

Forecasting ENSO Impacts in the California Current System

Guest Editors: Emanuele Di Lorenzo¹ and Art Miller²

¹Georgia Institute of Technology, ²Scripps Institution of Oceanography

The North Pacific eastern boundary upwelling system is one of the most ecologically productive, economically relevant, and well-studied systems in the world. Over the last 60 years, a wide range of observations have documented the significant impacts of the El Niño Southern Oscillation (ENSO) on marine ecosystems along the US West Coast. Yet there has been no systematic attempt to use this knowledge to explicitly forecast local marine ecosystem responses to individual ENSO events.

A recent workshop co-sponsored by US CLIVAR, OCB, NOAA, PICES, and ICES, [Forecasting ENSO impacts on marine ecosystems of the US West Coast](#), attempted to develop a framework for using ENSO forecasts from climate and statistical models in order to predict changes in key components of the marine ecosystem in the California Current System.

This set of articles published jointly between OCB and US CLIVAR (in their newsletter [Variations](#)) features participants from the workshop, including biologists and physical climate scientists, who were involved in advancing the discussion and outcomes. After describing a strategy to understand and quantify the predictable components of the ecosystem response to ENSO along the US West Coast (Di Lorenzo and Miller), this issue discusses the need to identify target ecosystem indicators or populations that respond to ENSO and are societally relevant, such as exploitable species that are regulated by federal and state agencies (Ohman et al.).

A major challenge for understanding the predictability of targeted ecosystem indicators is identification of the dominant regional physical, biogeochemical, and lower trophic processes that carry the ENSO predictable response in the marine ecosystem (Jacox et al.; Anderson et al.). These processes are sensitive to the different flavors of ENSO teleconnections originating in the tropical Pacific (Capotondi et al.). Exploiting ENSO predictability dynamics can add skill to current seasonal forecasts of large marine ecosystems in the California Current (Tommasi et al.) and improve existing modeling tools for managing top predators (Hazen et al.).



A framework for ENSO predictability of marine ecosystem drivers along the US West Coast

Emanuele Di Lorenzo¹ and Arthur J. Miller²

¹Georgia Institute of Technology, ²Scripps Institution of Oceanography

The US West Coast eastern boundary upwelling system supports one of the most productive marine ecosystems in the world and is a primary source of ecosystem services for the US (e.g., fishing, shipping, and recreation). Long-term historical observations of physical and biological variables in this region have been collected since the 1950s (e.g., the [CalCOFI program](#) and now including the [coastal ocean observing systems](#)), leading to an excellent foundation for understanding the ecosystem impacts of dominant climate fluctuations such as the El Niño-Southern Oscillation (ENSO). In the northeast Pacific, ENSO impacts a wide range of physical and biotic processes, including temperature, stratification, winds, upwelling, and primary and secondary production. The El Niño phase of ENSO, in particular, can result in extensive geographic habitat range displacements and altered catches of fishes and invertebrates, and impact vertical and lateral export fluxes of carbon and other elements (Jacox et al., this is-

sue; Anderson et al., this issue; Ohman et al., this issue). However, despite empirical observations and increased understanding of the coupling between climate and marine ecosystems along the US West Coast, there has been no systematic attempt to use this knowledge to forecast marine ecosystem responses to individual ENSO events. [ENSO forecasting](#) has become routine in the climate community. However, little has been done to forecast the impacts of ENSO on ecosystems and their services. This becomes especially important considering the occurrence of recent strong El Niño events (such as 2015-16) and climate model projections that suggest that ENSO extremes may become more frequent (Cai et al. 2015).

The joint US CLIVAR/OCB/NOAA/PICES/ICES workshop on *Forecasting ENSO impacts on marine ecosystems of the US West Coast* (Di Lorenzo et al. 2017) held in La Jolla, California, in August 2016 outlined a three-step strategy to better understand and quantify the ENSO-

related predictability of marine ecosystem drivers along the US West Coast (Figure 1). The first step is to use a high-resolution ocean reanalysis to determine the association between local ecosystem drivers and regional forcing patterns (RFPs). The identification of ecosystem drivers will depend on the ecosystem indicators or target species selected for prediction (Ohman et al., this issue). The second step is to objectively identify the tropical sea surface temperature (SST) patterns that optimally force the RFPs along the US West Coast region using available long-term large-scale reanalysis products. While the goal of the first two steps is to understand the dynamical basis for predictability (Figure 1, blue path), the final third step (Figure 1, orange path) aims at quantifying the predictability of the RFPs and estimating their prediction skill at seasonal timescales. This third step can be implemented using the output of multi-model ensemble forecasts such as the North America Multi-Model Ensemble (NMME) or by building efficient statistical prediction models such as Linear Inverse Models (LIMs; Newman et

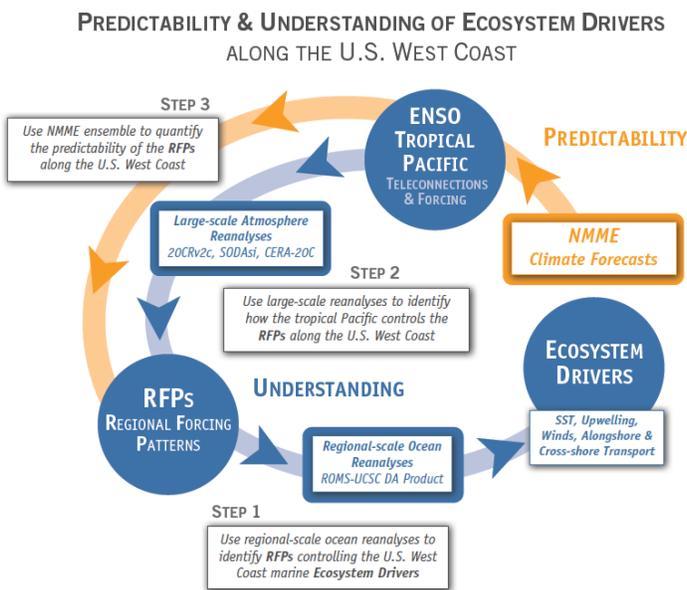


Figure 1. Framework for understanding and predicting ENSO impacts on ecosystem drivers. Blue path shows the steps that will lead to Understanding of the ecosystem drivers and their dependence on tropical Pacific anomalies. Orange path shows the steps that will lead to quantifying the Predictability of marine ecosystem drivers along the US West Coast that are predictable from large-scale tropical teleconnection dynamics.

al. 2003).

Important to the concept of ENSO predictability is the realization that the expressions of ENSO are very diverse and cannot be identified with a few indices (Capotondi et al. 2015; Capotondi et al., this issue). In fact, different expressions of sea surface temperature anomalies (SSTa) in the tropics give rise to oceanic and atmospheric teleconnections that generate different coastal impacts in the northeast Pacific. For this reason, we will refer to ENSO as the collection of tropical Pacific SSTa that lead to deterministic and predictable responses in the regional ocean and atmosphere along the US West Coast.

In the sections below, we articulate in more detail the elements of the framework for quantifying the predictability of ENSO-related impacts on coastal ecosystems along the US West Coast (Figure 1). Our focus will be on the California Current System (CCS), reflecting the regional expertise of the workshop participants. Specifically, we discuss (1) the ecosystem drivers and what is identified as such; (2) RFP definitions; and (3) the teleconnections from the tropical Pacific and their predictability.

Ecosystem drivers in the California Current System

The impacts of oceanic processes on the CCS marine ecosystem have been investigated since the 1950s when the long-term California Cooperative Oceanic Fisheries Investigations (CalCOFI) began routine seasonal sampling of coastal ocean waters. The CalCOFI program continues today and has been augmented with several other sampling programs (e.g., the coastal ocean observing network), leading to an unprecedented understanding of how climate and physical ocean processes, such as upwelling, drive ecosystem variability and change (e.g., see more recent reviews from King et al. 2011; Ohman et al. 2013; Di Lorenzo et al. 2013).

The dominant physical oceanographic drivers of ecosystem variability occur on seasonal, interannual, and decadal timescales and are associated with changes in (1) SST; (2) upwelling velocity; (3) alongshore transport; (4) cross-shore transport; and (5) thermocline/nutricline depth (see Ohman et al., this issue). This set of ecosystem drivers emerged from discussions among experts at the workshop. Ecosystem responses to these drivers include multiple trophic levels, including phytoplankton, zooplankton, small pelagic fish, and top predators, and several examples have been identified for the CCS (see summary table in Ohman et al., this issue).

While much research has focused on diagnosing the mechanisms by which these physical drivers impact marine ecosystems, less is known about the dynamics con-

trolling the predictability of these drivers. As highlighted in Ohman et al. (this issue), most of the regional oceanographic drivers (e.g., changes in local SST, upwelling, transport, thermocline depth) are connected to changes in large-scale forcings (e.g., winds, surface heat fluxes, large-scale SST and sea surface height patterns, freshwater fluxes, and remotely forced coastally trapped waves entering the CCS from the south). In fact, several studies have documented how large-scale changes in wind patterns associated with the Aleutian Low and the North Pacific Oscillation drive oceanic modes of variability such as the Pacific Decadal Oscillation and the North Pacific Gyre Oscillation (Mantua et al. 1997; Di Lorenzo et al. 2008; Chhak et al. 2009; Ohman et al., this issue; Jacox et al., this issue; Anderson et al., this issue; Capotondi et al., this issue) that influence the CCS. However, these large-scale modes only explain a fraction of the ecosystem's atmospheric forcing functions at the regional-scale. Thus, it is important to identify other key forcings to gain a more complete mechanistic understanding of CCS ecosystem drivers (e.g., Jacox et al. 2014; 2015).

Atmospheric and oceanic regional forcing patterns

The dominant large-scale quantities that control the CCS ecosystem drivers are winds, heat fluxes, and remotely forced coastally trapped waves (Hickey 1979). Regional expressions or patterns of these large-scale forcings have been linked to changes in local stratification and thermocline depth (Veneziani et al. 2009a; 2009b; Combes et al. 2013), cross-shore transport associated with mesoscale eddies (Kurian et al. 2011; Todd et al. 2012; Song et al. 2012; Davis and Di Lorenzo 2015b), and along-shore transport (Davis and Di Lorenzo 2015a; Bograd et al. 2015). For this reason, we define the regional expressions of the atmospheric and remote wave forcing that are optimal in driving SST, ocean transport, upwelling, and thermocline depth as the RFPs. To clarify this concept, consider the estimation of coastal upwelling velocities. While a change in the position and strength in the Aleutian Low has been related to coastal upwelling in the northern CCS, a more targeted measure of the actual upwelling vertical velocity and nutrient fluxes that are relevant to primary productivity can only be quantified by taking into account a combination of oceanic processes that depend on multiple RFPs such as thermocline depth (e.g., remote waves), thermal stratification (e.g., heat fluxes), mesoscale eddies, and upwelling velocities (e.g., local patterns of wind stress curl and alongshore winds; see Gruber et al 2011; Jacox et al. 2015; Renault et al. 2016). In other words, if we consider the vertical coastal upwell-

ing velocity (w) along the northern CCS, a more adequate physical description and quantification would be given from a linear combination of the different regional forcing functions $w = \sum_n \alpha_n * RFP_n$ rather than $w = \alpha * Aleutian\ Low$.

The largest interannual variability in the Pacific that impacts the RFPs is ENSO, which also constitutes the largest source of seasonal (3-6 months) predictability. During El Niño and La Niña, atmospheric and oceanic teleconnections from the tropics modify large-scale and local surface wind patterns and ocean currents of the CCS and force coastally trapped waves.

ENSO teleconnections and potential seasonal predictability of the regional forcing patterns

While ENSO exerts important controls on the RFPs in the CCS, it has become evident that ENSO expressions in the tropics vary significantly from event to event, leading to different responses in the CCS (Capotondi et al., this issue). Also, as previously pointed out, the CCS is not only sensitive to strong ENSO events but more generally responds to a wide range of tropical SSTa variability that is driven by ENSO-type dynamics in the tropical and subtropical Pacific. For this reason, we define an “ENSO teleconnection” as any RFP response that is linked to ENSO-type variability in the tropics.

ENSO can influence the upwelling and circulation in the CCS region through both oceanic and atmospheric pathways. It is well known that equatorial Kelvin waves, an integral part of ENSO dynamics, propagate eastward along the Equator and continue both northward (and southward) along the coasts of the Americas as coastally trapped Kelvin waves after reaching the eastern ocean boundary. El Niño events are associated with downwelling Kelvin waves, leading to a deepening of the thermocline, while La Niña events produce a shoaling of the thermocline in the CCS (Simpson 1984; Lynn and Bograd 2002; Huyer et al. 2002; Bograd et al. 2009; Her-

mann et al. 2009; Miller et al. 2015). The offshore scale of coastal Kelvin waves decreases with latitude, and the waves decay while propagating northward along the coast due to dissipation and radiation of westward propagating Rossby waves. In addition, topography and bathymetry can modify the nature of the waves and perhaps partially impede their propagation at some location. Thus, the efficiency of coastal waves of equatorial origin in modifying the stratification in the CCS is still a matter of debate. To complicate matters, regional wind variability south of the CCS also excites coastally trapped waves, which supplement the tropical source.

In the tropics, SST anomalies associated with ENSO change tropical convection and excite mid-troposphere stationary atmospheric Rossby waves that propagate signals to the extratropics, the so-called atmospheric ENSO teleconnections (Capotondi et al., this issue). Through these atmospheric waves, warm ENSO events favor a deepening and southward shift of the Aleutian Low pressure system

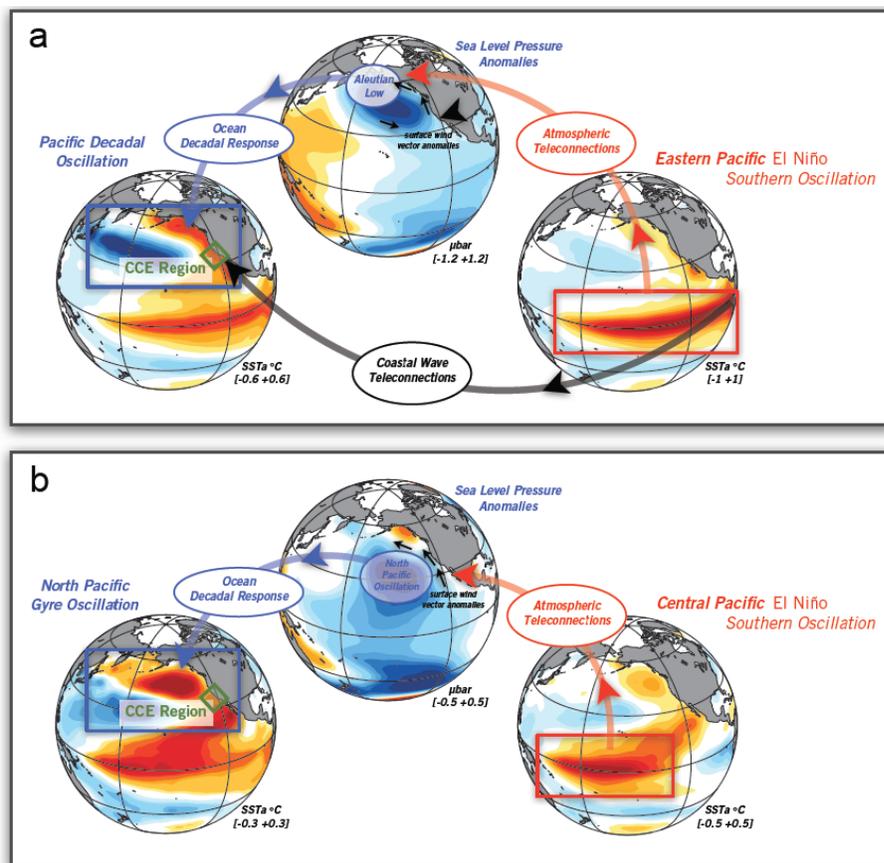


Figure 2. Depth-integrated balance of autotrophic and heterotrophic acquisition of N and C by nanoplankton (2 - 20 μm) in a global marine ecosystem model (12). The left-hand panels correspond to a model with mutually exclusive phytoplankton and zooplankton. The right-hand panels correspond to a model with only mixotrophic plankton. Black dots in panel c indicate sites where *in situ* nutrient addition experiments have identified (at least occasional) limitation by that nutrient element (26). Figure adapted from Ref. (12).

that is dominant during winter, as well as changes in the North Pacific Subtropical High that is dominant during spring and summer, resulting in a weakening of the alongshore winds, reduced upwelling, and warmer surface water. These changes are similar to those induced by coastal Kelvin waves of equatorial origin, making it very difficult to distinguish the relative importance of the oceanic and atmospheric pathways in the CCS. In addition, due to internal atmospheric noise, the details of the ENSO teleconnections can vary significantly from event to event and result in important differences along the California Coast (Figure 2).

El Niño events exhibit a large diversity in amplitude, duration, and spatial pattern (Capotondi et al. 2015). The amplitude and location of the maximum SST anomalies, whether in the eastern (EP) or central (CP) Pacific, can have a large impact on ENSO teleconnections (Ashok et al. 2007; Larkin and Harrison 2005). While “canonical” EP events induce changes in the Aleutian Low (Figure 2b), CP events have been associated with a strengthening of the second mode of North Pacific atmospheric variability, the North Pacific Oscillation (NPO; Figure 2a; Di Lorenzo et al. 2010; Furtado et al. 2012). In addition, it is conceivable that EP events have a larger Kelvin wave signature than CP events, resulting in different oceanic influences in the CCS.

In summary, while the ENSO influence on the CCS physical and biological environments is undeniable, several sources of uncertainty remain about the details of that influence. This uncertainty arises in the physical environment on seasonal timescales from many sources, including the diversity of ENSO events, the intrinsic unpredictable components of the atmosphere, and the intrinsic unpredictable eddy variations in the CCS. We also need to distinguish between physically forced ecosystem response versus intrinsic biological variability, which is potentially nonlinear and likely unpredictable. Skill levels need to be quantified for each step of the prediction process (i.e., ENSO, teleconnections, local oceanic response, local ecosystem response) relative to a baseline—for example the persistence of initial condition, which is also being exploited for skillful predictions of the large marine ecosystem at the seasonal timescale (Tommasi et al., this issue). The target populations should be exploitable species that are of interest to federal and state agencies that regulate certain stocks. Models are currently being developed to use ocean forecasts to advance top predator management (Hazen et al., this issue). The implementation of this framework (Figure 1) for practical uses will require a collaborative effort between physical climate scientists with expertise in

predicting and understanding ENSO and biologists who have expertise in understanding ecosystem response to physical climate forcing.

References

- Ashok, K., S.K. Behera, S.A. Rao, H. Weng, and T. Yamagata, 2007: El Niño Modoki and its possible teleconnections. *J. Geophys. Res.*, 112, doi:10.1029/2006JC003798
- Bograd, S. J., M. Pozo Buil, E. Di Lorenzo, C. G. Castro, I. D. Schroeder, R. Goericke, C. R. Anderson, C. Benitez-Nelson, and F. A. Whitney, 2015: Changes in source waters to the Southern California Bight. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.*, 112, 42-52, doi:10.1016/j.dsr2.2014.04.009.
- Bograd, S. J., I. Schroeder, N. Sarkar, X. Qiu, W. J. Sydeman, and F. B. Schwing, 2009: Phenology of coastal upwelling in the California Current. *Geophys. Res. Lett.*, 36, doi: 10.1029/2008GL035933.
- Cai, W. J., and Coauthors, 2015: ENSO and greenhouse warming. *Nature Climate Change*, 5, 849-859, doi:10.1038/nclimate2743.
- Capotondi, A., and Coauthors, 2015: Understanding ENSO Diversity. *Bull. Amer. Meteor. Soc.*, 96, 921-938, doi:10.1175/BAMS-D-13-00117.1.
- Chhak, K. C., E. Di Lorenzo, N. Schneider, and P. F. Cummins, 2009: Forcing of low-frequency ocean variability in the northeast Pacific. *J. Climate*, 22, 1255-1276, doi:10.1175/2008jcli2639.1.
- Davis, A., and E. Di Lorenzo, 2015a: Interannual forcing mechanisms of California Current transports I: Meridional Currents. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.*, 112, 18-30, doi:10.1016/j.dsr2.2014.02.005.
- Davis, A., and E. Di Lorenzo, 2015b: Interannual forcing mechanisms of California Current transports II: Mesoscale eddies. *Deep-Sea Res. Part II-Top. Stud. Oceanogr.*, 112, 31-41, doi:10.1016/j.dsr2.2014.02.004.
- Di Lorenzo, E., and Coauthors, 2017: Forecasting ENSO impacts on marine ecosystems of the US West Coast, Joint US CLIVAR/NOAA/PICES/ICES Report, <https://usclivar.org/meetings/2016-enso-ecosystems>, forthcoming.
- Di Lorenzo, E., and Coauthors, 2008: North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys. Res. Lett.*, 35, doi:10.1029/2007gl032838.
- Di Lorenzo, E., and Coauthors, 2013: Synthesis of Pacific Ocean climate and ecosystem dynamics. *Oceanogr.*, 26, 68-81, doi: 10.5670/oceanog.2013.76.
- 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 Ocean. *Nature Geosci.*, 3, 762-765, doi:10.1038/ngeo984.
- 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 Dyn.*, 39, 2833-2846, doi:10.1007/s00382-011-1245-4.

- Gruber, N., Z. Lachkar, H. Frenzel, P. Marchesiello, M. Munnich, J. C. McWilliams, T. Nagai, and G. K. Plattner, 2011: Eddy-induced reduction of biological production in eastern boundary upwelling systems. *Nature Geosci.*, 4, 787-792, doi:10.1038/ngeo1273.
- Hermann, A. J., E. N. Curchitser, D. B. Haidvogel, and E. L. Dobbins, 2009: A comparison of remote vs. local influence of El Niño on the coastal circulation of the northeast Pacific. *Deep Sea Res. Part II: Top. Stud. Oceanogr.*, 56, 2427-2443, doi: 10.1016/j.dsr2.2009.02.005.
- Hickey, B. M., 1979. The California Current system—hypotheses and facts. *Prog. Oceanogr.*, 8, 191-279, doi: 10.1016/0079-6611(79)90002-8.
- Huyer, A., R. L. Smith, and J. Fleischbein, 2002: The coastal ocean off Oregon and northern California during the 1997–8 El Niño. *Prog. Oceanogr.*, 54, 311-341, doi: 10.1016/S0079-6611(02)00056-3.
- Jacox, M. G., A. M. Moore, C. A. Edwards, and J. Fiechter, 2014: Spatially resolved upwelling in the California Current System and its connections to climate variability. *Geophys. Res. Lett.*, 41, 3189-3196, doi:10.1002/2014gl059589.
- Jacox, M. G., J. Fiechter, A. M. Moore, and C. A. Edwards, 2015: ENSO and the California Current coastal upwelling response. *J. Geophys. Res.-Oceans*, 120, 1691-1702, doi:10.1002/2014jc010650.
- Jacox, M. G., S. J. Bograd, E. L. Hazen, and J. Fiechter, 2015: Sensitivity of the California Current nutrient supply to wind, heat, and remote ocean forcing. *Geophys. Res. Lett.*, 42, 5950-5957, doi:10.1002/2015GL065147.
- Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd, 2016: Impacts of the 2015-2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophys. Res. Lett.*, 43, 7072-7080, doi:10.1002/2016GL069716.
- King, J. R., V. N. Agostini, C. J. Harvey, G. A. McFarlane, M. G. G. Foreman, J. E. Overland, E. Di Lorenzo, N. A. Bond, and K. Y. Aydin, 2011: Climate forcing and the California Current ecosystem. *Ices J. Mar. Sci.*, 68, 1199-1216, doi:10.1093/icesjms/fsr009.
- Kurian, J., F. Colas, X. Capet, J. C. McWilliams, and D. B. Chelton, 2011: Eddy properties in the California Current System. *J. Geophys. Res.-Oceans*, 116, doi:10.1029/2010jc006895.
- Larkin, N. K. and D. E. Harrison, 2005: On the definition of El Niño and associated seasonal average US weather anomalies. *Geophys. Res. Lett.* 32, doi: 10.1029/2005GL022738.
- Lynn, R. J. and S. J. Bograd, 2002: Dynamic evolution of the 1997–1999 El Niño–La Niña cycle in the southern California Current system. *Prog. Oceanogr.*, 54, 59-75, doi: 10.1016/S0079-6611(02)00043-5.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis, 1997: A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Amer. Meteorol. Soc.*, 78, 1069-1079, doi:10.1175/1520-0477(1997)078<1069:apicow>2.0.co;2.
- Marchesiello, P., J. C. McWilliams, and A. Shchepetkin, 2003: Equilibrium structure and dynamics of the California Current System. *J. Phys. Oceanogr.*, 33, 753-783, doi: 10.1175/1520-0485(2003)33<753:ESADOT>2.0.CO;2.
- McCreary, J. P., P. K. Kundu, and S. Y. Chao, 1987: On the dynamics of the California Current System. *J. Mar. Res.*, 45, 1-32, doi: 10.1357/002224087788400945.
- Miller, A. J., H. Song, and A. C. Subramanian, 2015: The physical oceanographic environment during the CCE-LTER Years: Changes in climate and concepts. *Deep Sea Res. Part II: Top. Stud. Oceanogr.*, 112, 6-17, doi: 10.1016/j.dsr2.2014.01.003.
- Newman, M., and Coauthors, 2016: The Pacific Decadal Oscillation, Revisited. *J. Climate*, 29, 4399-4427, doi:10.1175/jcli-d-15-0508.1.
- Ohman, M. D., K. Barbeau, P. J. S. Franks, R. Goericke, M. R. Landry, and A. J. Miller, 2013: Ecological transitions in a coastal upwelling ecosystem. *Oceanogr.*, 26, 210-219, doi: 10.5670/oceanogr.2013.65.
- Renault, L., C. Deutsch, J. C. McWilliams, H. Frenzel, J.-H. Liang, and F. Colas, 2016: Partial decoupling of primary productivity from upwelling in the California Current system. *Nature Geosci.*, 9, 505-508, doi:10.1038/ngeo2722.
- Simpson, J. J., 1984; El Niño-induced onshore transport in the California Current during 1982-1983. *Geophys. Res. Lett.*, 11, 233-236, doi: 10.1029/GL011i003p00233.
- Song, H., A. J. Miller, B. D. Cornuelle, and E. Di Lorenzo, 2011: Changes in upwelling and its water sources in the California Current System driven by different wind forcing. *Dyn. Atmos. Oceans*, 52, 170-191, doi:10.1016/j.dynatmoce.2011.03.001.
- Todd, R. E., D. L. Rudnick, M. R. Mazloff, B. D. Cornuelle, and R. E. Davis, 2012: Thermohaline structure in the California Current System: Observations and modeling of spice variance. *J. Geophys. Res.-Oceans*, 117, doi:10.1029/2011jc007589.
- Veneziani, M., C. A. Edwards, J. D. Doyle, and D. Foley, 2009: A central California coastal ocean modeling study: 1. Forward model and the influence of realistic versus climatological forcing. *J. Geophys. Res.-Oceans*, 114, doi:10.1029/2008jc004774.
- Veneziani, M., C. A. Edwards, and A. M. Moore, 2009: A central California coastal ocean modeling study: 2. Adjoint sensitivities to local and remote forcing mechanisms. *J. Geophys. Res.-Oceans*, 114, doi:10.1029/2008jc004775.

ENSO impacts on ecosystem indicators in the California Current System

Mark D. Ohman¹, Nate Mantua², Julie Keister³, Marisol Garcia-Reyes⁴, Sam McClatchie²

¹Scripps Institution of Oceanography, ²NOAA Southwest Fisheries Science Center, ³University of Washington, ⁴Farallon Institute

El Niño-Southern Oscillation (ENSO) events activate long-distance teleconnections through the atmosphere and ocean that can dramatically impact marine ecosystems along the West Coast of North America, affecting diverse organisms ranging from plankton to exploitable and protected species. Such ENSO-related changes to marine ecosystems can ultimately affect humans in many ways, including via depressed plankton and fish production, dramatic range shifts for many protected and exploited species, inaccessibility of traditionally fished resources, more prevalent harmful algal blooms, altered oxygen and pH of waters used in mariculture, and proliferation of pathogens. The principal objective of the Forecasting ENSO Impacts on Marine Ecosystems of the US West Coast workshop was to develop a scientific framework for building an ENSO-related forecast system of ecosys-

tem indicators along the West Coast of North America, including major biological and biogeochemical responses. Attendees realized that a quantitative, biologically-focused forecast system is a much more challenging objective than forecasting the physical system alone; it requires an understanding of the ocean-atmospheric physical system and of diverse organism-level, population-level, and geochemical responses that, in aggregate, lead to altered ecosystem states.

In the tropical ocean, important advances have been made in developing both intensive observational infrastructure (Global Tropical Moored Buoy Array) and diverse dynamical and statistical models that utilize these data in ENSO forecasting. These forecasts are made widely available (e.g., NOAA's Climate Prediction Center). The most sophisticated ENSO-forecasting efforts use global, coupled ocean-atmosphere climate models that extend ENSO-forecasting skill into seasonal climate forecasting skill for other regions, including the California Current System (CCS). However, both these measurement systems and forecast models are restricted to the physical dynamics of ENSO, rather than biotic and biogeochemical consequences.

El Niño impacts on pelagic ecosystems

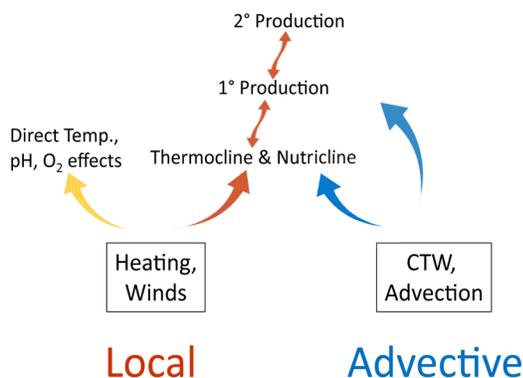


Figure 1. Schematic illustration of dominant mechanisms through which ENSO impacts biological and biogeochemical processes in the California Current System. Processes include both local effects (e.g., heat budget, winds) and advective effects. Such processes can influence organisms via: (1) (yellow arrow) direct physiological responses to changes in temperature, O₂, pH, etc.; (2) (orange arrows) effects that propagate through the food web, as successive trophic levels affect their predators (bottom up, upward-facing orange arrows) or prey (top down, downward-facing orange arrows); (3) (blue arrows) direct transport effects of advection. Top predators are not included here. CTW indicates coastally trapped waves.

Primary modes of influence of El Niño on marine organisms

In this brief discussion, we focus primarily on the warm (El Niño) phases of ENSO, which can have large and generally negative ecosystem consequences, although changes accompanying the cold phases (La Niña) can also be significant. We primarily address pelagic ocean processes, which merely reflect the expertise of the participants at the workshop. Physical mechanisms by which ENSO impacts the U.S. West Coast are more completely explained in Jacox et al. (this issue).

El Niño affects organisms and biogeochemistry via both local and advective processes (Figure 1). ENSO-related changes in the tropics can affect the CCS through an atmospheric teleconnection (Alexander et al. 2002) to alter local winds and surface heat fluxes, and through upper ocean processes

(thermocline and sea level displacements and geostrophic currents) forced remotely by poleward propagating coastally trapped waves (CTWs) of tropical origin (Enfield and Allen 1980; Frischkencht et al. 2015; Figure 1). It is important to recognize that ecosystem effects will occur through three primary mechanisms: (1) via the direct action of altered properties like temperature, dissolved O₂, and pH on the physiology and growth of marine organisms; (2) through food web effects as changes in successive trophic levels affect their predators (bottom up) or prey (top down); and (3) through changes in advection related to the combination of locally forced Ekman transport and remotely forced geostrophic currents, typically involving poleward and/or onshore transport of organisms. Advective effects can be pronounced, transporting exotic organisms into new regions and altering the food web if these imported species have significant impacts as predators, prey, competitors, parasites, or pathogens.

I. Poleward and onshore transport

Active, mobile marine fishes, seabirds, reptiles, and mammals may move into new (or away from old) habitats in the CCS as ENSO-related changes occur in the water column and render the physical-chemical characteristics and prey fields more (or less) suitable for them. Planktonic organisms are often critical prey and are, by definition,

subject to geographic displacements as a consequence of altered ocean circulation that accompanies El Niño events. Most commonly, lower latitude organisms are transported poleward to higher latitudes in either surface flows or in an intensified California Undercurrent (Lynn and Bograd 2002). However, some El Niño events are accompanied by onshore flows (Simpson 1984), potentially displacing offshore organisms toward shore (Keister et al. 2005).

Two of the most celebrated examples of poleward transport come from distributions of pelagic red crabs (*Pleuroncodes planipes*) and the subtropical euphausiid (or krill, *Nyctiphanes simplex*), both of which have their primary breeding populations in waters off Baja California, Mexico (Boyd 1967; Brinton et al. 1999). Pelagic red crabs were displaced approximately 10° of latitude, from near Bahia Magdalena, Baja California, northward to Monterey, California (Glynn 1961; Longhurst 1967) during the El Niño of 1958-1959. This early event was particularly well documented because of the broad latitudinal coverage of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises at the time. Such El Niño-related northward displacements have been documented repeatedly over the past six decades (McClatchie et al. 2016), partly because the red crabs often strand in large windrows on beaches and are conspicuous to the general public. The normal range of the euphausiid *Nyctiphanes*

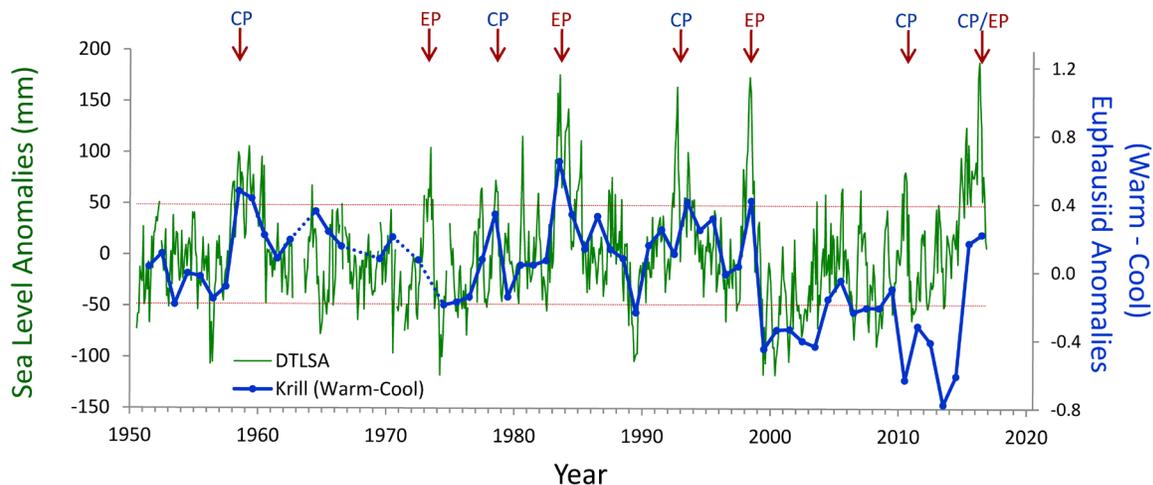


Figure 2. Covariability of California Current euphausiids (krill, blue lines) with an index of ENSO off California (de-trended sea level anomaly [DTSLA] at San Diego, green lines). Note the markedly different relationship between euphausiids and DTSLA after 2000. Sustained excursions of DTSLA exceeding one standard deviation (i.e., above upper dotted red line) are expressions of El Niño (or of the warm anomaly of 2014-2015). Red arrows indicate specific events categorized as either eastern Pacific (EP) or central Pacific (CP) El Niño events (Yu et al. 2012), apart from 2015-2016 which could be either CP or EP. The Warm-Cool euphausiid index is based on the difference in average log carbon biomass anomaly of the four dominant warm water euphausiids in the CCS minus the average anomaly of the four dominant cool water euphausiids (species affinities from Brinton and Townsend 2003). Euphausiid carbon biomass from springtime CalCOFI cruises off Southern California, lines 77-93, nighttime samples only. Dotted blue lines indicate years of no samples (Ohman, personal communication).

simplex is centered at 25-30°N (Brinton et al. 1999). *N. simplex* has been repeatedly detected far to the north of this range during El Niño, extending at least to Cape Mendocino (40.4°N) in 1958 (Brinton 1960), to northern Oregon (46.0°N) in 1983 (Brodeur 1986), and to Newport, Oregon (44.6°N; Keister et al. 2005) and northwest Vancouver Island (50.7°N; Mackas and Galbraith 2002) in 1998. In spring of 2016, *N. simplex* were extremely abundant in the southern California region (M. Ohman and L. Sala, personal communication) and detected as far north as Trinidad Head (41.0°N) but not in Newport, Oregon (W. Peterson, personal communication). Sometimes such El Niño-related occurrences of subtropical species are accompanied by declines in more boreal species (e.g., Mackas and Galbraith 2002; Peterson et al. 2002), although this is not always the case.

Among the organisms displaced during El Niños, the consequences of transport of predators are poorly understood but likely significant in altering the food web. Subtropical fishes can be anomalously abundant in higher latitudes during El Niño (Hubbs 1948; Lluch-Belda et al. 2005; Pearcy and Schoener 1987; Pearcy 2002; Brodeur et al. 2006), with significant consequences for the resident food web via selective predation on prey populations.

II. Habitat compression

Many species are confined to a specific habitat that may compress during El Niño. This phenomenon has been observed repeatedly for species and processes related to coastal upwelling in the CCS. During major El Niño events, as the offshore extent of upwelled waters is reduced and becomes confined close to the coast, the zone of elevated phytoplankton (observed as Chl-a) compresses markedly to a narrow zone along the coastal boundary (e.g., Kahru and Mitchell 2000; Chavez et al. 2002). For example, during the strong El Niño spring of 1983, the temperate euphausiid *Euphausia pacifica* was present in low densities throughout Central and Southern California waters, but 99% of the biomass was unusually concentrated at a single location (station 80.51) very close to Point Conception, where upwelling was still pronounced (E. Brinton, personal communication). The spawning habitat of the Pacific sardine (*Sardinops sagax*) was narrowly restricted to the coastal boundary during El Niño 1998, but one year later during La Niña 1999, the spawning habitat extended a few hundred kilometers farther offshore (Lo et al. 2005). Market squid, *Doryteuthis opalescens*, show dramatically lower catches during El Niño years (Reiss et al. 2004), but in 1998, most of the catch was confined to a small region in Central California (Reiss et al. 2004).

During the El Niño in spring 2016, vertical particle fluxes measured by sediment traps were reduced far offshore but remained elevated in the narrow zone of coastal upwelling very close to Point Conception (M. Stukel, personal communication).

III. Altered winds and coastal upwelling

Upwelling-favorable winds along the US West Coast may decline during El Niño conditions (Hayward 2000, but see Chavez et al. 2002) and vertical transports can be reduced (Jacox et al. 2015), mainly during the winter and early spring (Black et al. 2011). Independent of any changes in density stratification (considered below), these decreased vertical velocities can lead to diminished nutrient fluxes, reduced rates of primary production, and a shift in the size composition of the plankton community to smaller phytoplankton and zooplankton (Ryckaczewski and Checkley 2008). Such changes at the base of the food web can have major consequences for a sequence of consumers at higher trophic levels, as both the concentration and suitability of prey decline.

However, there are potential compensatory effects of reduced rates of upwelling. Diminished upwelling also means less introduction of CO₂-rich, low-oxygen waters to coastal areas (Feely et al. 2008; Bednaršek et al. 2014), with potential benefits to organisms that are sensitive to calcium carbonate saturation state or hypoxic conditions. Furthermore, reduced upwelling implies lower Ekman transport and potentially reduced cross-shore fluxes far offshore within coastal jets and filaments (cf., Keister et al. 2009).

IV. Increased stratification and deepening of nutricline

El Niño-related warming of surface waters and increased density stratification can result from advection of warmer waters and/or altered local heating. Evidence suggests that the pycnocline (Jacox et al. 2015) and nitracline (Chavez et al. 2002) deepen during stronger El Niños. This effect, independent of variations in wind stress, also leads to diminished vertical fluxes of nitrate and other limiting nutrients and suppressed rates of primary production. Decreased nitrate fluxes appear to explain elevated 15N in California Current zooplankton (Ohman et al. 2012) and decreased krill abundance (Lavaniegos and Ohman 2007; Garcia-Reyes et al. 2014) during El Niño years. For example, the 2015-16 El Niño resulted in a pronounced warming of surface waters and depressed Chl-a concentrations across a broad region of the CCS (McClatchie et al. 2016).

V. Direct physiological responses to altered temperature, dissolved O₂, pH

Most organisms in the ocean—apart from some marine vertebrates—are ectothermic, meaning they have no capability to regulate their internal body temperature. Heating or cooling of the ocean therefore directly influences their rates of metabolism, growth, and mortality. Most organisms show not only high sensitivity to temperature variations but nonlinear responses. A typical temperature response curve or “thermal reaction norm” (e.g., of growth rate) is initially steeply positive with increasing temperature, followed by a narrow plateau, then abruptly declines with further increases in temperature (e.g., Eppley 1972). Different species often show different thermal reaction norms. Hence, El Niño-related temperature changes may not only alter the growth rates and abundances of organisms, but also shift the species composition of the community due to differential temperature sensitivities.

Similarly, El Niño-induced variations in dissolved oxygen concentration and pH can have marked consequences for physiological responses of planktonic and sessile benthic organisms and, for active organisms, potentially lead to migrations into or out of a suitable habitat. Interactions between variables (Boyd et al. 2010) will also lead to both winners and losers in response to major ENSO-related perturbations.

VI. Altered parasite, predator populations, and harmful algal blooms

ENSO-related changes can favor the in situ proliferation or introduction of predators, parasites, pathogens, and harmful algal blooms. Such outbreaks can have major consequences for marine ecosystems, although some are relatively poorly studied. For example, a recent outbreak of sea star wasting disease thought to be caused by a densovirus adversely affected sea star populations at numerous locations along the West Coast (Hewson et al. 2014). While not specifically linked to El Niño, this outbreak was likely tied to warmer water temperatures. Because some sea stars are keystone predators capable of dramatically restructuring benthic communities (Paine 1966), such pathogen outbreaks are of considerable concern well beyond the sea stars themselves.

Domoic acid outbreaks, produced by some species of the diatom genus *Pseudo-nitzschia*, can result in closures of fisheries for razor clams, Dungeness crab, rock crab, mussels, and lobsters, resulting in significant economic losses. While the causal mechanisms leading to domoic acid outbreaks are under discussion (e.g., Sun et al. 2011; McCabe et al. 2016), warmer-than-normal ocean conditions in northern regions of the CCS have been linked to

domoic acid accumulation in razor clams, especially when El Niño conditions coincide with the warm phase of the Pacific Decadal Oscillation (McKibben et al. 2017).

ENSO diversity, non-stationarity, and consequences of secular changes

There is considerable interest in understanding the underlying dynamical drivers that lead to different El Niño events (Singh et al. 2011; Capotondi et al. 2015). Although there appears to be a continuum of El Niño expression along the equatorial Pacific, some simplify this continuum to a dichotomy between Eastern Pacific (EP) and Central Pacific (CP) events (Capotondi et al. 2015). Whether EP and CP El Niños have different consequences for mid-latitude ecosystems like the California Current Ecosystem is an area of open research, but some evidence suggests that differences in timing and intensity of biological effects may exist (cf. Fisher et al. 2015). While some studies (e.g., Lee and McPhaden 2010) suggest that the frequency of CP El Niños is increasing, the evidence is not definitive (Newman et al. 2011). In addition to questions about the ecosystem consequences of El Niño diversity, there are unknowns regarding interactions between El Niño, decadal-scale variability (Chavez et al. 2002), and secular changes in climate (Figure 2, Ohman, unpubl.), which suggest a non-stationary relationship between California Current zooplankton and El Niño. An index of the dominance of warm water krill from CalCOFI sampling in Southern California shows that for the first 50 years there was a predictable positive relationship between these warm water krill and El Niño. This relationship held during both EP and CP El Niño events from 1950-2000. However, the relationship appeared to weaken after 2000. The warm water krill index was negatively correlated with the moderate El Niño of 2009-10. While the krill index again responded to the major El Niño of 2015-16 and the preceding year of warm anomalies (Bond et al. 2015; Zaba and Rudnick 2016), the magnitude of the response was not comparable to what had been seen in earlier decades. It is unclear whether such results are merely the consequence of interannual variability in the mode of El Niño propagation (Todd et al. 2011) or a change in the relationship between El Niño forcing and ecosystem responses.

Conclusions

While the potential modes of El Niño influence on biological and biogeochemical processes in the CCS are numerous, not all processes are of first order consequence to all organisms. Forecasting ENSO effects on a given target species will likely focus on a limited number of governing processes. Table 1 illustrates some of the specific

types of organisms susceptible to El Niño perturbations and the suspected dominant mechanism. We look forward to developing a framework for forecasting such responses in a quantitative manner.

Ecosystem indicator	Region and season	Change during El Niño	Time scale of response	Regional ocean processes
Primary production	Entire CCS winter, spring, summer	Declines	Variable lag; Instantaneous or time-lagged	Reduced upwelling, nutrient fluxes; Deeper nutricline and weaker winds
<i>Pseudo-nitzschia</i> diatoms; Domoic Acid	Entire CCS spring-summer	Blooms	1-3 month lag	Elevated temperature; Altered nutrient stoichiometry
Copepod assemblage	NCCS spring-summer	Warm water species appear	Nearly instantaneous	Poleward advection; Reduced upwelling, warmer temperature
Subtropical euphausiids	SCCS spring-summer	Increase	Nearly instantaneous; persists beyond Niño event	Poleward advection
Cool water euphausiids	Entire CCS spring-summer	Decrease	Time-lagged	Reduced upwelling; Anomalous advection
Pelagic red crabs	SCCS & CCCS winter, spring, summer	Increase	Nearly instantaneous	Poleward advection
Market squid	CCCS & SCCS winter & spring	Collapse	Instantaneous for distribution; time-lagged for recruitment	Warmer temperature/deeper thermocline; Reduces spawning habitat
Pacific sardine	Entire CCS winter-spring	Changes in distribution; Compression of spawning habitat	Instantaneous for spawning and distribution, recruitment time- lagged, biomass is time-integrated	Wind stress, cross-shore transport
Northern anchovy	CCCS & SCCS winter-spring	Changes in distribution; Compression of spawning habitat	Instantaneous for spawning and distribution, recruitment time- lagged, biomass is time-integrated	Reduced upwelling; Anomalous advection
Juvenile salmon survival	NCCS spring-summer	Decrease in Pacific NW	Time-integrated	Reduce river flow, decreased food supply in ocean
Adult sockeye salmon (Fraser River)	NCCS summer	Return path deflected northward to Canadian waters	Time-integrated	Ocean temperature, including Ekman controls
Warm assemblage of mesopelagic fish	SCCS spring (?)	Increase	Lagged 0-3 months	Poleward and onshore advection
Common murre (reproductive success)	CCCS winter-spring	Decrease	Time-lagged, time-integrated	Prey (fish) availability; Thermocline depth; Decreased upwelling?
Top predator reproduction and abundance	Entire CCS	Species-dependent	Time-integrated	Advection of prey, altered temperature, upwelling, mesoscale structure
Top predator distribution	Entire CCS	Altered geographic distributions	Instantaneous or time-lagged	Advection of prey, altered temperature, upwelling, mesoscale structure

Table 1. Examples of water column biological processes and organisms known to be affected by El Niño in the California Current System. Columns indicate the type of organism; approximate geographic region and season of the effect; direction of change in response to El Niño; temporal pattern of response (immediate, time-lagged, time-integrated); and the hypothesized oceanographic processes driving the organism response. CCS = California Current System; NCCS, CCCS, and SCCS denote northern, central, and southern sectors of the CCS.

References

- 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, 2205-2231, doi: 10.1175/1520-0442(2002)015<2205:TABTIO>2.0.CO;2
- Bednaršek, N., R. A. Feely, J. C. P. Reum, B. Peterson, J. Menkel, S. R. Alin, and B. Hales, 2014: *Limacina helicina* shell dissolution as an indicator of declining habitat suitability owing to ocean acidification in the California Current Ecosystem. *Proc. Roy. Soc. B-Biol. Sci.*, 281, doi: 10.1098/rspb.2014.0123.
- Black, B. A., I. D. Schroeder, W. J. Sydeman, S. J. Bograd, B. K. Wells, and F. B. Schwing, 2011: Winter and summer upwelling modes and their biological importance in the California Current Ecosystem. *Glob. Change Bio.*, 17, 2536-2545, doi: 10.1111/j.1365-2486.2011.02422.x.
- Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua, 2015: Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys. Res. Lett.*, 42, 3414-3420, doi: 10.1002/2015GL063306.
- Boyd, C. M., 1967: The benthic and pelagic habitats of the red crab, *Pleuroncodes planipes*. *Pacific Science*, 21, 394-403.
- Boyd, P. W., R. Strzpek, F. X. Fu, and D. A. Hutchins, 2010: Environmental control of open-ocean phytoplankton groups: Now and in the future. *Limnol. Oceanogr.*, 55, 1353-1376, doi: 10.4319/lo.2010.55.3.1353.
- Brinton, E., 1960: Changes in the distribution of euphausiid crustaceans in the region of the California Current. *CalCOFI Reports*, 7, 137-146, http://www.calcofi.org/publications/calcofireports/v07/Vol_07_Brinton.pdf.
- Brinton, E., M. D. Ohman, A. W. Townsend, M. D. Knight, and A. L. Bridgeman, 1999: *Euphausiids of the World Ocean*. Vol. CD-ROM, MacIntosh version 1.0, UNESCO Publishing.
- Brodeur, R. D., 1986: Northward displacement of the euphausiid *Nyctiphanes simplex* Hansen to Oregon and Washington waters following the El Niño event of 1982-83. *J. Crustacean Bio.*, 6, 686-692, doi: 10.2307/1548382.
- Brodeur, R. D., S. Ralston, R. L. Emmett, M. Trudel, T. D. Auth, and A. J. Phillips, 2006: Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California Current in 2004 and 2005. *Geophys. Res. Lett.*, 33, doi:10.1029/2006gl026614.
- Capotondi, A., and Coauthors, 2015: Understanding ENSO Diversity. *Bull. Amer. Meteor. Soc.*, 96, 921-938, doi: 10.1175/BAMS-D-13-00117.1.
- Chavez, F. P., and Coauthors, 2002: Biological and chemical consequences of the 1997-1998 El Niño in central California waters. *Prog. Oceanogr.*, 54, 205-232, doi: 10.1016/S0079-6611(02)00050-2.
- Enfield, D., and J. Allen, 1980: On the structure and dynamics of monthly mean sea-level anomalies along the Pacific coast of North and South America. *J. Phys. Oceanogr.*, 10, 557-578, doi: 10.1175/1520-0485(1980)010<0557:OTSADO>2.0.CO;2.
- Eppley, R. W., 1972: Temperature and phytoplankton growth in the sea. *Fish. Bull.*, 70, 1063-1085, <http://fishbull.noaa.gov/70-4/eppley.pdf>.
- Feely, R. A., C. L. Sabine, J. M. Hernandez-Ayon, and D. H. Ianson, B., 2008: Evidence for upwelling of corrosive "acidified" water onto the continental shelf. *Science*, 320, 1490-1492, doi: 10.1126/science.1155676.
- Fisher J. L., W. T. Peterson, and R. R. Rykaczewski, 2015: The impact of El Niño events on the pelagic food chain in the northern California Current. *Glob. Change Bio.*, 21, 4401-4414, doi: 10.1111/gcb.13054.
- Frischknecht, M., M. Münnich, and N. Gruber, 2015: Remote versus local influence of ENSO on the California Current System, *J. Geophys. Res. Oceans*, 120, 1353-1374, doi:10.1002/2014JC010531.
- García-Reyes, M., J. L. Largier, and W. J. Sydeman, 2014: Synoptic-scale upwelling indices and predictions of phyto- and zooplankton populations. *Prog. Oceanogr.*, 120, 177-188, doi: 10.1016/j.pcean.2013.08.004.
- Glynn, P. W., 1961: The first recorded mass stranding of pelagic red crabs, *Pleuroncodes planipes*, at Monterey Bay, California, since 1859, with notes on their biology. *Cal. Fish Game*, 47, 97-101.
- Hayward, T. L., 2000: El Niño 1997-98 in the coastal waters of Southern California: a timeline of events. *CalCOFI Reports*, 41, 98-116, http://www.calcofi.org/publications/calcofireports/v41/Vol_41_Hayward.pdf.
- Hewson, I., and Coauthors, 2014: Densovirus associated with sea-star wasting disease and mass mortality. *Proc. Nat. Acad. Sci.*, 111, 17278-17283, doi: 10.1073/pnas.1416625111.
- Hubbs, C. L., 1948: Changes in the fish fauna of western North America correlated with changes in ocean temperature, *J. Mar. Res.*, 7, 459-482, <http://www.nativefishlab.net/library/text-pdf/20041.pdf>.
- Jacox, M. G., J. Fiechter, A. M. Moore, and C. A. Edwards, 2015: ENSO and the California Current coastal upwelling response. *J. Geophys. Res. Oceans*, 120, 1691-1702, doi: 10.1002/2014JC010650.
- Jacox, M.G. [this issue of Variations] PLEASE ADD FULL REFERENCE
- Kahru, M., E. Di Lorenzo, M. Manzano-Sarabia, and B. G. Mitchell, 2012: Spatial and temporal statistics of sea surface temperature and chlorophyll fronts in the California Current. *J. Plank. Res.*, 34, 749-760, doi: 10.1093/plankt/fbs010.
- Kahru, M., and B. G. Mitchell, 2000: Influence of the 1997-98 El Niño on the surface chlorophyll in the California Current. *Geophys. Res. Lett.*, 27, 2937-2940, doi: 10.1029/2000GL011486
- Keister, J. E., T. J. Cowles, W. T. Peterson, and C. A. Morgan, 2009: Do upwelling filaments result in predictable biological distri-

- butions in coastal upwelling ecosystems? *Prog. Oceanogr.*, 83, 303-313, doi: 10.1016/j.pocean.2009.07.042.
- Keister, J. E., T. B. Johnson, C. A. Morgan, and W. T. Peterson, 2005: Biological indicators of the timing and direction of warm-water advection during the 1997/1998 El Niño off the central Oregon coast, USA. *Mar. Ecol. Prog. Ser.*, 295, 43-48, <http://hdl.handle.net/1957/26294>.
- Lavaniegos, B. E., and M. D. Ohman, 2007: Coherence of long-term variations of zooplankton in two sectors of the California Current System. *Prog. Oceanogr.*, 75, 42-69, doi: 10.1016/j.pocean.2007.07.002.
- Lee, T., and M. J. McPhaden, 2010: Increasing intensity of El Niño in the central-equatorial Pacific. *Geophys. Res. Lett.*, 37, doi: 10.1029/2010gl044007.
- Lluch-Belda, D., D. B. Lluch-Cota, and S. E. Lluch-Cota, 2005: Changes in marine faunal distributions and ENSO events in the California Current. *Fish. Oceanogr.*, 14, 458– 467, doi: 10.1111/j.1365-2419.2005.00347.x.
- Lo, N. C. H., B. J. Macewicz, and D. A. Griffith, 2005: Spawning biomass of Pacific sardine (*Sardinops sagax*), from 1994–2004 off California. *CalCOFI Reports*, 46, 93-112, <https://swfsc.noaa.gov/publications/TM/SWFSC/NOAA-TM-NMFS-SWFSC-463.pdf>.
- Longhurst, A. R., 1967: The pelagic phase of Pleuroncodes planipes Stimpson (Crustacea, Galatheidae) in the California Current. *Cal. Coop. Ocean. Fish. Invest. Rep.*, 11, 142-154, <https://decapoda.nhm.org/pdfs/29796/29796.pdf>.
- Lynn, R. J., and S. J. Bograd, 2002: Dynamic evolution of the 1997-1999 El Niño-La Niña cycle in the southern California Current System. *Prog. Oceanogr.*, 54, 59-75, doi: 10.1016/S0079-6611(02)00043-5.
- Mackas, D. L., and M. Galbraith, 2002: Zooplankton community composition along the inner portion of Line P during the 1997-1998 El Niño event. *Prog. Oceanogr.*, 54, 423-437, doi: 10.1016/S0079-6611(02)00062-9.
- McCabe, R. M., and Coauthors, 2016: An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. *Geophys. Res. Lett.*, 43, 10366-10376, doi: 10.1002/2016gl070023
- McClatchie, S., and Coauthors, 2016: State of the California Current 2015-16: Comparisons with the 1997-98 El Niño. *CalCOFI Reports*, 57, 1-57, http://calcofi.org/publications/calcofireports/v57/Vol57-SOTCC_pages.5-61.pdf.
- McKibben, S. M., W. Peterson, M. Wood, V. L. Trainer, M. Hunter, and A. E. White, 2017: Climatic regulation of the neurotoxin domoic acid. *Proc. Nat. Acad. Sci.*, 114, 239-244, doi: 10.1073/pnas.1606798114.
- Newman, M., S.-I. Shin, and M. A. Alexander, 2011: Natural variation in ENSO flavors. *Geophys. Res. Lett.*, 38, doi:10.1029/2011GL047658.
- Ohman, M. D., G. H. Rau, and P. M. Hull, 2012: Multi-decadal variations in stable N isotopes of California Current zooplankton. *Deep Sea Res. I*, 60, 46-55, doi: 10.1016/j.dsr.2011.11.003.
- Paine, R. T., 1966: Food web complexity and species diversity. *Amer. Natural.*, 100, 65-75, <http://www.jstor.org/stable/2459379>.
- Pearcy, W. G., 2002: Marine nekton off Oregon and the 1997 – 98 El Niño. *Prog. Oceanogr.*, 54, 399-403, doi: 10.1016/S0079-6611(02)00060-5.
- Pearcy, W. G., and A. Schoener, 1987: Changes in the marine biota coincident with the 1982–1983 El Niño in the northeastern subarctic Pacific Ocean. *J. Geophys. Res.*, 92, 14,417– 14,428, doi: 10.1029/JC092iC13p14417.
- Peterson, W. T., J. E. Keister, and L. R. Feinberg, 2002: The effects of the 1997-99 El Niño/La Niña events on hydrography and zooplankton off the central Oregon coast. *Prog. Oceanogr.*, 54, 381-398, doi: 10.1016/S0079-6611(02)00059-9.
- Reiss, C. S., M. R. Maxwell, J. R. Hunter, and A. Henry, 2004: Investigating environmental effects on population dynamics of *Loligo opalescens* in the Southern California Bight. *CalCOFI Reports*, 45, 87-97, http://web.calcofi.org/publications/calcofireports/v45/Vol_45_Reiss.pdf.
- Rykaczewski, R. R., and D. M. Checkley, Jr., 2008: Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proc. Nat. Acad. Sci.*, 105, 1965-1970, doi: 10.1073/pnas.0711777105.
- Simpson, J. J., 1984: El Niño-induced onshore transport in the California Current during 1982-1983. *Geophys. Res. Lett.*, 11, 241-242, doi: 10.1029/GL011i003p00233.
- Singh, A., T. Delcroix, and S. Cravatte, 2011: Contrasting the flavors of El Niño-Southern Oscillation using sea surface salinity observations. *J. Geophys. Res.*, 116, doi:10.1029/2010JC006862.
- Sun, J., D. A. Hutchins, Y. Y. Feng, E. L. Seubert, D. A. Caron, and F. X. Fu, 2011: Effects of changing pCO₂ and phosphate availability on domoic acid production and physiology of the marine harmful bloom diatom *Pseudo-nitzschia multiseries*. *Limnol. Oceanogr.*, 56, 829-840, doi: 10.4319/lo.2011.56.3.0829.
- Todd, R. E., D. L. Rudnick, R. E. Davis, and M. D. Ohman, 2011: Underwater gliders reveal rapid arrival of El Niño effects off California's coast. *Geophys. Res. Lett.*, 38, doi: 10.1029/2010gl046376.
- Yu, J. Y., Y. H. Zou, S. T. Kim, and T. Lee, 2012: The changing impact of El Niño on US winter temperatures. *Geophys. Res. Lett.*, 39, doi: 10.1029/2012gl052483.
- Zaba, K. D., and D. L. Rudnick, 2016: The 2014–2015 warming anomaly in the Southern California Current System observed by underwater gliders. *Geophys. Res. Lett.*, 43, 1241-1248, doi: 10.1002/2015GL067550.

Dominant physical mechanisms driving ecosystem response to ENSO in the California Current System

Michael G. Jacox^{1,2}, Daniel L. Rudnick³, and Christopher A. Edwards¹

¹University of California, Santa Cruz, ²Southwest Fisheries Science Center, NOAA, ³Scripps Institution of Oceanography

The El Niño–Southern Oscillation (ENSO) is a dominant driver of interannual variability in the physical and biogeochemical state of the northeast Pacific, and, consequently, exerts considerable control over the ecological dynamics of the California Current System (CCS). In the CCS, upwelling is the proximate driver of elevated biological production, as it delivers nutrients to the sunlit surface layer of the ocean, stimulating growth of phytoplankton that form the base of the marine food web. Much of the ecosystem variability in the CCS can, therefore, be attributed to changes in bottom-up forcing, which regulates biogeochemical dynamics through a range of mechanisms. Of particular relevance to ENSO-driven variability are the influences of surface winds (which drive upwelling and downwelling), remote oceanic forcing by coastal wave propagation, and alongshore advection. While the relative importance of these individual forcing mechanisms has long been a topic of study, there is general consensus on the qualitative nature of each, and we discuss them in turn below.

Wind

One of the canonical mechanisms by which ENSO events generate an oceanographic response in the CCS is through modification of the surface winds and resultant upwelling. During El Niño, tropical convection excites atmospheric Rossby waves that strengthen and displace the Aleutian low, producing anomalously weak equatorward (or strong poleward) winds, which in turn drive anomalously weak upwelling (or strong downwelling) through modification of cross-shore Ekman transport near the surface (Alexander et al. 2002; Schwing et al. 2002). The opposite response is associated with La Niña. This tropical-extratropical communication through the atmosphere has been given the shorthand name “atmospheric teleconnection.” When equatorward winds are anomalously weak, as they were for example during the 2009–2010 El Niño (Todd et al. 2011), there is a twofold impact on the nutrient flux to the euphotic zone and, consequently, the potential primary productivity. First, weaker winds

produce weaker coastal upwelling; independent of changes in the nutrient concentration of upwelling source waters, a reduction in vertical transport translates directly to a reduction in vertical nutrient flux. Second, the nutrient concentration of source waters is altered by the strength of the wind; weak upwelling draws from shallower depths than strong upwelling, and the water that is upwelled is relatively nutrient-poor. Both of these effects tend to limit potential productivity during El Niño. Conversely, La Niña events are associated with anomalously strong equatorward winds, vigorous coastal upwelling, and an ample supply of nutrients to the euphotic zone. However, winds that are too strong can also export nutrients and plankton rapidly offshore, resulting in relatively low phytoplankton biomass in the nearshore region (Figure 1; Jacox et al. 2016a).

In addition to the magnitude of alongshore wind stress, its spatial structure is also important in dictating the ocean’s physical and biogeochemical response. Off the US West Coast, the first mode of interannual upwelling variability is a cross-shore dipole, where anomalously strong nearshore upwelling (within ~50 km of the coast) is accompanied by anomalously weak upwelling farther offshore (Jacox et al. 2014). In terms of the surface wind field, this pattern represents a fluctuation between cross-shore wind profiles with (i) weak nearshore winds and a wide band of positive wind stress curl, and (ii) strong nearshore winds and a narrow band of positive curl. The former, which is associated with positive phases of the Pacific Decadal Oscillation (PDO) and ENSO and negative phases of the North Pacific Gyre Oscillation (NPGO), may favor smaller phyto- and zooplankton, while the latter, associated with negative phases of the PDO and ENSO and positive phases of the NPGO, may favor larger phyto- and zooplankton (Rykaczewski and Checkley 2008).

Remote ocean forcing

As the atmospheric teleconnection transmits tropical variability to CCS winds, an oceanic teleconnection ex-

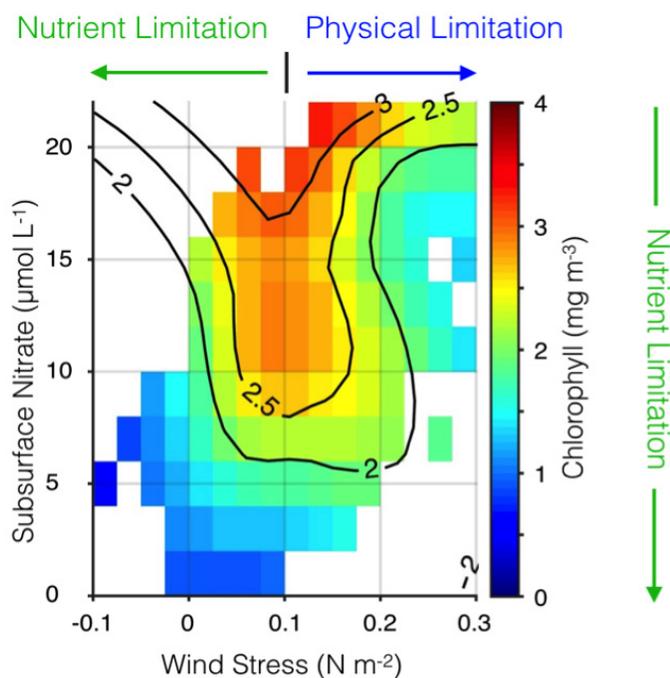


Figure 1. Surface chlorophyll plotted as a function of alongshore wind stress and subsurface nitrate concentration in the central CCS. Wind stress is from the UC Santa Cruz Regional Ocean Model System (ROMS) CCS reanalysis (oceanmodeling.ucsc.edu); nitrate comes from the CCS reanalysis combined with a salinity-temperature-nitrate model developed with World Ocean Database data; and chlorophyll is from the SeaWiFS ocean color sensor. Surface chlorophyll is highest when winds are moderate and subsurface nutrient concentrations are high. Phytoplankton biomass can be hindered by weak upwelling, nitrate-poor source waters, or physical processes (subduction or rapid offshore advection of nutrients and/or phytoplankton, light limitation due to a deep mixed layer) driven by strong winds. Adapted from Jacox et al. (2016a).

ists in the form of coastally trapped waves that propagate poleward along an eastern ocean boundary and thus approach the CCS from the south (Enfield and Allen 1980; Meyers et al. 1998; Strub and James 2002). During an El Niño, these waves tend to deepen the pycnocline and nutricline, which renders upwelling less effective at drawing nutrients to the surface and, therefore, limits potential productivity. While coastally trapped waves that reach the CCS may originate as far away as the equator, topographic barriers exist, notably at the mouth of the Gulf of California (Ramp et al. 1997; Strub and James 2002) and at Point Conception. Since coastally trapped waves that reach a particular location in the CCS can be generated by wind forcing anywhere along the coast equatorward of that location, the oceanic teleconnection may be thought of as an integration of wind forcing experienced along the equator and all the way up the coast to the CCS. Efforts to separate the effects of local wind forcing from coastally trapped waves are complicated by the strong correlation of

alongshore wind along the coast, the fast poleward propagation speed of coastally trapped waves, and the fact that both produce similar effects during canonical El Niño and La Niña events. The 2015-16 El Niño is one example in which warm water and deep isopycnals were observed in the southern CCS despite anomalous local upwelling-favorable winds (Jacox et al. 2016b). In this case, the local winds may have dampened the influence of the oceanic teleconnection (Frischknecht et al. 2017).

Coastally trapped waves are also likely important in setting up an alongshore pressure gradient. The barotropic alongshore pressure gradient influences local upwelling dynamics, as it is balanced primarily by the Coriolis force associated with onshore flow (Connolly et al. 2014). This onshore geostrophic flow acts in opposition to the wind-driven offshore Ekman transport, such that net offshore transport (and consequently upwelling) is less than the Ekman transport (Marchesiello and Estrade 2010). The magnitude of the alongshore pressure gradient is positively correlated with ENSO indices, so it tends to further reduce upwelling during El Niño events, exacerbating the influence of anomalously weak equatorward winds (Jacox et al. 2015).

Alongshore transport

Anomalous alongshore transport has on several occasions been implicated in major ecosystem changes in the CCS. In the case of anomalous advection from the north, as observed in 2002 (Freeland et al. 2003), the CCS is supplied by cold, fresh, and nutrient-rich subarctic water that can stimulate high productivity, even in the absence of strong upwelling. Conversely, anomalous advection of surface waters from the south, as observed during the 1997-98 El Niño (Bograd and Lynn 2001; Lynn and Bograd 2002; Durazo and Baumgartner 2002) may amplify surface warming and water column stratification, intensifying nutrient limitation and biological impacts associated with the atmospheric and oceanic teleconnections.

The poleward flowing California Undercurrent (CUC) may also be modulated by ENSO variability. In particular, there is evidence that strong El Niño events can intensify the CUC (Durazo and Baumgartner 2002; Lynn and Bograd 2002; Gomez-Valdivia et al. 2015), which transports relatively warm, salty, and nutrient-rich water along the North American coast from the tropical Pacific as far north as Alaska (Thomson and Krassovski 2010). Anomalously warm salty water was observed on subsur-

face isopycnals in the southern CUC during 2015-2016 (Rudnick et al. 2016), suggesting anomalous advection from the south. It is unclear whether coastal upwelling can reach deep enough during El Niño events to draw from the CUC, but if so, the CUC intensification could be a mechanism for modifying upwelling source waters and partially mitigating the previously described impacts on nutrient supply.

Finally, in addition to influencing the ecosystem through bottom-up forcing, anomalous surface and subsurface currents can directly influence the ecological landscape by transporting species into the CCS from the north, south, or west. For example, positive phases of ENSO and the PDO are associated with higher biomass of warm-water 'southern' copepods, while negative phases of ENSO and the PDO are associated with increases in cold-water 'northern' copepods (Hooff and Peterson 2006). Importantly, northern copepods are much more lipid-rich than southern copepods; thus, changes in the copepod composition alter the energy available to higher trophic levels and have been implicated in changing survival for forage fish, salmon, and seabirds (Sydeman et al. 2011). During El Niño events, the appearance of additional warm water species (e.g., pelagic red crabs) off the California coast has also been attributed to anomalous poleward

advection, though further research is needed to support this hypothesis.

Measuring ENSO's physical impact on the CCS

While El Niño and La Niña events have specific global and regional patterns associated with them, each ENSO event is unique, both in its evolution and its regional impacts (Capotondi et al. 2015), exemplified by events of the past several years. The tropical evolution of the 2015-16 El Niño was reasonably well predicted by climate models (L'Heureux et al. 2016), in contrast to 2014-15 when a predicted El Niño failed to materialize (McPhaden 2015). However, even in the strong 2015-16 El Niño there were notable exceptions from the expected effects of a strong El Niño, including a lack of increased precipitation over the Southwestern and South Central United States (L'Heureux et al. 2016). Similarly, subsurface ocean anomalies off Central and Southern California were weaker in 2015-16 than they were during the 1982-83 and 1997-98 El Niños (Jacox et al. 2016b), and the 2015-16 El Niño occurred against a backdrop of widespread pre-existing anomalous conditions in the northeast Pacific.

In light of ENSO's diverse expressions in the CCS, it is desirable to develop indices that capture variability in the CCS rather than to rely solely on tropical indices

with uncertain connections to the North American West Coast. For one such index, we turn to data from the California Underwater Glider Network (CUGN), which has sustained observations along California Cooperative Oceanic Fisheries Investigations (CalCOFI) lines 66.7 (Monterey Bay), 80.0 (Point Conception), and 90.0 (Dana Point) since 2007. The temperature anomaly at 50 m depth averaged over the inshore 50 km is calculated using a climatology of CUGN data (Figure 2; Rudnick et al. 2016). The choice of 50 m depth is consistent with the mean depth of the thermocline, and averaging over the inshore 50 km is intended to focus on the region of coastal upwelling. Anomalously warm water is largely the result of anomalously weak upwelling or strong downwelling. Results from all three lines are shown along with the Oceanic Niño Index, a measure of sea surface temperature in the central equatorial Pacific (Figure 2). The major

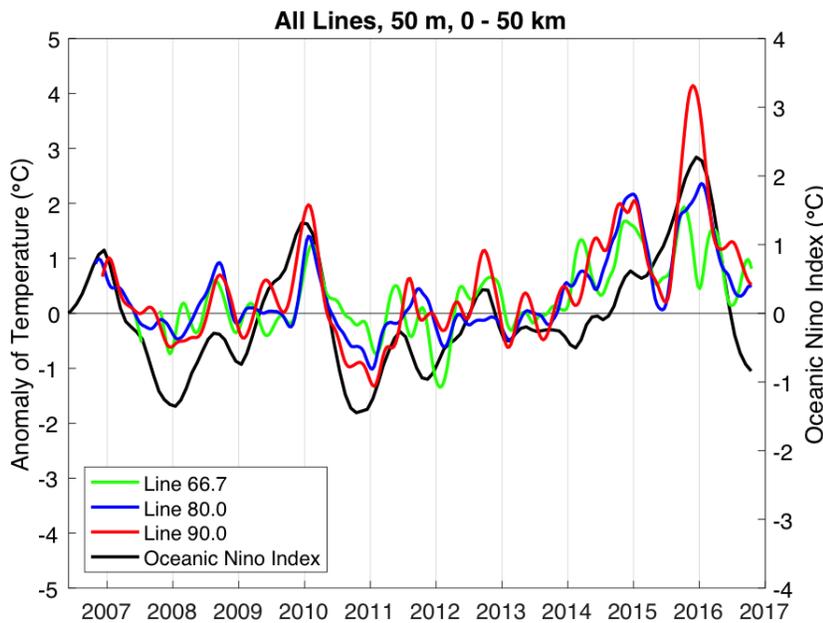


Figure 2. Temperature anomaly at 50 m depth from the California Underwater Glider Network, averaged over the inshore 50 km and filtered with a 3-month running mean. Lines have traditional CalCOFI designations 66.7 (Monterey Bay), 80.0 (Point Conception), and 90.0 (Dana Point). The Oceanic Niño Index (a 3-month running mean of the Niño 3.4 SST anomaly) is plotted for reference.

events of the past decade include the El Niño/La Niña of 2009-11, and the dramatic recent warming that started in 2014 and extended through the El Niño that ended in 2016. The two recent warm periods of 2014-15 (Zaba and Rudnick 2016) and 2015-16 are of note, as they extended along the coast between lines 90.0 and 66.7. While the equatorial Pacific is experiencing La Niña conditions, as of December 2016, anomalous warmth is lingering in the CCS. Time-series such as those in Figure 2 demonstrate the value of the CUGN, which provides direct observations of the vertical structure of the ocean and has been sustained over the past decade along three transects in the CCS. These observations can also be used in conjunction with ocean models and observations from other platforms to observe the physical state of the CCS in near real-time and place it in the context of historical variability, including ENSO-driven variability, spanning decades (e.g. Jacox et al., 2016b).

References

- Alexander, M. A., I. Bladé, 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. *J. Climate*, 15, 2205–2231, doi: 10.1175/1520-0442(2002)015<2205:TABTIO>2.0.CO;2.
- Bograd, S. J., and R. J. Lynn, 2001: Physical-biological coupling in the California Current during the 1997–1999 El Niño-La Niña cycle. *Geophys. Res. Lett.*, 28, 275–278, doi: 10.1029/2000GL012047.
- Capotondi, A., and Coauthors 2015: Understanding ENSO diversity. *Bull. Amer. Meteor. Soc.*, 96, 921-938, doi: 10.1175/BAMS-D-13-00117.1.
- Connolly, T. P., B. M. Hickey, I. Shulman, and R. E. Thomson, 2014: Coastal trapped waves, alongshore pressure gradients, and the California undercurrent. *J. Phys. Oceanogr.*, 44, 319-342, doi: 10.1175/JPO-D-13-095.1.
- Durazo, R., and T. Baumgartner, 2002: Evolution of oceanographic conditions off Baja California: 1997–1999. *Prog. Oceanogr.*, 54, 7–31, doi: 10.1016/S0079-6611(02)00041-1.
- Enfield, D., and J. Allen, 1980: On the structure and dynamics of monthly mean sea-level anomalies along the Pacific coast of North and South-America. *J. Phys. Oceanogr.*, 10. Doi: 10.1175/1520-0485(1980)010<0557:OTSADO>2.0.CO;2.
- Frischknecht, M., M. Münnich, and N. Gruber, 2017: Local atmospheric forcing driving an unexpected California Current System response during the 2015–2016 El Niño. *Geophys. Res. Lett.*, doi: 10.1002/2016GL071316.
- Freeland, H. J., G. Gatién, A. Huyer, and R. L. Smith, 2003: Cold halocline in the northern California Current: An invasion of subarctic water. *Geophys. Res. Lett.* 30, doi: 10.1029/2002GL016663.
- Gómez-Valdivia, F., A. Parés-Sierra, and A. L. Flores-Morales, 2015: The Mexican Coastal Current: A subsurface seasonal bridge that connects the tropical and subtropical Northeastern Pacific. *Contin. Shelf Res.*, 110, 100-107, doi: 10.1016/j.csr.2015.10.010.
- Hooff, R. C., and W. T. Peterson, 2006: Copepod biodiversity as an indicator of changes in ocean and climate conditions of the northern California current ecosystem. *Limnol. Oceanogr.*, 51, 2607-2620, doi: 10.4319/lo.2006.51.6.2607.
- Jacox, M. G., A. M. Moore, C. A. Edwards, and J. Fiechter, 2014: Spatially resolved upwelling in the California Current System and its connections to climate variability. *Geophys. Res. Lett.*, 41, 3189–3196, doi:10.1002/2014GL059589.
- Jacox, M. G., S. J. Bograd, E. L. Hazen, and J. Fiechter, 2015: Sensitivity of the California Current nutrient supply to wind, heat, and remote ocean forcing. *Geophys. Res. Lett.*, 42, 5950–5957, doi:10.1002/2015GL065147.
- Jacox, M., E. Hazen, and S. Bograd, 2016a: Optimal environmental conditions and anomalous ecosystem responses: Constraining bottom-up controls of phytoplankton biomass in the California Current System. *Sci. Rep.*, 6, 7612-27612, doi:10.1038/srep27612.
- Jacox, M., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd, 2016b: Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophys. Res. Lett.* 43, 7072-7080, doi:10.1002/2016GL069716.
- L’Heureux, M., and Coauthors, 2016: Observing and predicting the 2015-16 El Niño. *Bull. Amer. Meteor. Soc.* doi:10.1175/BAMS-D-16-0009.1.
- Lynn, R. J., and S. J. Bograd, 2002: Dynamic evolution of the 1997–1999 El Niño-La Niña cycle in the southern California Current System. *Prog. Oceanogr.*, 54, 59–75, doi: 10.1016/S0079-6611(02)00043-5.
- Marchesiello, P., and P. Estrade, 2010: Upwelling limitation by onshore geostrophic flow. *J. Mar. Res.*, 68, 37-62, doi: 10.1357/002224010793079004.
- McPhaden, M. J., 2015: Playing hide and seek with El Niño. *Nature Climate Change*, 5, 791-795, doi:10.1038/nclimate2775.
- Meyers, S. D., A. Melsom, G. T. Mitchum, and J. J. O’Brien, 1998: Detection of the fast Kelvin wave teleconnection due to El Niño-Southern Oscillation. *J. Geophys. Res.*, 103, 27,655–27,663, doi:10.1029/98JC02402.
- Ramp, S. R., J. L. McClean, C. A. Collins, A. J. Semtner, and K. A. S. Hays, 1997: Observations and modeling of the 1991–1992 El Niño signal off central California. *J. Geophys. Res.*, 102, 5553–5582, doi:10.1029/96JC03050.
- Rudnick, D. L., K. D. Zaba, R. E. Todd, and R. E. Davis, 2016: A climatology of the California Current System from a network of underwater gliders. *Prog. Oceanogr.*, submitted.
- Rykaczewski, R. R., and D. M. Checkley, 2008: Influence of ocean

- winds on the pelagic ecosystem in upwelling regions. *Proc. Natl. Acad. Sci.*, 105, 1965–1970, doi: 10.1073/pnas.0711777105.
- Schwing, F., T. Murphree, L. DeWitt, and P. Green, 2002: The evolution of oceanic and atmospheric anomalies in the northeast Pacific during the El Niño and La Niña events of 1995–2001. *Prog. Oceanogr.*, 54, 459–491, doi:10.1016/S0079-6611(02)00064-2.
- Strub, P., and C. James, 2002: The 1997–1998 oceanic El Niño signal along the southeast and northeast Pacific boundaries—An altimetric view. *Prog. Oceanogr.*, 54, 439–458, doi: 10.1016/S0079-6611(02)00063-0.
- Sydeman, W. J., S. A. Thompson, J. C. Field, W. T. Peterson, R. W. Tanasichuk, H. J. Freeland, S. J. Bograd, and R. R. Rykaczewski, 2011: Does positioning of the North Pacific Current affect downstream ecosystem productivity?. *Geophys. Res. Lett.*, 38, doi: 10.1029/2011GL047212.
- Thomson, R. E., and M. V. Krassovski, 2010: Poleward reach of the California Undercurrent extension. *J. Geophys. Res.: Oceans*, 115, doi: 10.1029/2010JC006280
- Todd, R. E., D. L. Rudnick, R. E. Davis, and M. D. Ohman, 2011: Underwater gliders reveal rapid arrival of El Niño effects off California’s coast. *Geophys. Res. Lett.*, 38, doi:10.1029/2010GL046376.
- Zaba, K. D., and D. L. Rudnick, 2016: The 2014-2015 warming anomaly in the Southern California Current System observed by underwater gliders. *Geophys. Res. Lett.*, 43, 1241-1248, doi:10.1002/2015GL067550.

ENSO diversity and its implications for US West Coast marine ecosystems

Antonietta Capotondi¹, Kris Karnauskas², Arthur Miller³, and Aneesh Subramanian⁴

¹NOAA Earth System Research Laboratory, ²University of Colorado, Boulder ³Scripps Institution of Oceanography, ⁴University of Oxford, UK

The El Niño-Southern Oscillation (ENSO) is the dominant mode of tropical Pacific climate variability at interannual timescales, with profound influences on seasonal weather and ecosystems worldwide. In particular, the physical and biological conditions along the US West Coast, an area that supports one of the most productive marine ecosystems in the world, are strongly influenced by ENSO. Specifically, during El Niño events, along-shore winds weaken and upwelling is reduced, resulting in warmer surface waters, reduced nutrient supply to the euphotic zone, and reduced biological productivity. While these conditions during El Niño events are well known, the exact mechanisms involved and the origin of event-to-event differences in ENSO impacts are not fully understood. Here, we review our current state of knowledge on ENSO and its different expressions, the mechanisms by which ENSO influences the US West Coast, and possible approaches for understanding the predictability of those impacts.

ENSO dynamics and oceanic teleconnections

Tropical Pacific interannual variations involve changes in the thermocline, namely the interface between the warmer upper ocean layer and the colder deeper ocean. In its neutral state, the tropical Pacific is characterized by a shallower thermocline in the eastern Pacific and deeper thermocline in the western Pacific, with a zonal (east-west) slope that is in equilibrium with the surface easterly wind stress. Surface waters are thus colder in the eastern Pacific “Cold Tongue,” and much warmer west of the dateline in the western

Pacific “Warm Pool.” ENSO events are disruptions of this neutral state. During warm events, the El Niño phase, the easterly trades weaken, reducing upwelling in the Cold Tongue region. The thermocline deepens in the east and shoals in the west (Figure 1) and the zonal temperature gradient is reduced. The initial deepening of the eastern Pacific thermocline is achieved through the eastward propagation of downwelling Kelvin waves, excited by high-frequency winds in the form of westerly wind events (WWEs) in the western Pacific (McPhaden 1999, Roundy and Kiladis 2006), and amplified by slower-building wind anomalies (known as the Bjerknes feedback). After

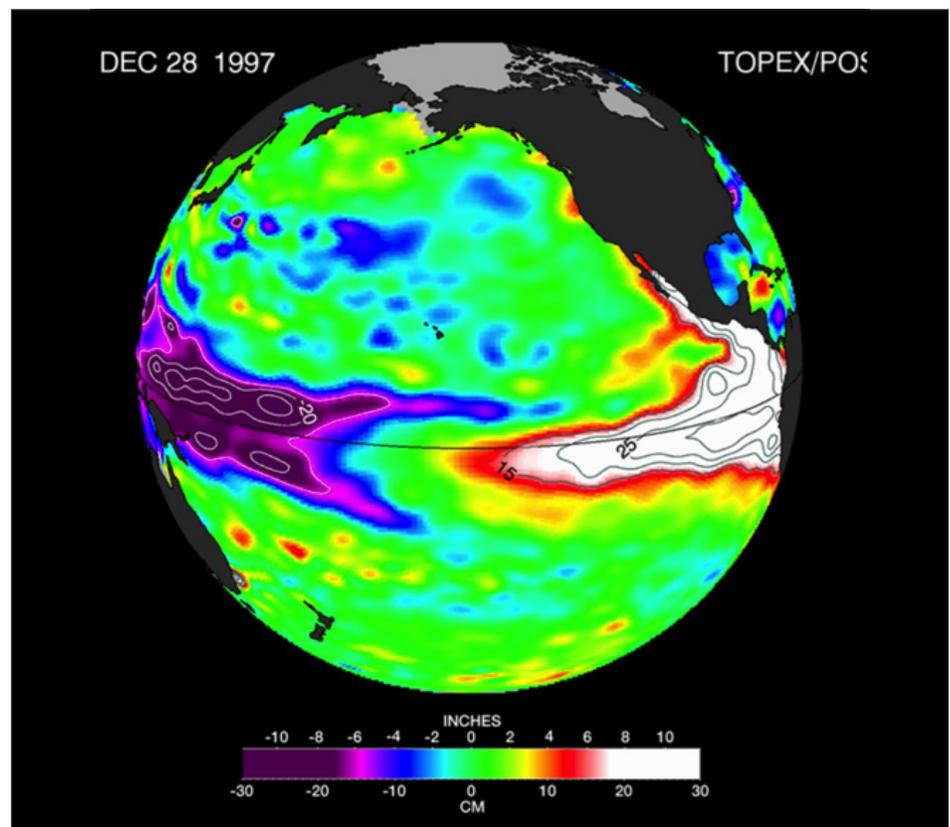


Figure 1. Canonical oceanic teleconnection pattern associated with coastally trapped Kelvin waves emanating from the tropical and subtropical eastern Pacific during the 1997-98 El Niño, as revealed by sea surface height altimeter observations (Credit: NASA/JPL-Caltech). These boundary-trapped waves have the potential to travel from the Equatorial region to the California Coast (and beyond) where they can alter thermocline depth, SST, mixed-layer depth, and currents. Atmospheric teleconnections, however, can also drive regional oceanic anomalies that mimic this same type of response.

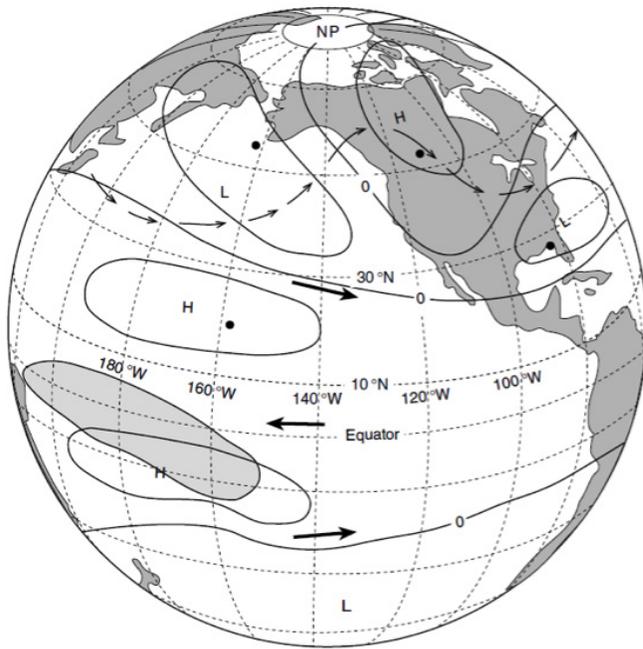


Figure 2. Canonical wintertime atmospheric teleconnection pattern associated with ENSO as a response to tropical heating, also known as the Pacific North American (PNA) pattern, as schematically illustrated by Horel and Wallace (1981). The contour lines represent middle troposphere geopotential height anomalies that occur in response to warm SST in the tropical Pacific near the dateline during an El Niño (shaded area). The Rossby wave-like pattern includes high-pressure anomalies in the Northern Hemispheric subtropics and low-pressure anomalies in the North Pacific, with a ridge over Canada and an anomalous low-pressure region in the Southeastern US. The dark arrows depict the strengthened subtropical jets and easterlies near the dateline. The lighter arrows indicate the distorted mid-tropospheric streamlines due to troughing and ridging.

reaching the eastern ocean boundary, these Kelvin waves continue poleward along the coastlines of the Americas as coastally trapped Kelvin waves, depressing the thermocline, and reducing upwelling along the west coast of North and South America. The coastal wave propagation north of the Equator can clearly be seen in Figure 1 all the way to Baja California. In contrast, upwelling Kelvin waves during La Niña conditions induce a shoaling of the thermocline in the eastern equatorial Pacific and along the west coast of the Americas, resulting in increased upwelling (Simpson 1984; Lynn and Bograd 2002; Huyer et al. 2002; Bograd et al. 2009; Hermann et al. 2009; Miller et al. 2015).

The changes in upwelling associated with the coastal Kelvin waves can directly impact the biogeochemistry of the waters along the US West Coast. However, the offshore scale of the waves decreases with latitude, and the

waves decay while propagating northward due to dissipation and radiation of energy by the generation of westward propagating Rossby waves (Marchesio et al. 2003). In addition, topography and bathymetry can modify the nature of the waves and perhaps partially impede their propagation at some locations, casting some doubt on the effectiveness of coastal waves of equatorial origin to substantially alter the stratification along the US West Coast and modulate the local marine ecosystem.

Atmospheric teleconnections

Equatorial sea surface temperature (SST) anomalies associated with ENSO also influence remote weather and climate through large-scale atmospheric teleconnections. Variations in convection trigger atmospheric stationary Rossby wave trains that alter the Pacific North America Pattern (PNA, Figure 2), a mode of North Pacific geopotential height variability (Horel and Wallace 1981), and induce variations in the regional atmospheric circulation. In particular, El Niño events are associated with an intensification and southward shift of the Aleutian Low (AL) pressure system and changes in the eastern Pacific subtropical high, which conspire to weaken the alongshore winds off the US West Coast, resulting in reduced upwelling and warmer SST. These changes associated with the local atmospheric forcing are similar to those induced by coastal Kelvin waves of equatorial origin, making it very difficult to distinguish the relative importance of the oceanic and atmospheric pathways in this region, especially observationally. In addition, large uncertainties exist surrounding the atmospheric mid-latitude response to tropical SST anomalies. Results from a recent study based on both observations and climate model ensemble simulations indicate that uncertainties in the sea level pressure (SLP) response to ENSO arise primarily from atmospheric internal variability rather than diversity in ENSO events (Deser et al. 2017). Thus, the details of the ENSO teleconnections can vary significantly and randomly from event to event and result in important differences along the California Coast.

ENSO diversity and its implications for impacts on the US West Coast

As already noted by Wyrtki (1975), “No two El Niño events are quite alike.” Indeed, ENSO events differ in amplitude, duration, and spatial pattern, and several studies have suggested that such differences may play an important role in ENSO impacts (see Capotondi et al. 2015 for a review). Special emphasis has been given to the location of the maximum equatorial SST anomalies, as this is an aspect that is readily observed and may influence atmospheric teleconnections (Ashok et al. 2007; Larkin and Harrison 2005). Although the longitudinal position of the maximum SST anomalies along the equator varies from event to event in a quasi-continuum fashion, for practical purposes, events are often grouped depending on whether the largest anomalies are located in the eastern Pacific (“EP” events), or in the central Pacific (“CP” events). Here, we use the relative amplitudes of SST anomalies in the Niño-3 (5°S-5°N, 150°W-90°W) and Niño-4 (5°S-5°N, 160°E-150°W) regions to classify the events as “EP” or “CP”. Figure 3 shows the equatorial

profiles of SST anomalies for the two groups of events in the Simple Ocean Data Assimilation (SODA; Carton and Giese 2008) reanalysis over the period 1958-2007 (Figure 3a) and in 500 years of a pre-industrial control simulation of the National Center for Atmospheric Research (NCAR) Community Climate System Model version 4 (CCSM4; Figure 3b). We notice that there is a large overlap between the two groups of events, which is indicative of the large spread in event longitudinal distribution, although events peaking in the eastern Pacific can achieve larger amplitudes than those peaking in the central Pacific. This difference in amplitude is not as pronounced in the precipitation profiles (Figure 3c), suggesting that in spite of their weaker SST anomaly signature, CP events may still have a large influence on the atmosphere due to their position in a region of warmer background SST.

Do different types of ENSO events have different impacts on the climate and marine ecosystems of the US West Coast? In terms of atmospheric teleconnections, “canonical” EP events have been associated with changes in the AL, while CP events may produce a strengthening

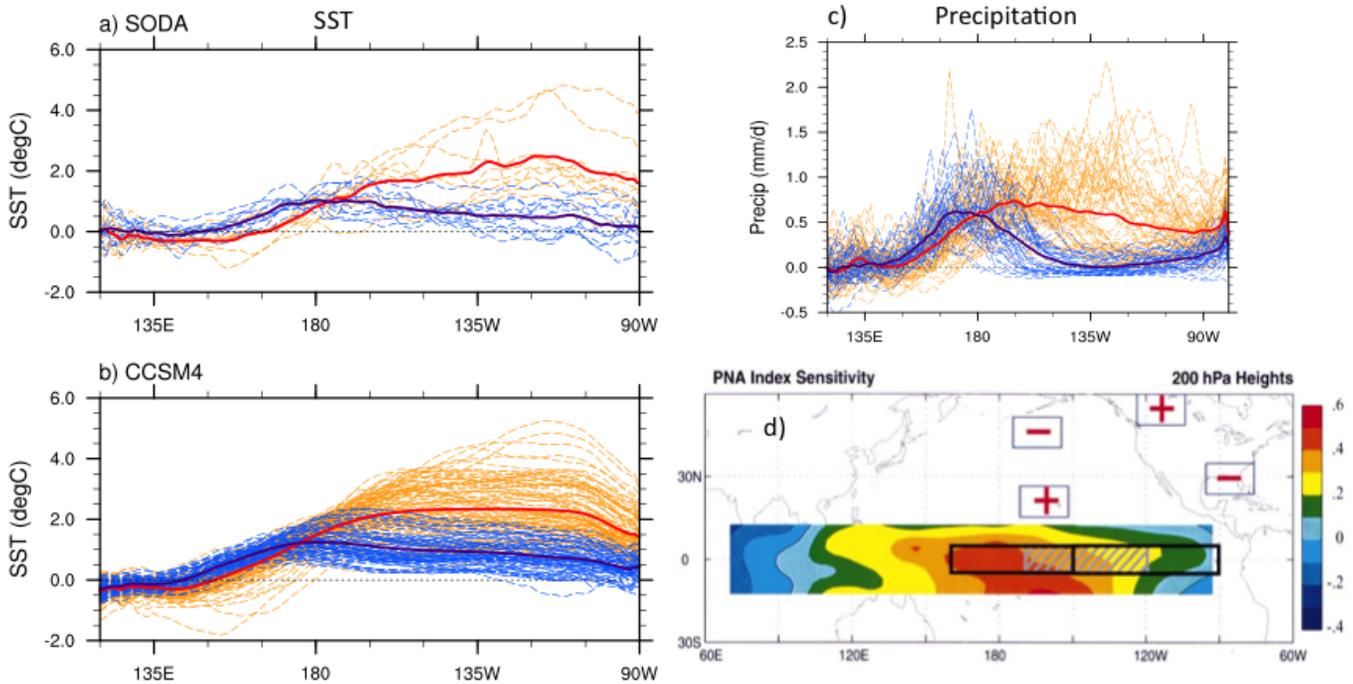


Figure 3. a) Equatorial SST anomaly profiles for El Niño events with largest SST anomalies in the Niño-3 region (EP events, thin dashed orange lines) and in the Niño-4 region (CP events, thin dashed blue lines) from the SODA ocean reanalysis over the period 1958-2007. The thick red and blue lines are the composites of the thin orange and blue lines, respectively. b) Same as in a, but for a 500-year preindustrial simulation of the NCAR-CCSM4 climate model. c) Same as in b, but for precipitation anomalies rather than SST anomalies. The a), b) and c) panels are adapted from Capotondi (2013). d) Tropical SST anomaly pattern, or “sensitivity pattern,” that exerts the largest influence on the PNA (the “+” and “-” signs indicate the PNA highs and lows as shown in Figure 2), as computed by Barsugli and Sardeshmukh (2002) using ensembles of atmospheric model simulations forced by a set of SST anomaly patches over the tropical Pacific. Panel c) is adapted from Barsugli and Sardeshmukh (2002).

of the second mode of North Pacific atmospheric variability, the North Pacific Oscillation (NPO; Di Lorenzo et al. 2013). AL variability is associated with the Pacific Decadal Oscillation, while the NPO appears to provide the atmospheric forcing for the North Pacific Gyre Oscillation (Di Lorenzo et al. 2008), a mode of variability that is largely correlated with biologically relevant quantities along the West Coast of the US. However, the event-to-event differences in teleconnections, associated with intrinsic atmospheric variability, may obscure differences in atmospheric response to different event types.

EP and CP events have different subsurface characteristics as well so that the oceanic pathways between the tropical Pacific and the US West Coast can also be expected to differ in the two cases. While EP events are characterized by large equatorial thermocline anomalies across the basin, which evolve consistently with the recharge oscillator paradigm (Jin 1997), thermocline depth anomalies during CP events tend to be confined to the central part of the basin and do not undergo the large variations associated with the meridional warm water volume transport. As a result, the Kelvin wave signature in the eastern equatorial Pacific, and the resulting amplitude of the coastal Kelvin wave can be expected to be weaker during CP events. Indeed, a recent study (Fischer et al. 2015) has shown that temperature anomalies (and associated zooplankton composition) in the northern California Current responded very rapidly to EP El Niño events with a peak during boreal winter, whereas CP events were accompanied by a delayed response with a peak during boreal spring. The most recent 2015/16 El Niño provides another compelling example of diversity in ENSO influences. In spite of the magnitude of the event, which was comparable to the previous two extreme events on record, the 1982/83 and 1997/98, the changes in temperature, thermocline/nutricline depth, and alongshore winds associated with this event were much smaller than during the two previous cases (Jacox et al. 2016). These differences are perhaps due to the unique nature of this event, whose spatial pattern has elements of both EP and CP El Niño types, with, in particular, a weaker thermocline depth anomaly in the eastern equatorial Pacific relative to the 1982/83 and 1997/98 cases. This question remains open and is the subject of intense research.

How well can we predict different types of ENSO events? Several studies have attempted to determine specific precursors for EP- and CP-type events. SST and wind stress anomalies propagating southwestward from the Southern California coast to the central equatorial Pacific, a pattern known as the “Pacific Meridional Mode”

(PMM; Chiang and Vimont 2004) has been suggested as a possible precursor for CP events (Yu and Kim 2011; Vimont et al. 2014), while SST and wind stress anomalies extending northward along the coast of South America toward the eastern equatorial Pacific (the “South Pacific Meridional Mode” or SPMM; Zhang et al. 2014) have been considered as candidate precursors for EP-type events. While these modes of variability do produce initial SST anomalies either in the central or eastern Pacific, these anomalies can propagate along the equator and maximize at a different longitude in the mature phase of the event. For example, the strong 1982/83 EP El Niño developed from anomalous SSTs in the central Pacific in the late spring of 1982, which propagated eastward to achieve their largest amplitude near the South American coast in the following winter (Xue and Kumar 2016). In late spring 2015, on the other hand, anomalies exceeding 2°C appeared in the far eastern Pacific and then propagated westward to reach their largest amplitude in the central Pacific in winter (Xue and Kumar 2016). While several studies have emphasized SST precursors, thermocline conditions two seasons prior to the peak of an event appear to play an important role in the development of the two types of events (Capotondi and Sardeshmukh 2015). Deeper than average initial thermocline conditions in the eastern Pacific favor EP-type events and shallower than average eastern Pacific thermocline depth favors CP-type events. The results of Capotondi and Sardeshmukh (2015) were obtained using a combination of multiple linear regressions and linear inverse modeling (Penland and Sardeshmukh 1995), thus objectively providing the initial state that will optimally evolve, two seasons later, in either an EP- or CP-type event.

Given the remaining uncertainties in the exact triggers of ENSO diversity, as well as the large noise level of atmospheric teleconnections, how can we isolate the predictable component of the ENSO influence on the US West Coast physical and biogeochemical conditions in the Pacific? In other words, even if we could perfectly predict ENSO in all its diversity and atmospheric teleconnections, how well could we predict the ecosystem responses? One possible approach is to determine the SST pattern to which a given target quantity (e.g., a mode of atmospheric variability or some local ecosystem forcing function) is most sensitive. The SST anomalies that are most effective in influencing specific “target” regions do not necessarily coincide with the anomalies typical of “canonical” ENSO events (Rasmussen and Carpenter 1982). In fact, as shown by Barsugli and Sardeshmukh (2002) the PNA pattern is particularly sensitive to SST anomalies in the Niño-4 re-

the sensitivity pattern relative to stronger EP events, and be as (if not more) effective in influencing atmospheric teleconnections like the PNA (compare Figures 3a,b with Figure 3d). Similar sensitivity patterns could be determined for key regional forcing function along the US West Coast, either using the approach outlined in Barsugli and Sardeshmukh (2002) or via multiple linear regression (e.g., Capotondi and Sardeshmukh 2015).

Conclusions

In summary, ENSO can provide a large source of potential predictability for the physics and the biology of the US West Coast. However, in light of the large uncertainties associated with ENSO diversity and atmospheric teleconnections, novel approaches need to be developed to isolate the robust predictable components of ENSO influences and inform forecast development.

References

- Ashok, K., S. K. Behera, S. A. Rao, H. Weng, and T. Yamagata, 2007: El Niño Modoki and its possible teleconnections. *J. Geophys. Res.*, 112, doi:10.1029/2006JC003798.
- Barsugli, J. J., and P. D. Sardeshmukh, 2002: Global atmospheric sensitivity to tropical SST anomalies throughout the Indo-Pacific basin. *J. Climate*, 15, 3427-3442, doi: 10.1175/1520-0442(2002)015<3427:GASTTS>2.0.CO;2.
- Bograd, S. J., I. Schroeder, N. Sarkar, X. Qiu, W. J. Sydeman, and F. B. Schwing, 2009: Phenology of coastal upwelling in the California Current. *Geophys. Res. Lett.*, 36, doi: 10.1029/2008GL035933.
- Capotondi, A., 2013: ENSO diversity in the NCAR CCSM4 climate model. *J. Geophys. Res. Oceans*, 118, 4755-4770, doi:10.1002/jgrc.20335.
- Capotondi, A., and Coauthors, 2015: Understanding ENSO Diversity. *Bull. Amer. Meteor. Soc.*, 96, 921-938, doi:10.1175/BAMS-D-13-00117.1.
- Capotondi, A., and P. D. Sardeshmukh, 2015: Optimal precursors of different types of ENSO events. *Geophys. Res. Lett.*, 42, doi:10.1002/2015GL066171.
- Carton, J. A., and B. S. Giese, 2008: A reanalysis of ocean climate using simple ocean data assimilation (SODA). *Mon. Wea. Rev.*, 136, 2999-3017, doi:10.1175/2007MWR1978.1.
- Chiang, J. C. H., and D. J. Vimont, 2004: Analogous Pacific and Atlantic meridional modes of tropical atmosphere-ocean variability. *J. Climate*, 17, 4143-4158, doi: 10.1175/JCLI4953.1.
- Deser, C., I. R. Simpson, K. A. McKinnon, and A. S. Phillips, 2017: The Northern Hemisphere extra-tropical atmospheric circulation response to ENSO: How well do we know it and how do we evaluate models accordingly? *J. Climate*, submitted.
- Di Lorenzo, E., and Coauthors, 2008: North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys. Res. Lett.*, 35, doi:10.1029/2007gl032838.
- Di Lorenzo, E., and Coauthors, 2013: Synthesis of Pacific Ocean climate and ecosystem dynamics. *Oceanogr.*, 26, 68-81, doi: 10.5670/oceanog.2013.76.
- Fischer, J. L., W. T. Peterson, and R. R. Rykaczewski, 2015: The impact of El Niño events on the pelagic food chain in the northern California Current. *Glob. Change Bio.*, 21, 4401-4414, doi:10.1111/gbc.13054.
- Hermann, A. J., E. N. Curchitser, D. B. Haidvogel, and E. L. Dobbins, 2009: A comparison of remote vs. local influence of El Niño on the coastal circulation of the northeast Pacific. *Deep Sea Res. Part II: Top. Stud. Oceanogr.*, 56, 2427-2443, doi: 10.1016/j.dsr2.2009.02.005.
- Horel, J. D., and J. M. Wallace, 1981: Planetary-scale atmospheric phenomena associated with the Southern Oscillation. *Mon. Wea. Rev.*, 109, 813-829, doi: 10.1175/1520-0493(1981)109<0813:PSAPAW>2.0.CO;2.
- Huyer, A., R. L. Smith, and J. Fleischbein, 2002: The coastal ocean off Oregon and northern California during the 1997-8 El Niño. *Prog. Oceanogr.*, 54, 311-341, doi: 10.1016/S0079-6611(02)00056-3.
- Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd, 2016: Impacts of the 2015-2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophys. Res. Lett.*, 43, 7072-7080, doi:10.1002/2016GL069716.
- Jin, F.-F., 1997: An equatorial ocean recharge paradigm for ENSO. Part I: Conceptual model. *J. Atmos. Sci.*, 54, 811-829, doi: 10.1175/1520-0469(1997)054<0811:AEORPF>2.0.CO;2.
- Larkin, N. K., and D. E., Harrison, 2005: On the definition of El Niño and associated seasonal average U.S. weather anomalies. *Geophys. Res. Lett.* 32, doi:10.1029/2005GL022738.
- Lynn, R. J., and S. J. Bograd, 2002: Dynamic evolution of the 1997-1999 El Niño-La Niña cycle in the southern California Current system. *Prog. Oceanogr.*, 54, 59-75, doi: 10.1016/S0079-6611(02)00043-5.
- Marchesiello, P., J. C. McWilliams, and A. Shchepetkin, 2003: Equilibrium structure and dynamics of the California Current System. *J. Phys. Oceanogr.*, 33, 753-783, doi: 10.1175/1520-0485(2003)33<753:ESADOT>2.0.CO;2.
- McPhaden, M. J., 1999: Climate oscillations – Genesis and evolution of the 1997-98 El Niño. *Science*, 283, 950-954.
- Miller, A. J., H. Song, and A. C. Subramanian, 2015: The physical oceanographic environment during the CCE-LTER Years: Changes in climate and concepts. *Deep Sea Res. Part II: Top. Stud. Oceanogr.*, 112, 6-17, doi: 10.1016/j.dsr2.2014.01.003.

- Penland, C., and P. D. Sardeshmukh, 1995: The optimal growth of tropical sea surface temperature anomalies. *J. Climate*, 8, 1999-2024, doi: 10.1175/1520-0442(1995)008<1999:TOGOTS>2.0.CO;2.
- Rasmusson, E. M., and T. H. Carpenter, 1982: Variations in tropical sea-surface temperature and surface wind fields associated with the Southern-Oscillation El Niño. *Mon. Wea. Rev.*, 110, 354-384, doi: 10.1175/1520-0493(1982)110<0354:VITSST>2.0.CO;2.
- Roundy, P. E., and G. N. Kiladis, 2006: Observed relationships between intraseasonal oceanic Kelvin waves and atmospheric forcing. *J. Climate*, 19, 5253-5272.
- Simpson, J. J., 1984. El Nino-induced onshore transport in the California Current during 1982-1983. *Geophys. Res. Lett.*, 11, 233-236, doi: 10.1029/GL011i003p00233.
- Vimont, D. J., M. A. Alexander, and M. Newman, 2014: Optimal growth of central and east Pacific ENSO events. *Geophys. Res. Lett.*, 41, doi:10.1002/2014GL059997.
- Wyrтки, K., 1975: El Niño – The dynamic response of the equatorial Pacific Ocean to atmospheric forcing. *J. Phys. Oceanogr.*, 5, 572-584, doi: 10.1175/1520-0485(1975)005<0572:ENTDRO>2.0.CO;2.
- Xue, Y., and A. Kumar, 2016: Evolution of the 2015-16 El Niño and historical perspective since 1979. *Sci. China, Earth Sci.*, doi:10.1007/s11430-016-0106-9.
- Yu., J.-Y., and S. T. Kim, 2011: Relationships between extratropical sea level pressure variations and the central-Pacific and eastern-Pacific types of ENSO. *J. Climate*, 24, 708-720, doi: 10.1175/2010JCLI3688.1.
- Zhang, H., A. Clement, and P. Di Nezio, 2014: The South Pacific Meridional Mode: A mechanism for ENSO-like variability. *J. Climate*, 27, 769-783, doi: 10.1175/JCLI-D-13-00082.1.

Impact of ENSO on biogeochemistry and lower trophic level response in the California Current System

Clarissa Anderson¹, Samantha Siedlecki², Cecile Rousseaux^{3,4}, Brian Powell⁵, Bill Peterson⁶, and Chris Edwards⁷

¹*Scripps Institution of Oceanography*, ²*University of Washington*, ³*NASA Goddard Space Flight Center*, ⁴*Universities Space Research Association*, ⁵*University of Hawaii, Manoa*, ⁶*NOAA Northwest Fisheries Science Center*, ⁷*University of California, Santa Cruz*

El Niño events are one of the “most spectacular instances of interannual variability in the ocean” with “profound consequences for climate and the ocean ecosystem” (Cane 1986). Perturbations in the atmosphere directly influence the ocean with long-term effects on environmental variability in the tropical Pacific Ocean as the El Niño-Southern Oscillation (ENSO) shifts between El Niño, neutral, and La Niña states on a timescale of two to seven years. On longer timescales, teleconnections from the tropics to extratropical regions drive Pacific decadal variability, and these can be both oceanic and atmospheric in nature. Mid-latitude variability of the Pacific Decadal Oscillation (PDO) has been associated with ENSO (e.g., Newman et al. 2003) and is distinguished from ENSO in part by its multidecadal timescale (20–30 years; 50 years). The PDO is dependent upon ENSO as a response to the combined effects of atmospheric noise (Newman et al. 2003), as well as the asymmetry of the ENSO cycle (Rodgers et al. 2004). Therefore, when discussing decadal variability of the northeast Pacific, we are referring to the delayed impacts of ENSO.

Ecosystem impacts of northeast Pacific variability

Given the complex influence of tropical climate on northeast Pacific ecosystems, there is significant overlap between ENSO signals and higher frequency modes of the PDO Index. It is widely recognized that interactions between these two climate modes drive substantial ecosystem variability on a range of time and space scales. Large regime shifts in the North Pacific that have reverberated throughout the ecosystem, from physics to fish, are recurring patterns now associated with low-frequency changes in sea surface temperature (SST) that characterize the PDO (e.g., Mantua et al. 1997). Some of the higher-frequency fluctuations in ecosystem variables of the northeast Pacific that have not been successfully attributed to PDO or ENSO are now thought to be driven by an intermediate mode of variability called the North Pacific Gyre Oscillation (NPGO). While the PDO is character-

ized as the first empirical orthogonal function (EOF) of SST, NPGO is defined as the first EOF of both SST and sea surface height (SSH) anomalies (Di Lorenzo et al. 2008). Compared to PDO and ENSO, NPGO is more closely tied to variations in salinity, nutrient upwelling, and chlorophyll a (chl-a) in the long-running California Cooperative Oceanic Fisheries Investigations (CalCOFI) time-series. DiLorenzo et al. (2008) suggest that major ecosystem regime shifts require a simultaneous and opposite sign reversal of the NPGO and PDO, as was seen shortly after the massive ENSO event of 1997/98, and all three indices relate back to dynamics in the tropical Pacific. The struggle is to understand how these low- to high(er)-frequency modes of variability in the climate and physics drive fluctuations in biogeochemistry and coastal ecology.

As discussed by Jacox et al. (this issue), there is an expected or canonical set of physical conditions associated with ENSO in the California Current System (CCS). This physical response to ENSO generally includes: 1) changes in surface wind stress that alter the strength of coastal upwelling and downwelling; 2) remote oceanic forcing by coastally trapped waves that propagate poleward along the US West Coast and modify thermocline depth and coastal stratification; and 3) changes to alongshore advection (Jacox et al., this issue). The ecological response of the coastal marine environment includes changes in primary production and the community composition of plankton and higher trophic levels that can be directly or more subtly related to these physical factors. Primary production is driven by vertical nutrient flux to well-lit surface waters; nutrient supply is related to upwelling magnitude, upwelling source depth, and nutrient concentrations at the source depth. ENSO-related processes are also important for interannual and seasonal variability of oxygen concentrations and carbonate biogeochemistry on the Washington and Oregon Shelves (Siedlecki et al. 2015). In this article, we highlight some of the modeling and observational studies that have successfully attributed ENSO-like vari-

ability to specific impacts on the biogeochemistry and lower-trophic level organisms of the northeast Pacific and CCS.

Carbon dioxide

Numerical models are widely employed to diagnose climatic forcing of the physical and biogeochemical conditions of the northeast Pacific. For instance, using a fully coupled ocean and biogeochemical model, Xiu and Chai (2014) found that after accounting for atmospheric effects, the air-sea flux and resulting $p\text{CO}_2$ of sea water in the Pacific was significantly correlated (0.6) to the Multivariate ENSO Index (MEI) with a lag of ten months. Similarly, Wong et al. (2010) found that sea surface $p\text{CO}_2$ was significantly correlated with the MEI in the northeast Pacific. Biogeochemical models of different complexity have also highlighted the connection between PDO and the interannual variability of air-sea CO_2 fluxes (e.g., McKinley et al. 2006). These studies also demonstrate that the individual components controlling surface ocean $p\text{CO}_2$ in the northeast Pacific respond to PDO with significant amplitudes, but that their combined influence has a relatively small effect on the CO_2 fluxes in this region. Xiu and Chai (2014) showed that the dominant driver of North Pacific $p\text{CO}_2$ variability is anthropogenic CO_2 , whereas air-sea CO_2 flux is more closely correlated with the PDO and the NPGO.

Nutrients and chlorophyll

In the coastal regions of the northeast Pacific, such as the CCS, ENSO significantly impacts the nutrient supply due to modifications of upwelling and source waters mentioned above (Jacox et al., this issue). At the peak of the El Niño season in December-January, Frischknecht et al. (2016) found a pattern in the development of chlorophyll events through a modeling study focused on the CCS. Around the onset of the El Niño year, chlorophyll anomalies were consistently low. This pattern was even more pronounced during the spring of the following year. In spring of the second year (i.e. with the onset of the upwelling season), all events shared the development of a strong negative chlorophyll anomaly. Frischknecht et al. (2016) attributed this phenomenon to a persistent lack of nutrients to support production driven by a combination of physical mechanisms impacting the thermocline (Jacox et al. 2015; 2016; this issue) and light limitation at the onset of the upwelling season. Consequently, El Niño events disrupt the biogeochemical cycling in these systems for months, even years, after the event is over. The observations in Oregon, from the Newport line in Fisher et al.

(2015), detail the nitrate anomalies from 1995 to 2015, and the nitrate anomalies remain negative long after the Niño-3.4 SST anomaly suggested that the event was over. This may contribute to the success surrounding seasonal forecast systems like J-SCOPE, in which forecasts of biogeochemical parameters (e.g., bottom oxygen) outperformed those of physical variables (e.g., SST) in terms of predictive skill (Siedlecki et al. 2016).

Oxygen and carbon

The relationship between ENSO and nutrient availability from source waters can serve as an analog for oxygen and carbon content. We would expect from observed stoichiometry that when nutrients are low, oxygen is relatively high and carbon is low. In California, this has been documented: El Niño events correlate to higher oxygen and pH, while La Niña events are correlated with lower oxygen and pH (e.g., Nam et al. 2011). In the northern CCS along the Washington and Oregon coasts, the interannual variability in oxygen content of source waters has been correlated to NPGO more than ENSO (Peterson et al. 2013). Consistent with these findings, oxygen has been increasing since 2010 and aragonite saturation state (a measure of the availability of carbonate ion to calcifying organisms) has been elevated in 2015-2016 relative to the year prior in both Oregon and California (McClatchie et al. 2016).

Primary production and particle export

As an eastern boundary upwelling region, the CCS is among the most productive in the world in terms of primary production and fisheries. The suppression of nutrient availability described above can be thought of as reduced “upwelling efficacy” that leads to reduced primary production in the CCS, while La Niña often has the opposite effect due to associated increases in the upwelling efficacy (Jacox et al. 2015). In the southern CCS, the 1997/1998 El Niño led to a significant deepening of the nutricline, with the strongest effects along CalCOFI Line 80, and a pronounced regional reduction of primary production (Bograd and Lynn 2001). The uptake of silicon increased in central California (Santa Barbara Channel) during the onset of the 1997 event, suggesting that diatoms were major drivers of the primary productivity prior to the 1998 spring season when overall productivity was reduced in response to density surface adjustments (Shipe and Brzezinski 2003). Despite reductions in surface layer primary productivity in response to the El Niño, export ratios of particulate organic carbon and particulate organic nitrogen increased during the spring of 1998 relative to the

1994-1997 period, while biogenic Si flux decreased in response to the El Niño (Shipe et al. 2002). This counterintuitive result appears to be due to an increase in particulate material exported to depth. By 1999, ratios of Si/N and Si/C had not recovered to pre-El Niño conditions.

Phytoplankton community composition

Warmer waters and changes in nutrient supply associated with ENSO can lead to phytoplankton community shifts such as an influx of coccolithophores or an increase in harmful algal blooms (HABs). The most common harmful algal bloom organism in the CCS is the diatom genus *Pseudo-nitzschia*. McCabe et al. (2016) recently observed a link between the Oceanic Niño Index (ONI), the *Pseudo-nitzschia* growth rate anomaly determined from temperature-growth relationships, and domoic acid levels in razor clams over a 16-year period (Figure 1), implicating El Niño-driven warming in the unprecedented 2015 HAB along the US West Coast. Similarly, McKibben et al. (2017) linked warm phases of the PDO and ONI to domoic acid in shellfish in the northern CCS. The toxic blooms off Newport in 2015 were the most prolonged (late-April through October 2015) and among the most toxic ever observed off Oregon (Du et al. 2015; McKibben et al. 2017). Conversely, Santa Barbara Basin sediment

trap data showed no significant correlation between a 15-year record of domoic acid levels and PDO, NPGO, or ENSO indices; however, there was a strong change point in the frequency and toxicity of these blooms following the 1997/1998 ENSO (Sekula-Wood et al. 2011).

Zooplankton community composition

Off the Oregon coast, a 21-year time-series of fortnightly hydrography and plankton sampling of shelf and slope waters showed that the water masses (and thus the plankton) that dominate shelf and slope waters vary seasonally, interannually, and on decadal scales. Thus, it is a simple matter to track the timing of summer or winter arrival, ENSO events, and changes in sign of the PDO (Figure 2). During summer months, northerly winds drive surface waters offshore (Ekman transport), which are replaced by the upwelling of cold nutrient-rich waters that penetrate the continental shelf and fuel high primary production. Northerly winds also enhance the southward transport of water (and plankton) from the coastal Gulf of Alaska into the coastal northern CCS, and these species are referred to as ‘cold water’ or ‘northern species.’ During winter, the winds reverse and the poleward Davidson current transports warm coastal water from southern California to the northern CCS, bringing with it ‘southern species’ of plankton. On longer timescales (5-10

years), cold-water, northern copepods are largely replaced by warm-water, southern copepods during El Niño events (Fisher et al. 2015) and during the positive phase of the PDO (Keister et al. 2011). Incorporating the physiological response of these zooplankton groups into biogeochemical-ecosystem models (in addition to the effects of physical transport) will be essential for advancing our predictive capacity of plankton communities in the CCS.

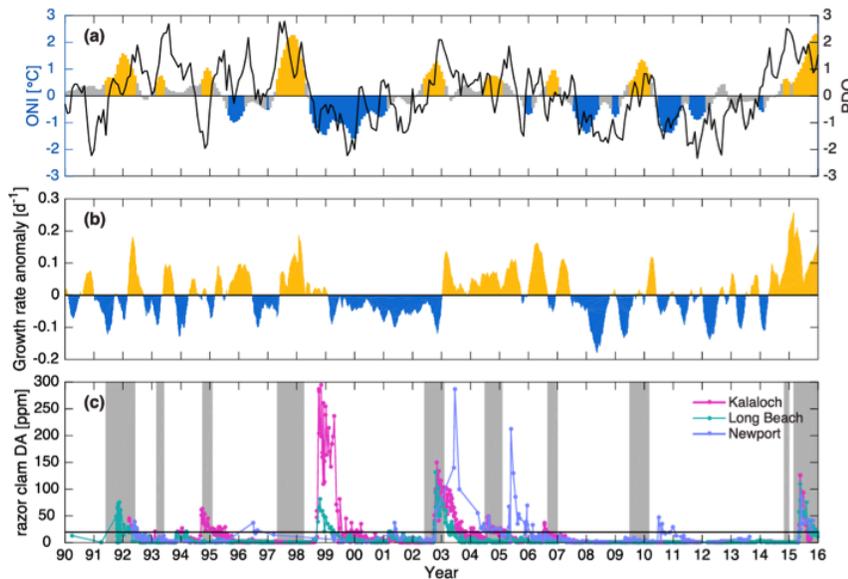


Figure 1. Records of razor clam toxicity and the potential growth rate anomaly for *Pseudo-nitzschia* spp. are plotted below the Oceanic Niño Index (gold = El Niño, blue = La Niña, gray = neutral) to illustrate the association between ENSO events and harmful algal blooms in the northern CCS. The potential for *Pseudo-nitzschia* growth does not always coincide with records of high domoic acid in shellfish, e.g., 1997 El Niño. Figure adapted from McCabe et al. (2016).

Predicting ecosystem response to ENSO: Now and in the future

State-of-the-art models, in situ measurements, and available satellite observations are all required to adequately characterize short- and long-term physical dynamics associated with ENSO and Pacific decadal variability. Seasonal-to-interannual forecasting of the ecosystem response

to ENSO in the CCS and throughout the northeast Pacific will depend on our understanding of how interannual climate variability alters ocean biogeochemistry and productivity at the base of the food web, and therefore how predictive models should be modified to capture the dynamic range introduced by these anomalous events. Unusual warm water anomalies, as observed during large ENSO events, may serve as important analogs for assessing the impacts of long-term warming on the pelagic ecosystem of the CCS. Regional simulations suggest similarities between the physical drivers leading to biogeochemical variability from ENSO and those in projected future upwelling systems (Ryckaczewski and Dunne 2010). Further exploration of the mechanisms and predictive skill of forecasts on seasonal timescales will enhance our understanding and improve our projections further into the future. Global climate models are unable to anticipate anomalous warming events such as major ENSO events. As such, they are unable to detect large-scale events related to shifts in the distribution of pelagic species or

track ecological changes associated with such events. Furthermore, the evaluation of model-based forecasts and projections of ecosystem variations and changes across timescales requires that long-term physical, biogeochemical, and ecological observation programs are maintained and others initiated. High-resolution modeling approaches for forecasts and projections should also be prioritized, so that ecosystem impacts of future climate anomalies can be anticipated and understood in greater detail.

References

- Bograd, S. J., & Lynn, R. J. (2001). Physical-biological coupling in the California Current during the 1997–99 El Niño-La Niña Cycle. *Geophysical Research Letters*, 28(2), 275-278.
- Cane, M. A., S. E. Zebiak, and S. C. Dolan, 1986: Experimental forecasts of El Niño. *Nature* 321, 827–832, doi:10.1038/321827a0.
- Di Lorenzo, E., and Coauthors, 2008: North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys. Res. Lett.*, 35, doi:10.1029/2007gl032838.
- Du, X., W. Peterson, and L. O’Higgins, 2015: Interannual variations in phytoplankton community structure in the northern California Current during the upwelling seasons of 2001-2010. *Mar. Ecol. Prog. Ser.*, 519, 75-87, doi: 10.3354/meps11097.
- Fisher, J. L., W. T. Peterson, and R. Ryckaczewski, 2015: The impact of El Niño events on the pelagic food chain in the northern California Current. *Global Change Bio.*, 21, 4401-4414, doi:10.1111/gbc.13054.
- Frischknecht, M., M. Münnich, and N. Gruber, 2016: Local atmospheric forcing driving an unexpected California Current System response during the 2015–2016 El Niño, *Geophys. Res. Lett.*, 43, doi:10.1002/2016GL071316.
- Jacox, M. G., J. Fiechter, A. M. Moore, and C. A. Edwards, 2015: ENSO and the California Current coastal upwelling response. *J. Geophys. Res.*, 120, 1691–1702, doi: 10.1002/2014JC010650.
- Jacox, M., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd, 2016: Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophys. Res. Lett.* 43, 7072-7080, doi:10.1002/2016GL069716.
- 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. *Glob. Change Bio.*, 17, 2498-2511, doi: 10.1111/j.1365-2486.2010.02383.x.
- Liu, Z., and M. Alexander, 2007: Atmospheric bridge, oceanic tunnel, and global climatic teleconnections. *Rev. Geophys.*, 45, doi: 10.1029/2005RG000172.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis, 1997: A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Amer. Meteorol. Soc.*, 78, 1069–1079, doi: 10.1175/1520-0477(1997)078<1069:APICOW>2

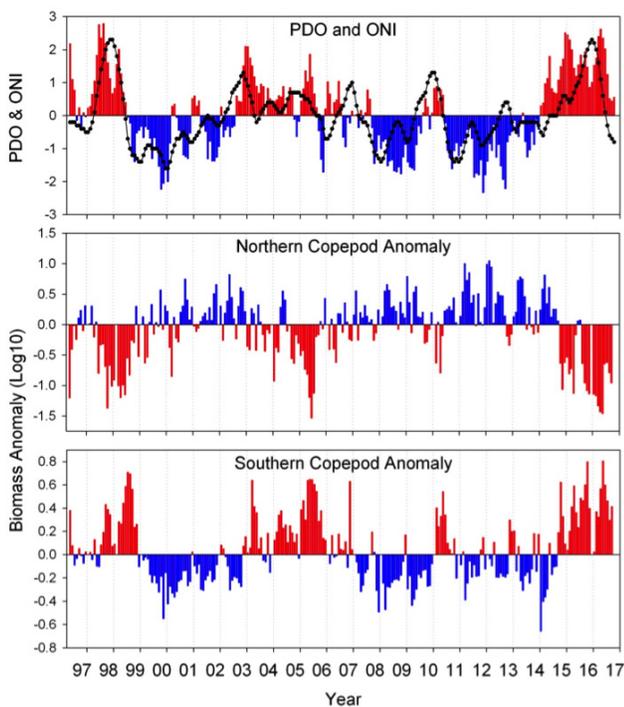


Figure 2. Monthly time series of the Pacific Decadal Oscillation and Oceanic Niño Index (upper) and monthly-averaged biomass anomalies of northern copepods (middle) and southern copepods (lower). Note the high coherence between the PDO and ONI with the copepod time series – positive anomalies of northern copepods are correlated with negative PDO and ONI; positive anomalies of southern copepods are correlated with positive PDO and ONI.

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- McCabe, R. M., and Coauthors, 2016: An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. *Geoph. Res. Lett.*, 43, doi: 10.1002/2016GL070023.
- McClatchie, S., A. R. Thompson, S. R. Alin, S. Siedlecki, W. Watson, and S. J. Bograd, 2016: The influence of Pacific Equatorial Water on fish diversity in the southern California Current System. *J. Geophy. Res.*, 121, 6121-6136, doi: 10.1002/2016JC011672.
- McKibben, S. M., W. Peterson, M. Wood, V. L. Trainer, M. Hunter, and A. E. White, 2017: Climatic regulation of the neurotoxin domoic acid. *Proc. Nat. Acad. Sci.*, 114, 239-244, doi: 10.1073/pnas.1606798114.
- McKinley, G. A., and Coauthors, 2006: North Pacific carbon cycle response to climate variability on seasonal to decadal timescales. *J. Geophy. Res.*, 111, doi: 10.1029/2005JC003173.
- Nam, S., H. J. Kim, and W. Send, 2011: Amplification of hypoxic and acidic events by La Niña conditions on the continental shelf off California. *Geophy. Res. Lett.*, 38, doi: 10.1029/2011GL049549.
- Newman, M., G. P. Compo, and M. A. Alexander, 2003: ENSO-forced variability of the Pacific decadal oscillation. *J. Climate*, 16, 3853-3857, doi: 10.1175/1520-0442(2003)016<3853:EVOTPD>2.0.CO;2.
- Peterson, J. O., C. A. Morgan, W. T. Peterson, and E. Di Lorenzo, 2013: Seasonal and interannual variation in the extent of hypoxia in the northern California Current from 1998–2012. *Limnol. Oceanogr.*, 58, 2279-2292, doi: 10.4319/lo.2013.58.6.2279.
- Rodgers, K. B., P. Friederichs, and M. Latif, 2004: Tropical Pacific decadal variability and its relation to decadal modulations of ENSO. *J. Climate*, 17, 3761-3774, doi: 10.1175/1520-0442(2004)017<3761:TPDVAI>2.0.CO;2.
- Rykaczewski, R. R., and J. P. Dunne, 2010: Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. *Geophy. Res. Lett.*, 37, doi: 10.1029/2010GL045019.
- Sekula-Wood, E., C. Benitez-Nelson, S. Morton, C. Anderson, C. Burrell, and R. Thunell, 2011: Pseudo-nitzschia and domoic acid fluxes in Santa Barbara Basin (CA) from 1993 to 2008. *Harmful Algae*, 10, 567–575, doi: 10.1016/j.hal.2011.04.009.
- Shipe, R. F., Passow, U., Brzezinski, M. A., Graham, W. M., Pak, D. K., Siegel, D. A., &
- Allredge, A. L. (2002). Effects of the 1997–98 El Niño on seasonal variations in suspended and sinking particles in the Santa Barbara basin. *Progress in Oceanography*, 54(1), 105-127.
- Shipe, R. F., and M. A. Brzezinski, 2003: Siliceous plankton dominate primary and new productivity during the onset of El Niño conditions in the Santa Barbara Basin, California. *J. Mar. Sys.*, 42, 127-143, doi: 10.1016/S0924-7963(03)00071-X.
- Siedlecki, S. A., N. S. Banas, K. A. Davis, S. Giddings, B. M. Hickey, P. MacCready, T. Connolly, and S. Geier, 2015: Seasonal and interannual oxygen variability on the Washington and Oregon continental shelves. *J. Geophy. Res.*, 120, 608-633, doi: 10.1002/2014JC010254.
- Siedlecki, S. A., I. C. Kaplan, A. J. Hermann, T. T. Nguyen, N. A. Bond, J. A. Newton, G. D. Williams, W. T. Peterson, S. R. Alin, and R. A. Feely, 2016: Experiments with seasonal forecasts of ocean conditions for the northern region of the California Current upwelling system. *Sci. Rep.*, 6, 27203, doi: 10.1038/srep27203.
- Valsala, V., S. Maksyutov, M. Telszewski, S. Nakaoka, Y. Nojiri, M. Ikeda, and R. Murtugudde, 2012: Climate impacts on the structures of the North Pacific air-sea CO₂ flux variability. *Biogeosci.*, 9, 477, doi: 10.5194/bg-9-477-2012.
- Xiu, P., and F. Chai, 2014: Variability of oceanic carbon cycle in the North Pacific from seasonal to decadal scales. *J. Geophy. Res.*, 119, 5270-5288, doi: 10.1002/2013JC009505.

Modeling to aid management of marine top predators in a changing climate

Elliott Hazen¹, Mike Alexander², Steven Bograd¹, Alistair J. Hobday³, Ryan Rykaczewski⁴, Kylie L. Scales⁵

¹Southwest Fisheries Science Center, NOAA, ²Earth System Research Laboratory, NOAA, ³CSIRO, Australia, ⁴University of South Carolina, ⁵University of the Sunshine Coast, Australia

Marine top predators can include species that occupy a high trophic level (e.g., predatory sharks), have few predators (e.g., marine turtles), or can exert top-down control on food webs due to their large energetic demands (e.g., whales). While many species in the open ocean are widely distributed (e.g., Read et al. 2013; Reygondeau et al. 2012), the higher trophic levels are noteworthy as they are also wide-ranging (e.g., tuna (Itoh et al. 2003; Block et al. 2011; Hobday et al. 2015), seabirds (Shaffer et al. 2006), turtles (Shillinger et al. 2008; Briscoe et al. 2016)). These wide-ranging species can serve as ecological linkages within and across ocean basins, through both ontogenetic (larvae to adult) and seasonal migrations (Boustany et al. 2010; Hobday et al. 2015; Briscoe et al. 2016). Many wide-ranging marine animals show site fidelity at particular times during their lives or have relatively small and well-defined areas of critical habitat, which facilitates both exploitation (e.g., Hobday et al. 2015) and protection (e.g., Ban et al. 2014). This fidelity can be related to the temporal and spatial predictability of their physical habitats, as evidenced by predictable seasonal aggregations of high-trophic fishes, birds, turtles, and mammals (Scales et al. 2014), which is aided by sensory capabilities that permit them to locate specific physical and biological features.

These species are also of interest, as they are often charismatic, providing commercial, cultural, or ecological value (e.g., Weng et al. 2015). Top predators in marine ecosystems are supported by the productivity of primary and secondary consumers; thus they integrate a range of processes across these lower levels in the trophic food web. Their relatively long life spans and wide-ranging movements mean that many marine predator populations integrate variability across larger spatial and temporal scales than many lower-trophic-level populations (Shaffer et al. 2006). Top predators also have movement and sensory capabilities that permit active targeting of biophysical features (Scales et al. 2014). These characteristics make assessments of top predator populations particularly valuable for investigations of large-scale ecosystem variability and change.

For example, in the California Current System (CCS),

plankton (Fisher et al. 2015; Lluch-Belda et al. 2005) and nekton (Lynn 2003; Phillips et al. 2007; Lluch-Belda et al. 2005) exhibit distributional shifts associated with El Niño-Southern Oscillation (ENSO) events, which are echoed by changes in the distribution of top predators. While the distribution of planktonic organisms is indicative of changes in circulation and habitat suitability, shifts in the distributions of top predators and other nekton are often the result of changes in migration patterns based on the availability of prey. Historical observations of the distributions of top predators indicate that along the West Coast of North America, populations are typically displaced poleward during El Niño events. Also, distributions of species with ranges that are typically offshore (e.g., highly migratory fishes) are contracted towards the West Coast, and the catch-per-unit-effort of tunas and yellowtail are often increased in response to the increased availability to nearshore fishers (Sydeman and Allen 1999; Benson et al. 2002; Henderson et al. 2014). Shifts in species distributions attributed to El Niño are often documented in local newspapers and fishing reports as well as in scientific publications (Lluch-Belda et al. 2005; Cavole et al. 2016). However, many predator populations resident to the CCS (e.g., common murre, Cassin's auklet, and splitnose rockfishes) exhibit extreme negative productivity anomalies during El Niño (Black et al. 2014), and these events are the most prominent anomalies in time-series spanning multiple decades. Mass strandings of pinnipeds (e.g., sea lions) and die-offs of seabirds have also been associated with El Niño events. These unusual mortality events have been attributed to reduced availability of forage fishes and the exacerbated effects of harmful algal blooms that accompanied past El Niño events (McCabe et al. 2016).

This nearshore compression of viable habitat can also expose these species to a range of relatively concentrated anthropogenic threats, including fishing, oil and gas exploration, transport, and pollution (e.g., Ban et al. 2014). For example, Maxwell et al. (2013) combined electronic tracking from eight top predator species in the CCS with data on 24 anthropogenic stressors to develop a metric of cumulative utilization and impact. The

distribution of these stressors and species showed that comprehensive management approaches are required, as no single approach was likely to be successful. Predicting the time-varying distribution and abundance of these and other high-trophic-level species may offer additional management insight, and allow a dynamic approach to management and conservation (e.g., Hobday et al. 2014; Scales et al. 2014; Lewison et al. 2015; Maxwell et al. 2015; Hazen et al. 2016).

Using top predators to monitor ocean changes

There is a suite of tools available for monitoring the response of top predator populations and distributions to variation in environmental conditions. At-sea surveys record the presence and abundance of air-breathing marine predators, such as seabirds, whales, sea turtles, and pinnipeds, which can be reliably sighted at the ocean surface or detected using acoustic methods. Standardized, repeat surveys such as the California Cooperative Oceanic Fisheries Investigations (CalCOFI; Bograd et al. 2003) and NOAA's Cetacean Ship Surveys (e.g., CalCurCEAS 2014; Rankin et al. 2016) provide longitudinal datasets informative for understanding population trends and regional habitat preferences (Forney et al. 2015; Sydeman et al. 2014). When combined with in situ measurements of physical conditions and prey distributions, survey datasets generate insight into the finer-scale biophysical mechanisms that underlie the dynamics of predator-prey interactions (Benoit-Bird et al. 2013; Embling et al. 2012). Over broader scales, aerial surveys are useful for mapping distributions of air-breathers (Barlow & Forney 2007), and as new technologies become more widely available—such as autonomous underwater vehicles (AUVs), unmanned aerial vehicles (UAVs) (Christiansen et al. 2016; White et al. 2016), and passive acoustics (Morano et al. 2012)—they are increasingly used to survey and study predator populations.

Animal tracking and telemetry allow for remote acquisition of data describing movements and behaviors of marine predators as they move freely through their natural environment. Tracking individuals of known age, sex, body condition, and breeding status has revealed previously cryptic at-sea behaviors (Block et al. 2011; Hazen et al. 2012; Hussey et al. 2015). For example, satellite telemetry has revealed the complexities of ocean-basin scale migrations in several populations (e.g., seabirds (Clay et al. 2016; Shaffer et al. 2006), sea turtles (Briscoe et al. 2016), and pinnipeds (Robinson et al. 2012)). Understanding migratory behaviors improves our knowledge of phenology (timing) and increases chances of detecting climate change

responses. Telemetry datasets have also proven particularly powerful in identifying important foraging habitats (e.g., Block et al. 2011; Grecian et al. 2016; Raymond et al. 2015). When linked with measures of body condition or population-level metrics, such as breeding success, tracking datasets provide novel insights into population status and responses to physical variability (e.g., Biuw et al. 2007). Together, these technologies have revolutionized understanding of at-sea habitat use by marine predator populations across the global ocean and hold promise for the use of top predators themselves as monitors of ecosystem change.

Additional statistical tools are necessary to relate predator distribution data to their prey and the environment. Species Distribution Models (SDMs) quantify predator habitat preferences by combining movement or distribution datasets with physical data from in situ measurements, satellite remote sensing, or ocean models (Robinson et al. 2011). A variety of techniques are used for modeling habitat preferences, such as Resource Selection Functions (e.g., generalized linear or additive models), machine learning (e.g., regression or classification trees; Elith & Leathwick 2009), and ensemble predictions from multiple algorithms (Scales et al. 2015). SDMs can enhance the value of tracking data in identifying foraging habitats and provide insight into how predictability in the locations of at-sea habitats links to persistence in the physical environment historically, in real-time, or for future projections (Hobday and Hartmann 2006; Hazen et al. 2013; Becker et al. 2014; Hazen et al. 2016). Individual-based or agent-based models link biological responses to heterogeneity and variability in the physical environment using sets of mechanistic rules that underlie biophysical interactions. To date, individual-based models have been used most extensively for lower trophic-level marine predators, such as small pelagic fish (e.g., Pethybridge et al. 2013), as the mechanisms that link the distributions of these organisms to biophysical conditions are generally better understood than for top predators. However, this approach has distinct advantages for modeling top predator habitat use as it explicitly includes prey-field dynamics, an aspect often missing from SDMs owing to the lack of empirical data describing broad-scale prey distributions. Recent advances using regional ocean models with an individual-based model framework have proven effective in modeling predator habitat selection (e.g., California sea lions (Fiechter et al. 2016)) and hold promise for forecasting top predator distributions in changing oceanic seascapes. In particular, a combination of statistical and mechanistic models can identify non-stationarity in

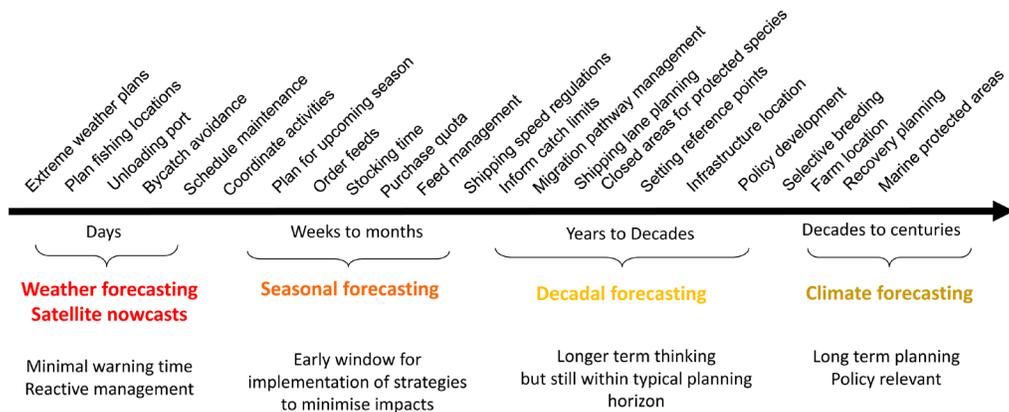


Figure 1. Decisions relevant to fisheries, aquaculture, and conservation sectors at forecasting timescales are noted above the time line. Seasonal forecasting is considered most useful for proactive marine management at this time, with decadal forecasting in its infancy. Modified from Hobday et al. 2016.

predator-environment relationships and can use energetic and movement rules to incorporate prey into predictive models (Muhling et al. 2016).

Managing for a changing climate

Marine top predators are actively managed in many regions to provide social (e.g., tourism), economic (e.g., harvesting), or ecological benefits (e.g., healthy reefs). Traditional management approaches remain an important tool for managing top predators exploited in marine fisheries and addressing conservation objectives. However, in regions with both short-term and long-term change, static spatial management may not represent the best solution when there are competing goals for ocean use (protection or exploitation), as oceanic habitats are mobile and static protection often requires large areas to cover all of the critical habitat for a particular time period (Hobday et al. 2014; Maxwell et al. 2015). Instead, dynamic spatial management may be a suitable alternative, provided that species movements are predictable and suitable incentives exist (Hobday et al. 2014; Maxwell et al. 2015; Lewison et al. 2015). Several approaches, using data and models described in the previous section, can be used to develop a dynamic management approach in response to variable species distributions, including those based on historical patterns (e.g., past responses to ENSO), real-time, and forecasted prediction of species occurrence. Real-time approaches can use observed data (e.g., satellite data or as-

simulated ocean model output), while seasonal and decadal approaches require validated models and forecasts of ocean state (Figure 1).

The longest standing real-time example comes from the Australian Eastern Tuna and Billfish Fishery (ETBF; Hobday and Hartmann 2006). Fishers in this multi-species longline fishery often target different species—yellowfin, bigeye, and southern bluefin tunas; marlin; and swordfish—depending on seasonal availability and prevailing ocean conditions, and are themselves subjected to management decisions that alter their fishing behavior. In this region, dynamic ocean management was first used in 2003 to reduce unwanted bycatch of quota-limited southern bluefin tuna (SBT). The distribution of likely SBT habitat, which can change rapidly with the movement of the East Australian Current, was used to dynamically regulate fisher access to east coast fishing areas. A habitat preference model was used to provide near real-time advice to management about the likely SBT habitat (Hobday et al. 2010). Managers use these habitat preference reports to frequently update spatial restrictions to fishing grounds, which involve dividing the ocean into a series of zones based on expected distribution of SBT. These restrictions limit unwanted interactions by fishers that do not hold SBT quota (SBT cannot be landed without quota and in that situation must be discarded) and allow access to those that do have SBT quota to operate efficiently (Hobday et al. 2010). The underlying habitat model has evolved

from a surface temperature-based model to an integrated surface and sub-surface model, and currently includes a seasonal forecasting element to aid managers and fishers planning for future changes in the location of the habitat zones (Hobday et al. 2011). This ongoing improvement and adaptation of the system has seen new oceanographic products tested and included in the operational model. This dynamic approach has reduced the need for large area closures while still meeting the management goal but does require more flexible fishing strategies to be developed, including planning vessel movements, home port selection, and quota purchase.

In parallel with improved biological data, numerical climate forecast systems have greatly improved over the last 30 years and now have the capability to provide useful seasonal forecasts (National Research Council, 2010). Dynamic forecast systems include i) global climate models (GCMs), which consist of atmosphere, ocean, land, and ice components; ii) observations from multiple sources (e.g., satellites, ships buoys); iii) an assimilation system to merge the observations with the model's "first guess" to initialize forecasts; and iv) post-processing software to display and disseminate the model output. Such systems

are currently used to make forecasts at scales on the order of 100 km on seasonal and even decadal timescales (e.g., Kirtman et al. 2014; Meehl et al. 2014; Stock et al. 2015). In addition, output from the GCMs is being used to drive much higher-resolution forecasts from regional ocean models (Siedlecki et al. 2016). Model skill on seasonal timescales is a function of persistence, multi-year climate modes (e.g., ENSO, IOD), and its teleconnections and transport by ocean currents. Model skill on decadal timescales arises due to anthropogenic climate change and slowly evolving ocean circulation features such as the Atlantic Meridional Overturning Circulation (AMOC; Salinger et al. 2016). GCM-based forecast systems are currently being used to predict sea surface temperature, sub-surface temperatures, and other ocean conditions that are subsequently used in marine resource applications described above (Hobday et al. 2011; Eveson et al. 2015, Figure 2). However, skill from statistical methods is currently on par with those from much more complex and computer-intensive numerical models (Newman 2013; Jacox et al. 2017), and forecast skill will always be limited regardless of the quality of both models and observations due to the chaotic elements of the climate system.

Ecosystem Prediction

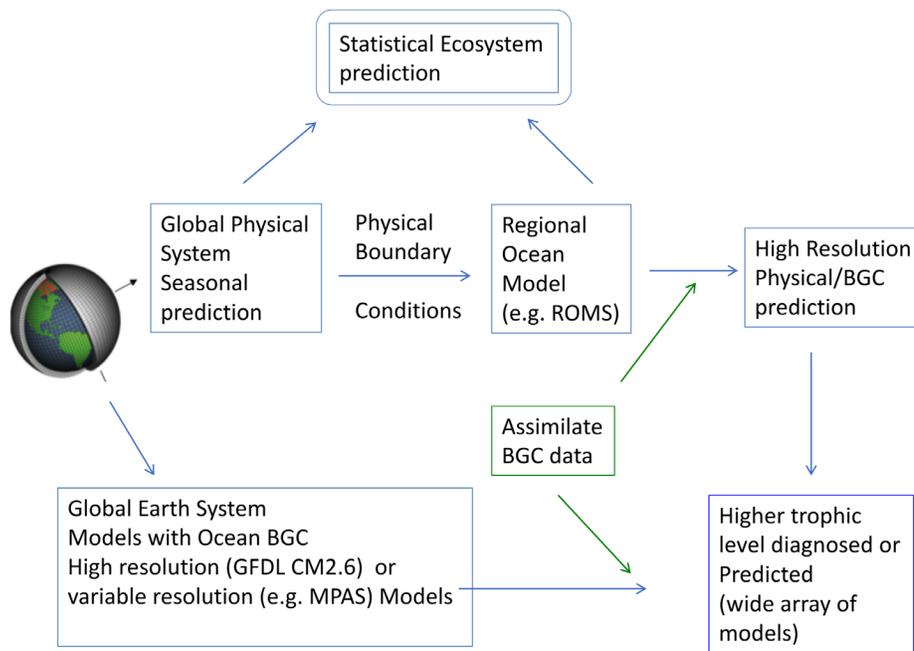


Figure 2. Ecosystem predictions require a suite of inputs and modeling steps to ensure both physical and biological components in the ecosystem are adequately represented. Physical models (from 1 degree to 1/10 degree downscaled models) can be used to predict higher trophic level distributions directly or can be used to drive individual based movement models of prey and predator to incorporate trophic dynamics in ecosystem predictions.

Where do we go from here?

As described above, ocean forecast systems and biological data are being linked to advance top predator management. Three priorities to strengthen this link and better inform management efforts include: (i) gather and share data, (ii) identify effective measures and improve mechanistic understanding of prey availability, and (iii) understand the spatial and temporal overlap between humans and particular focal species.

First, while the capacity to monitor marine top predators has made considerable strides in recent years (Hussey et al. 2015), juvenile portions of many top predator populations can be under-represented and need particular attention (Hazen et al. 2012). Tagging efforts provide detailed data on animal movement and can provide finer-scale data than traditional shipboard surveys. However, there are only a few examples of broad-scale tagging efforts that allow for measurement of diversity and multi-species habitat use, such as the Tagging of Pacific Predators and the Ocean Tracking Network (Block et al. 2011, Hussey et al. 2015). There is a growing trend for these data to be made widely available in repositories (e.g., Ocean Biogeographic Information System Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP), Seabird Tracking Database) that allow for greater synthesis than individual datasets alone (Halpin et al. 2006; Lascelles et al. 2016). This should be encouraged as standard practice, as in the oceanographic community (e.g., Global Ocean Ship-Based Hydrographic Investigations Program (GO-SHIP) database). Data collection must continue, as climate variability and change influence the relationship between top predators and their environment, and additional data are necessary to both test and refine predictive models.

Second, while the movements of many highly migratory predators are tied closely to prey availability, most models of marine top predator habitat use remotely sensed or in situ oceanographic measurements as proxies for prey distribution, which is rarely available. The difficulty is in measuring prey distribution at the scales appropriate for predators (e.g., Torres et al. 2008). We can measure fine-scale foraging behavior using archival tag data and associated prey measurements (e.g., Goñi et al. 2009; Hazen et al. 2009), but these ship-based approaches cannot provide data at the scales used in management-focused habitat models (see Lawson et al. 2015). We can model prey distributions mechanistically to inform models of top predator movements (Fiechter et al. 2016), but these approaches have not yet been coupled with real-time prediction. Prey data at migration-wide scales would greatly improve both

statistical and mechanistic models by offering insight to where residence times are highest, yet these data remain difficult beyond fine-spatial scales (Benoit-Bird et al. 2013; Boyd et al. 2015).

Finally, both animals and humans use the marine environment at multiple spatial and temporal scales. For example in the Pacific, blue whales migrate from high-latitude foraging grounds to tropical breeding grounds seasonally and travel to discrete foraging hotspots based on prey availability (Bailey et al. 2009), and container vessels are making decisions such as ship speed, choice of shipping lanes, and port of call on multiple time scales as well (Hazen et al. 2016). This requires information on long-term habitat pathways and high-use areas (e.g., for static protection), as well as the shorter-term (e.g., seasonal) triggers of migration and identification of ocean features that result in high prey aggregations and increased residence times. Comparably, a fisher may change her long-term investment decisions (e.g., quota purchase, hiring crew) based on projections of long-term stock dynamics, or may decide when to start fishing seasonally based on weather and proximity to port, or when to set a net based on when fish schools are plentiful (Figure 1). Thus, management approaches could also be nested to include real-time predictions, seasonal forecasts, and decadal projections to inform multiple management processes (Hobday and Hartmann 2006; Hobday et al. 2011; Salinger et al. 2016). This suite of dynamic spatial management tools would represent an adaptive strategy robust to shifting habitats and species in response to climate variability and change.

Conclusions

In summary, ENSO can provide a large source of potential predictability for the physics and the biology of the US West Coast. However, in light of the large uncertainties associated with ENSO diversity and atmospheric teleconnections, novel approaches need to be developed to isolate the robust predictable components of ENSO influences and inform forecast development.

References

- Ashok, K., S. K. Behera, S. A. Rao, H. Weng, and T. Yamagata, 2007: El Niño Modoki and its possible teleconnections. *J. Geophys. Res.*, 112, doi:10.1029/2006JC003798.
- Barsugli, J. J., and P. D. Sardeshmukh, 2002: Global atmospheric sensitivity to tropical SST anomalies throughout the Indo-Pacific basin. *J. Climate*, 15, 3427-3442, doi: 10.1175/1520-0442(2002)015<3427:GASTTS>2.0.CO;2.
- Bograd, S. J., I. Schroeder, N. Sarkar, X. Qiu, W. J. Sydeman, and F. B. Schwing, 2009: Phenology of coastal upwell-

- ing in the California Current. *Geophys. Res. Lett.*, 36, doi: 10.1029/2008GL035933.
- Capotondi, A., 2013: ENSO diversity in the NCAR CCSM4 climate model. *J. Geophys. Res. Oceans*, 118, 4755-4770, doi:10.1002/jgrc.20335.
- Capotondi, A., and Coauthors, 2015: Understanding ENSO Diversity. *Bull. Amer. Meteor. Soc.*, 96, 921-938, doi:10.1175/BAMS-D-13-00117.1.
- Capotondi, A., and P. D. Sardeshmukh, 2015: Optimal precursors of different types of ENSO events. *Geophys. Res. Lett.*, 42, doi:10.1002/2015GL066171.
- Carton, J. A., and B. S. Giese, 2008: A reanalysis of ocean climate using simple ocean data assimilation (SODA). *Mon. Wea. Rev.*, 136, 2999-3017, doi:10.1175/2007MWR1978.1.
- Chiang, J. C. H., and D. J. Vimont, 2004: Analogous Pacific and Atlantic meridional modes of tropical atmosphere-ocean variability. *J. Climate*, 17, 4143-4158, doi: 10.1175/JCLI4953.1.
- Deser, C., I. R. Simpson, K. A. McKinnon, and A. S. Phillips, 2017: The Northern Hemisphere extra-tropical atmospheric circulation response to ENSO: How well do we know it and how do we evaluate models accordingly? *J. Climate*, submitted.
- Di Lorenzo, E., and Coauthors, 2008: North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys. Res. Lett.*, 35, doi:10.1029/2007gl032838.
- Di Lorenzo, E., and Coauthors, 2013: Synthesis of Pacific Ocean climate and ecosystem dynamics. *Oceanogr.*, 26, 68-81, doi: 10.5670/oceanog.2013.76.
- Fischer, J. L., W. T. Peterson, and R. R. Rykaczewski, 2015: The impact of El Niño events on the pelagic food chain in the northern California Current. *Glob. Change Bio.*, 21, 4401-4414, doi:10.1111/gbc.13054.
- Hermann, A. J., E. N. Curchitser, D. B. Haidvogel, and E. L. Dobbins, 2009. A comparison of remote vs. local influence of El Niño on the coastal circulation of the northeast Pacific. *Deep Sea Res. Part II: Top. Stud. Oceanogr.*, 56, 2427-2443, doi: 10.1016/j.dsr2.2009.02.005.
- Horel, J. D., and J. M. Wallace, 1981: Planetary-scale atmospheric phenomena associated with the Southern Oscillation. *Mon. Wea. Rev.*, 109, 813-829, doi: 10.1175/1520-0493(1981)109<0813:PSAPAW>2.0.CO;2.
- Huyer, A., R. L. Smith, and J. Fleischbein, 2002: The coastal ocean off Oregon and northern California during the 1997-8 El Niño. *Prog. Oceanogr.*, 54, 311-341, doi: 10.1016/S0079-6611(02)00056-3.
- Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd, 2016: Impacts of the 2015-2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophys. Res. Lett.*, 43, 7072-7080, doi:10.1002/2016GL069716.
- Jin, F.-F., 1997: An equatorial ocean recharge paradigm for ENSO. Part I: Conceptual model. *J. Atmos. Sci.*, 54, 811-829, doi: 10.1175/1520-0469(1997)054<0811:AEORPF>2.0.CO;2.
- Larkin, N. K., and D. E., Harrison, 2005: On the definition of El Niño and associated seasonal average U.S. weather anomalies. *Geophys. Res. Lett.* 32, doi:10.1029/2005GL022738.
- Lynn, R. J., and S. J. Bograd, 2002: Dynamic evolution of the 1997-1999 El Niño-La Niña cycle in the southern California Current system. *Prog. Oceanogr.*, 54, 59-75, doi: 10.1016/S0079-6611(02)00043-5..
- Marchesiello, P., J. C. McWilliams, and A. Shchepetkin, 2003. Equilibrium structure and dynamics of the California Current System. *J. Phys. Oceanogr.*, 33, 753-783, doi: 10.1175/1520-0485(2003)33<753:ESADOT>2.0.CO;2.
- McPhaden, M. J., 1999: Climate oscillations – Genesis and evolution of the 1997-98 El Niño. *Science*, 283, 950-954.
- Miller, A. J., H. Song, and A. C. Subramanian, 2015: The physical oceanographic environment during the CCE-LTER Years: Changes in climate and concepts. *Deep Sea Res. Part II: Top. Stud. Oceanogr.*, 112, 6-17, doi: 10.1016/j.dsr2.2014.01.003.
- Penland, C., and P. D. Sardeshmukh, 1995: The optimal growth of tropical sea surface temperature anomalies. *J. Climate*, 8, 1999-2024, doi: 10.1175/1520-0442(1995)008<1999:TOGOTS>2.0.CO;2.
- Rasmusson, E. M., and T. H. Carpenter, 1982: Variations in tropical sea-surface temperature and surface wind fields associated with the Southern-Oscillation El Niño. *Mon. Wea. Rev.*, 110, 354-384, doi: 10.1175/1520-0493(1982)110<0354:VITSST>2.0.CO;2.
- Roundy, P. E., and G. N. Kiladis, 2006: Observed relationships between intraseasonal oceanic Kelvin waves and atmospheric forcing. *J. Climate*, 19, 5253-5272.
- Simpson, J. J., 1984. El Niño-induced onshore transport in the California Current during 1982-1983. *Geophys. Res. Lett.*, 11, 233-236, doi: 10.1029/GL011i003p00233.
- Vimont, D. J., M. A. Alexander, and M. Newman, 2014: Optimal growth of central and east Pacific ENSO events. *Geophys. Res. Lett.*, 41, doi:10.1002/2014GL059997.
- Wyrtki, K., 1975: El Niño – The dynamic response of the equatorial Pacific Ocean to atmospheric forcing. *J. Phys. Oceanogr.*, 5, 572-584, doi: 10.1175/1520-0485(1975)005<0572:ENTDRO>2.0.CO;2.
- Xue, Y., and A. Kumar, 2016: Evolution of the 2015-16 El Niño and historical perspective since 1979. *Sci. China, Earth Sci.*, doi:10.1007/s11430-016-0106-9.
- Yu., J.-Y., and S. T. Kim, 2011: Relationships between extra-tropical sea level pressure variations and the central-Pacific and eastern-Pacific types of ENSO. *J. Climate*, 24, 708-720, doi: 10.1175/2010JCLI3688.1.
- Zhang, H., A. Clement, and P. Di Nezio, 2014: The South Pacific Meridional Mode: A mechanism for ENSO-like variability. *J. Climate*, 27, 769-783, doi: 10.1175/JCLI-D-13-00082.1.

Seasonal forecasts of ocean conditions in the California Current Large Marine Ecosystem

Desiree Tommasi¹, Michael G. Jacox^{2,3}, Michael A. Alexander⁴, Samantha Siedlecki⁵, Francisco E. Werner³, Charles A. Stock⁶, Nicholas A. Bond⁵

¹Princeton University, ²University of California, Santa Cruz, ³Southwest Fisheries Science Center, NOAA, ⁴Earth System Research Laboratory, NOAA, ⁵University of Washington, ⁶Geophysical Fluid Dynamics Laboratory, NOAA

The California Current Large Marine Ecosystem (CCLME) is a productive coastal ecosystem extending from Baja California, Mexico, to British Columbia, Canada. High primary productivity is sustained by inputs of cooler, nutrient-rich waters during seasonal wind-driven upwelling in spring and summer. This high productivity fuels higher trophic levels, including highly valued commercial (\$3.5B yr⁻¹) and recreational (\$2.5B yr⁻¹) US fisheries (NOAA 2016). The CCLME system experiences large interannual and decadal variability in ocean conditions in response to the El Niño-Southern Oscillation (ENSO) and extratropical climate modes such as the Pacific Decadal Oscillation and the North Pacific Gyre Oscillation (Di Lorenzo et al. 2013). ENSO events affect productivity of the CCLME ecosystem through atmospheric and oceanic pathways. In the former, El Niño triggers a decrease in equatorward winds (Alexander et al. 2002), reducing upwelling and nutrient inputs to coastal surface waters (Schwing et al. 2002; Jacox et al. this issue). In the latter, El Niño events propagate poleward from the equator via coastally trapped Kelvin waves, increasing the depth of the thermocline, and hence decreasing the nutrient concentration of upwelled source waters during El Niño events (Jacox et al. 2015; Jacox et al. this issue). Thus, CCLME productivity, forage fish dynamics, and habitat availability for top predators can vary substantially between years (Chavez et al. 2002; Di Lorenzo et al. 2013; Hazen et al. 2013; Lindegren et al. 2013), and there is increasing recognition of the need to incorporate seasonal forecasts of ocean conditions into management frameworks to improve fisheries management and industry decisions (Hobday et al. 2016; Tommasi et al. 2017a). We describe herein recent improvements in the seasonal prediction of ENSO and how these advances have translated to skillful forecasts of oceanic conditions in the CCLME. We conclude by offering remarks on the implications for ecological forecasting and improved management of living marine resources in the CCLME.

Seasonal ENSO predictions

ENSO is the dominant mode of seasonal climate variability, and while it is a tropical Pacific phenomenon, its effects extend over the entire Pacific basin and even globally. ENSO and its teleconnections influence rainfall, temperature, and extreme events such as flooding, droughts, and tropical cyclones (Zebiak et al. 2015). Because of the extensive societal impacts associated with ENSO, its prediction has been central to the development of today's state-of-the-art seasonal climate prediction systems. The first attempts at ENSO prediction go back to the 1980s (Cane et al. 1986). Today, resulting from the development of an ENSO observing system located in the equatorial Pacific (McPhaden et al. 1998) and large improvements in our understanding of ENSO dynamics over the last two decades (Neelin et al. 1998; Latif et al. 1998; Chen and Cane 2008), prediction systems can, in general, skillfully predict ENSO up to about six months in advance (Tippett et al. 2012; Ludescher et al. 2014). While such skillful ENSO forecasts may also improve prediction of the extratropical ENSO response, intrinsic variability of the extratropical atmosphere and ocean, and the chaotic nature of weather, will limit extratropical prediction skill no matter how accurately the models—and observations initializing them—predict ENSO itself. ENSO operational forecasts from numerous climate modeling centers are made available in real-time from Columbia University's [International Research Institute for Climate and Society](#) and NOAA's [Climate Prediction Center](#).

Given its global impact, ENSO provides much of the climate forecasting skill on seasonal timescales (Goddard et al. 2001). While weather is only predictable over a timescale of days (up to about two weeks) owing to the chaotic nature of the atmosphere (Lorenz 1963), predictions of seasonal-scale anomalies are possible because of the ability of global dynamical prediction systems to model atmosphere-ocean coupling processes and other atmosphere forcing factors, such as land and sea ice, which vary more slowly than the atmosphere (Goddard 2001). Low-frequency variations in sea surface temperature

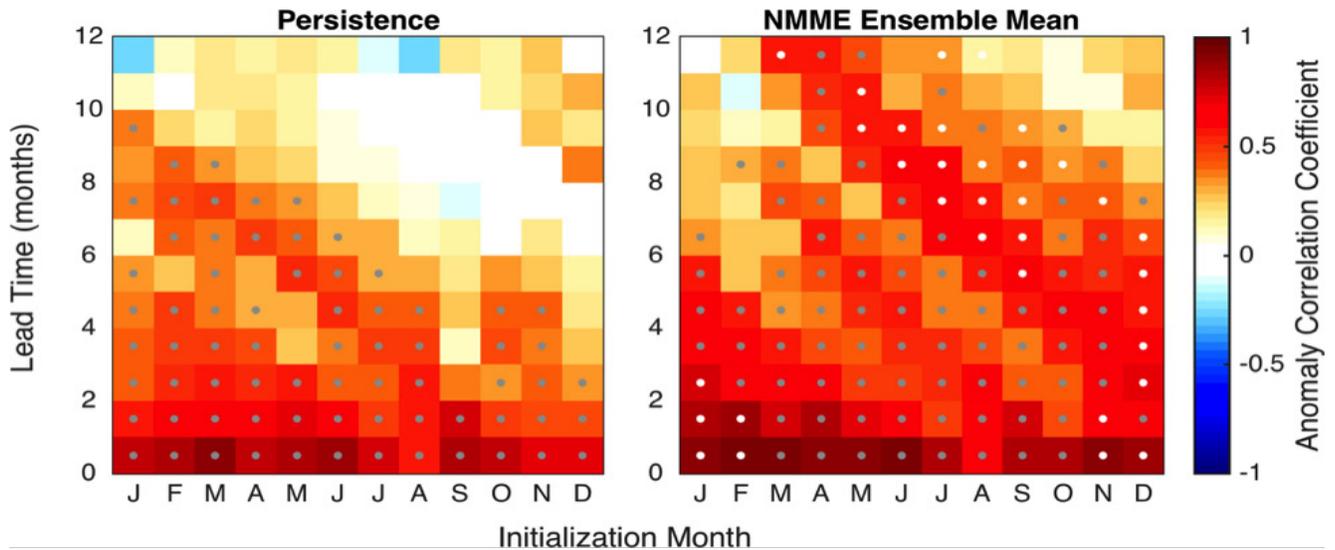


Figure 1. Anomaly correlation coefficients (ACCs) as a function of forecast initialization month (x-axis) and lead-time (y-axis) for (left) persistence and (right) NOAA NMME mean for the California Current system (US West Coast, less than 300 km from shore). Note the ridge of high SST anomaly prediction skill exceeding persistence at long lead-times (4-12 months) for late winter-early spring forecasts. Grey dots indicate ACCs significantly above zero at a 5% level; white dots indicate ACCs significantly above persistence at a 5% level. (Adapted from Jacox et al. 2017).

(SST), particularly in the tropics, can modulate the atmosphere (as is the case for ENSO), making some weather patterns more likely to occur over the next month or season. Therefore, the ability of the coupled global climate models to skillfully forecast the evolution of observed tropical SSTs, shifts the distribution of likely average weather over the next month or season may be, and allows for skillful prediction of seasonal climate anomalies.

While seasonal predictability is relatively high for SST due to the ocean’s large thermal inertia, assessments of SST predictability have largely been focused on ocean basin-scale modes of variability (e.g., ENSO), linked to regional rainfall and temperature patterns over land. However, recent work has demonstrated that seasonal SST predictions are also skillful in coastal ecosystems (Stock et al. 2015; Hervieux et al. 2017), and, as detailed in the next section, specifically for the CCLME (Jacox et al. 2017).

Seasonal climate predictions in the California Current Large Marine Ecosystem

Recent advances in ENSO prediction and global dynamical seasonal climate prediction systems have enabled skillful seasonal forecasts of SST anomalies in the CCLME after bias correcting the forecasts to remove model drift (Stock et al. 2015; Jacox et al. 2017; Hervieux et al. 2017). Skill of SST anomaly predictions produced by the National Oceanic and Atmospheric Administration (NOAA) North American Multi-Model Ensemble (NMME) is shown in Figure 1. Skill is evaluated through the anomaly correlation coefficient (ACC) between

monthly SST anomalies from retrospective forecasts from 1982 to 2009 and observed SST anomalies. Forecasts are skillful (ACC > 0.6) across initialization months for lead times up to about four months (Figure 1). Persistence of the initialized SST anomalies provides much of the prediction skill at these short lead times (Stock et al. 2015; Jacox et al. 2017). Preexisting temperature anomalies at depth may also provide some predictability. Skillful forecasts of February, March, and April SST extend to lead times greater than six months (Figure 1; Stock et al. 2015; Jacox et al. 2017). This ridge of enhanced predictive skill in winter to early spring forecasts is apparent across seasonal forecasting models and arises from the ability of the prediction systems to capture the wintertime coastal signature of predictable basin-scale SST variations (Stock et al. 2015; Jacox et al. 2017). Specifically, the models can skillfully forecast the predictable evolution of meridional winds during ENSO events and the associated changes in upwelling anomalies and SST in the CCLME (Jacox et al. 2017).

Owing to the severe ecological and economic consequences of extreme SST conditions in the CCLME (e.g., Cavole et al. 2016), it is also instructive to look at forecast performance over time, specifically during the CCLME extreme warm events of 1991-1992, 1997-1998, and 2014-2016, and the CCLME extreme cold events of 1988-1989, 1998-1999, and 2010-2011 (Figure 2). All of the cold events were associated with La Niña conditions, and the first two warm events and 2015-2016 were associated with El Niño. However, the anomalously warm conditions of 2014 and 2015, dubbed “the blob,” were caused by a

resilient ridge of high pressure over the North American West Coast that suppressed storm activity and mixing, and allowed a build-up of heat in the upper ocean (Bond et al. 2015).

The forecast system is highly skillful at one-month lead times. It is also skillful at longer lead times of three and six months, as seen by the forecasted February to April SSTs following the 2010-2011 La Niña and the 2015-2016 El Niño (Figure 2). However, at these longer lead times, the forecast system was unable to capture the extreme magnitude of the warm “blob” anomalies during 2014 and 2015 (Figure 2). Also, while fall to winter conditions during the 1991-1992 El Niño and the late winter-early spring conditions following the 1997-1998 El Niño were forecasted with a six-month lead time, the prolonged warm conditions over the 1992 summer and the early transition to anomalously warm conditions during the summer of 1997 were not (Figure 2).

Transitions in and out of the 1991 and 1997 El Niño events were particularly unusual also at the Equator, with El Niño conditions developing late in 1991 and persisting well into the summer of 1992, and El Niño conditions appearing early in summer 1997 (see Figure 2 in Jacox et al. 2015). The spring predictability barrier for ENSO (i.e., a dip in forecast skill for forecasts initialized over the ENSO transition period of March-May; Tippet et al. 2012), as well as weaker teleconnections to the extratropics in summer, may partly explain the lower forecast skill for these El Niño events during summer and fall, and the poorer forecast performance in predicting the early transition to La Niña conditions in 1998-1999 and 2010-2011 (Figure 2).

The forecast system was also unable to predict the cooler conditions over the ENSO-neutral spring and summer of 1991 (Figure 2). The conditional predictability of CCLME winds and SST on ENSO implies that during ENSO-neutral conditions, such as in 1991 and 2014, forecasts of winds are not skillful and SST forecast skill is therefore limited to lead times up to about four months (Jacox et al. 2017). Thus, skillfulness of the seasonal predictions

results from a complex interplay of factors that will require further study to identify the underlying mechanisms driving differing levels of robustness.

Seasonal forecasts for fisheries management applications

While seasonal prediction of living marine resources has been a goal for the past three decades (GLOBEC 1997), operational use of seasonal SST forecasts to inform dynamic management of living marine resources was pioneered in Australia (Hobday et al. 2011), where seasonal SST forecasts are now used to improve the decision making of the aquaculture industry (Spillman and Hobday 2014; Spillman et al. 2015), fishers (Eveson et al. 2015), and fisheries managers (Hobday et al. 2011). Through both increased awareness of climate prediction skill at fishery-relevant scales and of their value to ecosystem-based management, such efforts have now begun to expand to

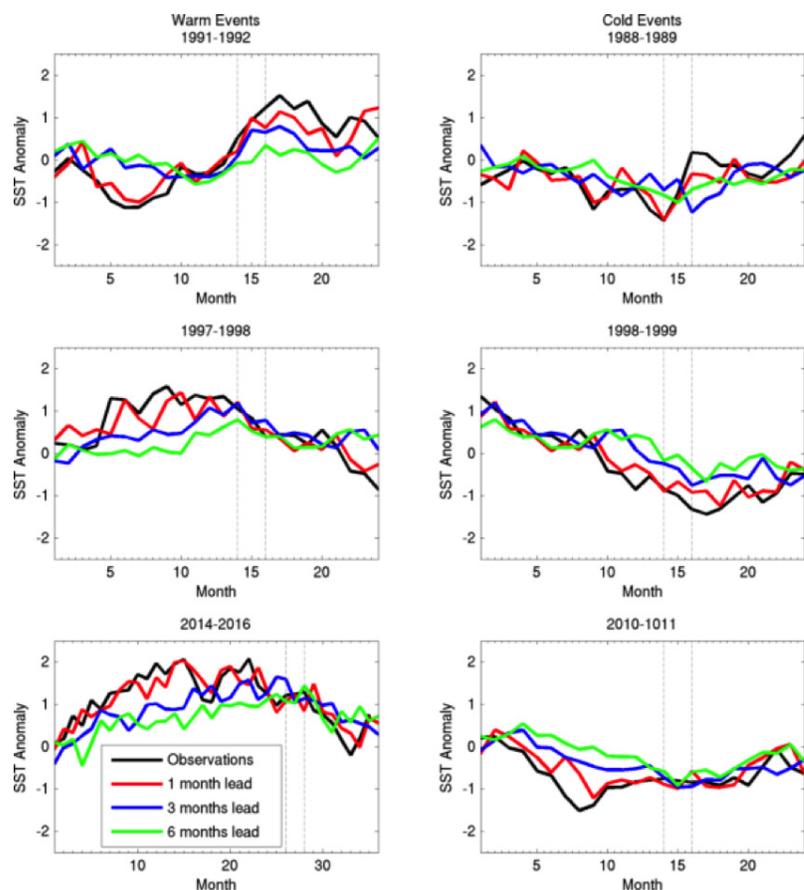


Figure 2. Predictions at 1-month (red line), 3-month (blue line), and 6-month (green line) lead times of SST anomalies (°C) for the CCLME from the NOAA Geophysical Fluid Dynamics Laboratory (GFDL) CM2.5 FLOR global climate prediction systems and Reynolds OISST.v2 observations (black line) for specific extreme events in the CCLME. Warm events are on the left; cold events are on the right. The dotted lines represent the February to April period of enhanced predictive skill following ENSO events. The x-axis is months since January 1 of the year in which the extreme event started.

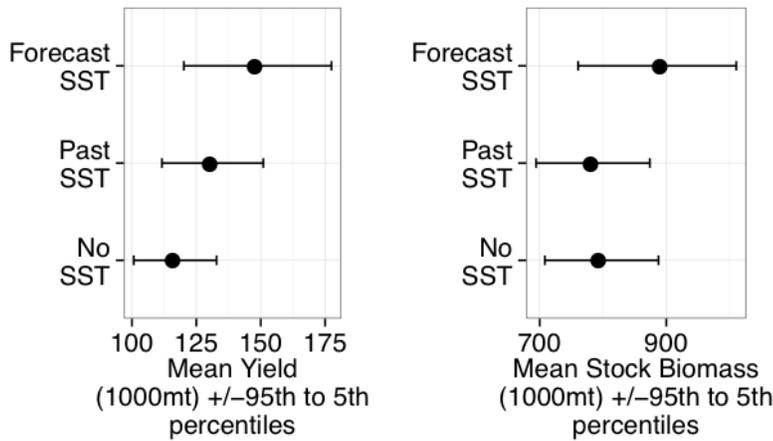


Figure 3. Mean long-term Pacific sardine catch and biomass following catch limit decisions integrating different levels of environmental information. The catch limit incorporating future SST information reflects the uncertainty of a 2-month lead forecast. (Adapted from Tommasi et al. 2017b).

other regions (see Tommasi et al. 2017a, and case studies therein). In the CCLME, recent work has demonstrated that integration of current March SST forecasts into fisheries models can provide useful information for catch limit decisions for the Pacific sardine fishery (i.e., how many sardines can be caught each year?) when combined with existing harvest cutoffs (Tommasi et al., 2017b). Knowledge of future SST conditions can improve predictions of future recruitment and stock biomass and allow for the development of a dynamic management framework, which could increase allowable fisheries harvests during periods of forecasted high productivity and reduce harvests during periods of low productivity (Tommasi et al. 2017b). Hence, integration of skillful seasonal forecasts into management decision strategies may contribute to greater long-term catches than those set by management decisions based solely on either past SST information or on no environmental information at all (Figure 3; Tommasi et al., 2017b).

Novel dynamical downscaling experiments in the Northern California Current as part of the JISAO Seasonal Coastal Ocean Prediction of the Ecosystem (J-SCOPE) project (Siedlecki et al. 2016) show that seasonal regional climate forecasts may also be of potential utility for dynamic spatial management strategies in the CCLME (Kaplan et al. 2016). Predictions of ocean conditions from a global dynamical climate prediction system (NOAA NCEP CFS) forced the Regional Ocean Modeling System (ROMS) with biogeochemistry to produce seasonal forecasts of ocean conditions, both at the surface

and at depth, with measureable skill up to a four-month lead time (Siedlecki et al. 2016). The downscaling both enables forecasts of fishery-relevant biogeochemical variables such as chlorophyll, oxygen, and pH not yet produced by global forecasting systems, and resolves the fine-scale physical and ecological processes influencing the distribution of managed species within the CCLME. For instance, high-resolution regional implementations of ROMS resolve upwelling and coastal wave dynamics (Jacox et al. 2015; Siedlecki et al. 2016), two processes that drive the CCLME response to ENSO variability, better than coarser-resolution global models. Downscaled forecasts have also driven prototype forecasts of Pacific sardine spatial distribution (Kaplan et al. 2016). Such forecasts have the potential to inform fishing operations, fisheries surveys, and US and Canadian quotas for this internationally shared stock (Kaplan et al. 2016; Siedlecki et al. 2016; Tommasi et al. 2017a).

These CCLME case studies suggest that with recent advancements in state-of-the-art global dynamical prediction systems and regional downscaling models, some skillful seasonal predictions of ocean conditions are possible (Siedlecki et al. 2016; Tommasi et al. 2017a).

Seasonal forecast skill may be further improved by improved representation of other features such as ocean eddies and gyre circulations in the extratropics and the basin-wide atmospheric response to SST anomalies in the Kuroshio-Oyashio region (Smirnov et al. 2015). Such skillful seasonal forecasts present opportunities for inclusion in adaptive management strategies for improved living marine resource management and better informed industry operations in the CCLME.

References

- Alexander, M. A., I. Bladé, 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. *J. Climate*, 15, 2205–2231, doi:10.1175/1520-0442(2002)015<2205:TABTIO>2.0.CO;2.
- Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua, 2015: Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys. Res. Lett.*, 42, 3414–3420, doi:10.1002/2015GL063306.
- Cane, M. A., S. E. Zebiak, and S. C. Dolan, 1986: Experimental forecasts of El Niño. *Nature* 321, 827–832, doi:10.1038/321827a0.
- Cavole, L. M., and Coauthors, 2016: Biological impacts of the

- 2013–2015 warm-water anomaly in the Northeast Pacific: Winners, losers, and the future. *Oceanogr.*, 29, 273–285, doi: 10.5670/oceanog.2016.32.
- Chavez, F. P., J. T. Pennington, C. G. Castro, J. P. Ryan, R. P. Michisaki, B. Schlining, P. Walz, K. R. Buck, A. McFadyen, and C. A. Collins, 2002: Biological and chemical consequences of the 1997–1998 El Niño in central California waters. *Prog. Oceanogr.*, 54, 205–232, doi: 10.1016/S0079-6611(02)00050-2.
- Chen, D., and M. A. Cane, 2008: El Niño prediction and predictability. *J. Comp. Phys.*, 227, 3625–3640, doi: 10.1016/j.jcp.2007.05.014.
- Di Lorenzo, E., and Coauthors, 2013: Synthesis of Pacific Ocean climate and ecosystem dynamics. *Oceanogr.* 26, 68–81, doi: 10.5670/oceanog.2013.76.
- Eveson, J. P., A. J. Hobday, J. R. Hartog, C. M. Spillman, and K. M. Rough, 2015: Seasonal forecasting of tuna habitat in the Great Australian Bight. *Fish. Res.*, 170, 39–49 doi: 10.1016/j.fishres.2015.05.008.
- Global Ocean Ecosystem Dynamics (GLOBEC), 1997: Global Ocean Ecosystem Dynamics Science Plan. R. Harris and the members of the GLOBEC Scientific Steering Committee, Eds., IGBP secretariat, Stockholm, Sweden, 83 pp.
- Goddard, L., S. J. Mason, S. E. Zebiak, C. F. Ropelewski, R. Basher, and M. A. Cane, 2001: Current approaches to seasonal-to-interannual climate predictions. *Int. J. Climatol.*, 21, 1111–1152, doi: 10.1002/joc.636.
- Hazen, E. L., and Coauthors, 2013: Predicted habitat shifts of Pacific top predators in a changing climate. *Nat. Climate Change*, 3, 234–238, doi:10.1038/nclimate1686.
- Hervieux, G., M. Alexander, C. Stock, M. Jacox, K. Pegion, and D. Tommasi, 2017: Seasonal sea surface temperature anomaly prediction skill for coastal ecosystems using the North American multi-model ensemble (NMME). *Climate Dyn.*, submitted.
- Hobday, A. J., J. R. Hartog, C. M. Spillman, and O. Alves, 2011: Seasonal forecasting of tuna habitat for dynamic spatial management. *Can. J. Fish. Aqu. Sci.*, 68, 898–911, doi: 10.1139/f2011-031.
- Hobday, A. J., C. M. Spillman, J. P. Eveson, and J. R. Hartog, 2016: Seasonal forecasting for decision support in marine fisheries and aquaculture. *Fish.*, *Oceanogr.*, 25, 45–56, doi: 10.1111/fog.12083.
- Jacox, M. G., J. Fiechter, A. M. Moore, and C. A. Edwards, 2015: ENSO and the California Current coastal upwelling response. *J. Geophys. Res. Oceans*, 120, 1691–1702, doi:10.1002/2014JC010650.
- Jacox, M., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd, 2016: Impacts of the 2015–2016 El Niño on the California Current System: Early assessment and comparison to past events. *Geophys. Res. Lett.* 43, 7072–7080, doi:10.1002/2016GL069716.
- Jacox, M. G., M. A. Alexander, C. A. Stock, and G. Hervieux, 2017: On the skill of seasonal sea surface temperature forecasts in the California Current System and its connection to ENSO variability. *Climate Dyn.*, in review.
- Kaplan, I. C., G. D. Williams, N. A. Bond, A. J. Hermann, and S. Siedlecki, 2016: Cloudy with a chance of sardines: forecasting sardine distributions using regional climate models. *Fish. Oceanogr.*, 25, 15–27, doi: 10.1111/fog.12131.
- Latif, M., A. Sterl, E. Maier-Reimer, and M. M. Junge, 1998: Climate variability in a coupled GCM. Part I: the tropical Pacific. *J. Climate*, 6, 5–21, doi: 10.1175/1520-0442(1993)006<0005:CVIACG>2.0.CO;2.
- Lindegren, M., D. M. Checkley Jr., T. Rouyer, A. D. MacCall, and N. C. Stenseth, 2013: Climate, fishing, and fluctuations of sardine and anchovy in the California Current. *Proc. Nat. Acad. Sci.*, 110, 13672–13677, doi: 10.1073/pnas.1305733110.
- Lorenz, E. N. 1963: Deterministic nonperiodic flow. *J. Atmos. Sci.*, 20, 130–141, doi: 10.1175/1520-0469(1963)020<0130:DNF>2.0.CO;2.
- Ludescher, J., A. Gozolchiani, M. Bogachev, A. Bunde, S. Havlin, and H. J. Schellnhuber, 2014: Very early warning of next El Niño. *Proc. Nat. Acad. Sci.*, 111, 2064–2066, doi: 10.1073/pnas.1323058111.
- McPhaden, M. J., and Coauthors, 1998: The TOGA observing system: a decade of progress. *J. Geophys. Res.*, 103, 14,169–14,240, doi: 10.1029/97JC02906.
- Neelin, J. D., D. S. Battisti, A. C. Hirst, F. F. Jin, Y. Wakata, T. Yamagata, and S. E. Zebiak, 1998: ENSO theory. *J. Geophys. Res.*, 103, 14261–14290, doi: 10.1029/97JC03424.
- NOAA, 2016: National Marine Fisheries Service Seafood Industry Impacts tool. <https://www.st.nmfs.noaa.gov/apex/?p=160:1>.
- Schwing, F. B., T. Murphree, L. DeWitt, and P. M. Green, 2002: The evolution of oceanic and atmospheric anomalies in the northeast Pacific during the El Niño and La Niña events of 1995–2001. *Prog. Oceanogr.*, 54, 459–491, doi:10.1016/S0079-6611(02)00064-2.
- Siedlecki, S. A., I. C. Kaplan, A. J. Hermann, T. T. Nguyen, N. A. Bond, J. A. Newton, G. D. Williams, W. T. Peterson, S. R. Alin, and R. A. Feely, 2016: Experiments with seasonal forecasts of ocean conditions for the northern region of the California Current upwelling system. *Sci. Rep.*, 6, 27203, doi: 10.1038/srep27203.
- Smirnov, D., M. Newman, M. A. Alexander, Y.-O. Kwon, and C. Frankignoul, 2015: Investigating the local atmospheric response to a realistic shift in the Oyashio sea surface temperature front. *J. Climate*, 28, 1126–1147, doi: 10.1175/JCLI-D-14-00285.1.
- Spillman, C. M., J. R. Hartog, A. J. Hobday, and D. Hudson, 2015: Predicting environmental drivers for prawn aquaculture production to aid improved farm management. *Aquaculture*, 447, 56–65, doi: 10.1016/j.aquaculture.2015.02.008.
- Spillman, C. M., and A. J. Hobday, 2014: Dynamical seasonal ocean forecasts to aid salmon farm management in a climate

- hotspot. *Climate Risk Management*, 1, 25-38, doi: 10.1016/j.crm.2013.12.001.
- Stock, C. A., K. Pegion, G. A. Vecchi, M. A. Alexander, D. Tommasi, N. A. Bond, P. S. Fratantoni, R. G. Gudgel, T. Kristiansen, T. D. O'Brien, Y. Xue, and X. Yang, 2015: Seasonal sea surface temperature anomaly prediction for coastal ecosystems. *Prog. Oceanogr.*, 137, 219-236, doi: 10.1016/j.pocean.2015.06.007.
- Tippett, M. K., A. G. Barnston, and S. Li, 2012: Performance of recent multi-model ENSO forecasts. *J. App. Meteorol. Climatol.*, 51, 637-654, doi: 10.1175/JAMC-D-11-093.1.
- Tommasi, D., and Coauthors, 2017a. Managing living marine resources in a dynamic environment: the role of seasonal to decadal climate forecasts. *Prog. Oceanogr.*, doi: 10.1016/j.pocean.2016.12.011.
- Tommasi, D., C. Stock, K. Pegion, G. A. Vecchi, R. D. Methot, M. Alexander, and D. Checkley, 2017b: Improved management of small pelagic fisheries through seasonal climate prediction. *Ecol. App.*, doi: 10.1002/eap.1458.
- Zebiak, S. E., B. Orlove, A. G. Muñoz, C. Vaughan, J. Hansen, T. Troy, M. C. Thomson, A. Lustig, and S. Garvin, 2015: Investigating El Niño-Southern Oscillation and society relationships. *WIREs Climate Change*, 6, 17-34, doi: 10.1002/wcc.294.