ENSO impacts on ecosystem indicators in the California Current System

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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 ecosystem 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.

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

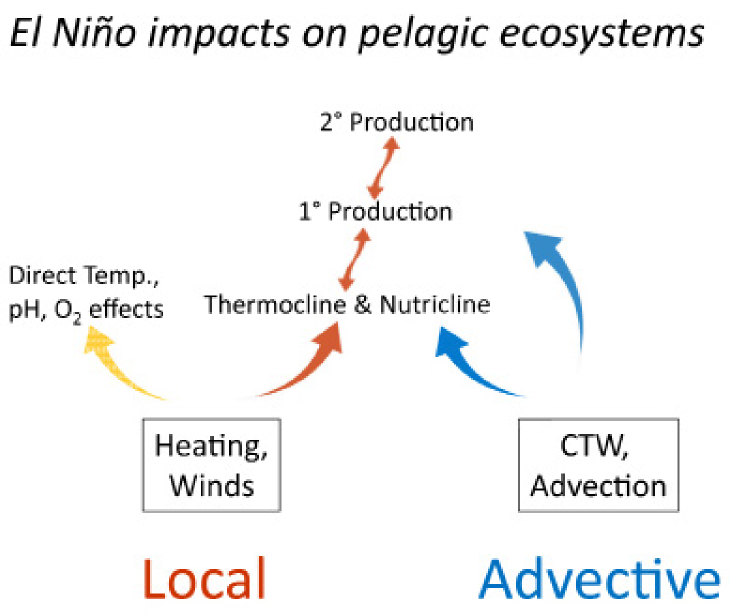

Figure 1. Schematic illustration of dominant mechanisms through which ENSO impacts biological and biogeochemical processes in the California Current System. Processes include both local effects (e.g., heat budget, winds) and advective effects. Such processes can influence organisms via: (1) (yellow arrow) direct physiological responses to changes in temperature, O_2, 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.

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 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 (Rykaczewski 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 CO_2-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 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 ^{15}N 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 oxygen, 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 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, unpublished), 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.

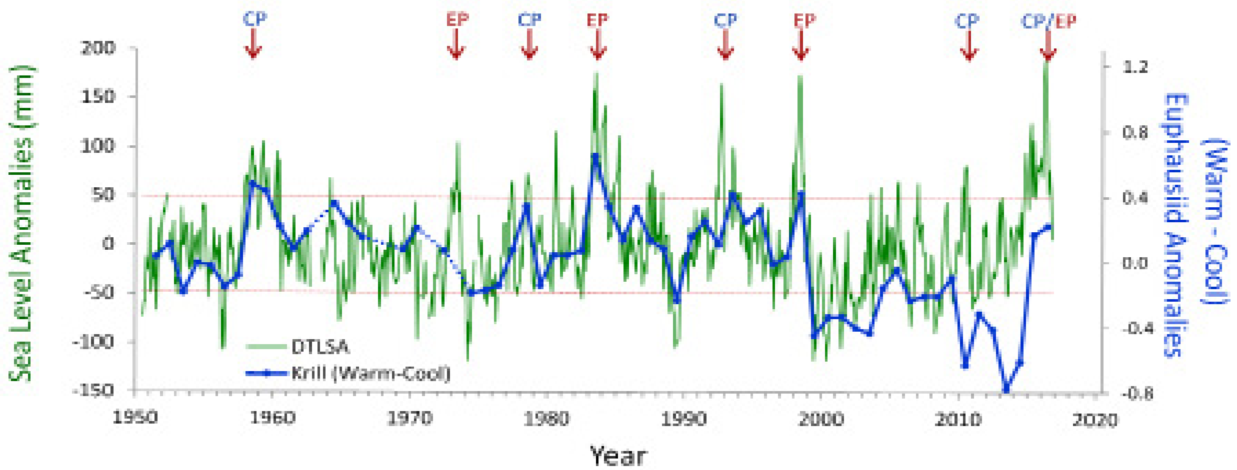

Figure 2. Covariability of California Current euphausiids (krill, blue lines) with an index of ENSO off California (de-trended sea level anomaly (DTSLA) at San Diego, green lines). Note the markedly different relationship between euphausiids and DTSLA after 2000. Sustained excursions of DTSLA exceeding one standard deviation (i.e., above upper dotted red line) are expressions of El Niño (or of the warm anomaly of 2014-15). Red arrows indicate specific events categorized as either eastern Pacific (EP) or central Pacific (CP) El Niño events (Yu et al. 2012), apart from 2015-16 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).

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.

Ecosystem indicator	Region & 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 & weaker winds
Pseudo-nitzschia diatoms; Domoic Acid	Entire CCS spring-summer	Blooms	1-3 month lag	Elevated temp; Altered nutrient stoichiometry
Copepod assemblage	NCCS spring-summer	Warm water species appear	Nearly instantaneous	Poleward advection; reduced upwelling, warmer temp
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 temp/deeper thermocline; reduces spawning habitat
Pacific sardine	Entire CCS winter-spring	Changes in distribution; compression of spawning habitat	Instantaneous for spawning & 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 & 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 temp, 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 temp, upwelling, mesoscale structure
Top predator distribution	Entire CCS	Altered geographic distributions	Instantaneous or time-lagged	Advection of prey, altered temp, upwelling, mesoscale structure

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 (see previous page) 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.

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ENSO diversity and its implications for US West Coast marine ecosystems

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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, alongshore 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 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

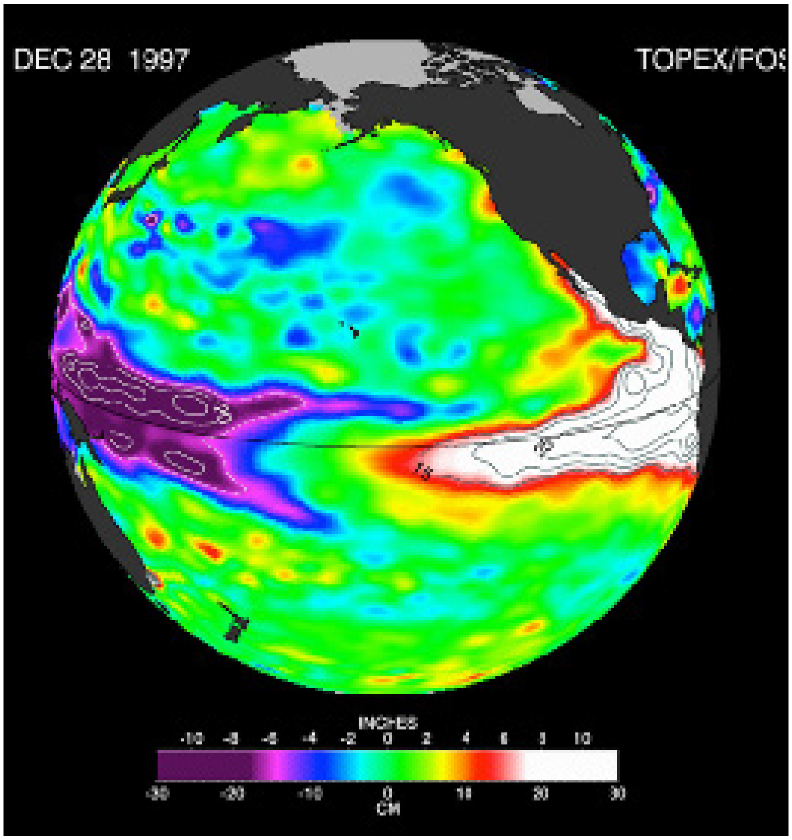

Figure 1. Canonical oceanic teleconnection pattern associated with coastally trapped Kelvin waves emanating from the tropical and subtropical eastern Pacific during the 1997-98 El Niño, as revealed by sea surface height altimeter observations (Credit: NASA/JPL-Caltech). These boundary-trapped waves have 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.

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 (Marchesiello 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 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.

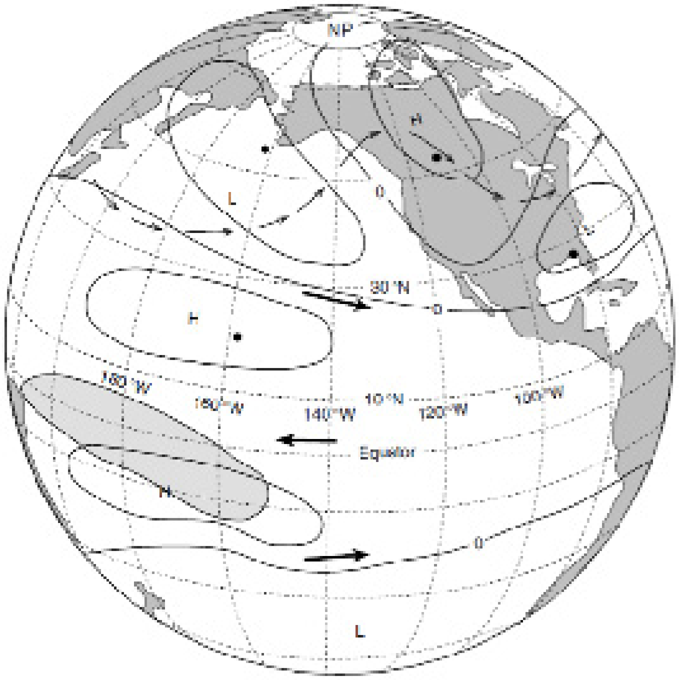

Figure 2. Canonical wintertime atmospheric teleconnection pattern associated with ENSO as a response to tropical heating, also known as the Pacific North American (PNA) pattern, as schematically illustrated by Horel and Wallace (1981). The contour lines represent middle troposphere geopotential height 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.

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 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

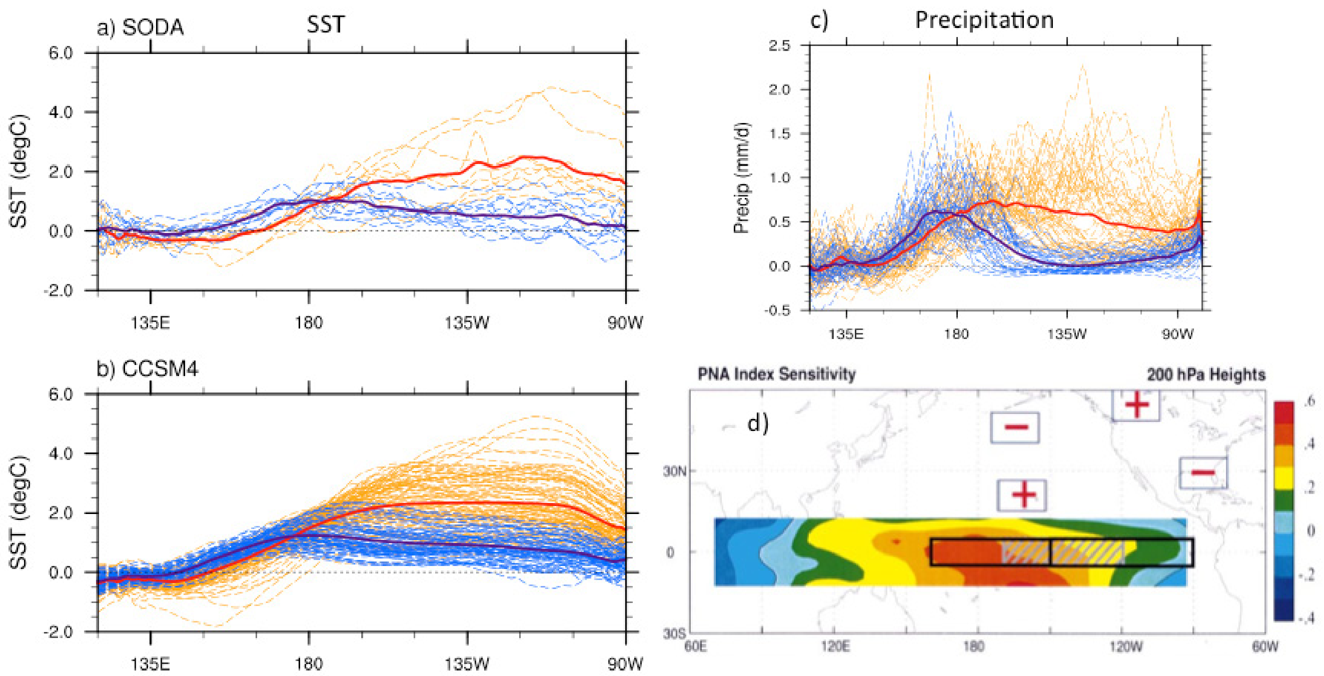

Figure 3. a) Equatorial SST anomaly profiles for El Niño events with largest SST anomalies in the Niño-3 region (EP events, thin dashed orange lines) and in the Niño-4 region (CP events, thin dashed blue lines) from the SODA ocean reanalysis over the period 1958-2007. The thick red and blue lines are 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).

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 region rather than the Niño-3 region where canonical "EP" events typically peak (Figure 3d). This implies that weaker CP El Niño events may exert a comparable influence on 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.

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