V

VARIABILITY, MULTIDECADAL

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Changes in climate, ocean circulation, and ocean ecosystems with periods of about 50 years have been recently recognized and referred to as Pacific multidecadal variability. These climate or regime shifts have particularly large impacts on small pelagic fish such as anchovies and sardines. These populations shift synchronously in Japan, California, and Peru, with sardines dominating for about 25 years and anchovies for the following 25 years. Impact on other ocean ecosystems, such as those on rocky shores, are unknown but likely.

NATURAL CLIMATE CHANGE

As farmers and fishermen have known for centuries, climate fluctuations are both important and normal. Climate varies on daily, weather-system, and seasonal time scales, and we are now learning about longer term fluctuations that occur within the bounds of natural variability. These cycles strongly affect humans, their economies, and the ecosystems on which they depend. But humans are also affecting climate by increasing atmospheric CO_2, and the biological consequences of the resulting global warming are not at present predictable and are potentially catastrophic. Understanding human-induced climate change will require characterization of natural climate variability and the use of natural cycles as models of climate change.

Prior to this growing awareness of natural climate variations, ecologists viewed the physical environment as a stable background against which biotic interactions drive population change and structure communities. Over the past two decades, strong El Niños, the ozone hole, and the looming specter of global warming forced the uncomfortable realization that the physical environment is changing, even on the relatively short time scales of ecological study, and that human activities may affect climate in unforeseen ways. Climate and the physical environment have thus reemerged as major themes in ecological science. In the oceans, it is clear that natural climate variability can have large impacts on ecosystem structure and biological productivity. The correlation between climate variability and the productivity and structure of ocean ecosystems has been well established. Climate-driven changes in ocean circulation, ocean mixing, dust deposition, or both, can regulate the overall productivity of an ocean ecosystem by changing the supply of a limiting nutrient. Changes in primary productivity then cascade through every trophic level. Climate can also influence animal populations directly through effects on recruitment, competitive advantages, or predation. Of particular interest are relationships between abiotic (bottom-up climate impacts on overall ecosystem productivity) and biotic (top-down climate impacts on competition and predation) effects.

CLIMATE IS NEVER AVERAGE

In general dictionaries, climate is defined as the average course or condition of the weather at a place, usually over a period of years as exhibited by temperature, wind velocity, and precipitation. However, the average itself changes, depending on the period used. For example, sea surface temperature (SST) for the coasts of Peru and California for the years 1993–1996 was warmer than during 1999–2003, and during the 1997–1998 El Niño, SST was extremely warm. These changes in temperature were accompanied by fluctuations in ocean productivity, with warmer years being less productive than cooler years. What causes climate to change from year to year and decade to decade? What are the consequences of this climate variability? Complete answers to these questions are still forthcoming, although significant progress has been made over the past several decades, particularly in understanding the consequences of climate variability. For example, the warm SST observed during 1997–1998 was a result of a strong El Niño that was well documented in the equatorial Pacific and along the west coast of the Americas. El Niño is a prime example of the insight gained on the consequences of climatic variability. Although El Niño had been recognized off Peru since the ancient civilizations of the Incas, it was the large 1957–1958 El Niño that brought international attention to the phenomenon. Following the 1982–1983 El Niño it became clear that the oceanic perturbations in the tropical Pacific had global effects on climate. Oceanic effects were originally thought to be restricted to the tropical and eastern Pacific, but careful studies in the center of the Pacific Ocean close to Hawaii uncovered El Niño effects there as well. The past several decades have seen growing awareness of La Niña, the counterpart or opposite condition of El Niño.

THE STORY OF EL VIEJO

Recently, focus has shifted to longer decade-scale changes that show remarkable basin-wide coherence and, again, strong impacts on oceans ecosystems. These multidecadal changes help explain the differences in SST observed before and after the 1997–1998 El Niño. The period prior to 1997–1998 was associated with a warm quarter century; the period after may be a cool one. This particular cycle, which is often referred to as the Pacific Decadal Oscillation (PDO), has a period of approximately 50 years (Fig. 1). Because of the similarity to El Niño and La Niña, the name El Viejo (the old man) for the warm eastern Pacific regime, and La Vieja (the old woman) for its counterpart, has been suggested. When the eastern Pacific is warmer than average, during El Viejo, El Niños may be more frequent and of greater intensity. Similarly, during La Vieja, La Niñas may be frequent or stronger. Longer time series, both historical and present, will enlighten us further on El Niño frequency and intensity and the potential effects of anthropogenic perturbations.

In a simplified conceptual view of the Pacific, the trade winds set up a basinwide slope in sea level, thermal structure, and—importantly for biology—nutrient structure. The shallow thermocline in the eastern tropical Pacific leads to enhanced nutrient supply and productivity. The El Viejo/La Vieja fluctuations have basinwide effects on SST and thermocline slope that are similar to El Niño and La Niña but on longer time scales. During the cool eastern boundary La Vieja regime, the basin-scale sea level slope is accentuated (sea level is lower in the eastern Pacific, higher in the western Pacific). Lower sea level is associated with a shallower thermocline and increased nutrient supply and productivity in the eastern Pacific; the inverse occurs in the western Pacific. In addition to thermocline and sea surface temperature, there are regime shift changes in the transport of boundary currents, equatorial currents, and of the major atmospheric pressure systems. Changes in the abundance of anchovies and sardines are only one of many biological perturbations associated with regime shifts, and these are reflected around the entire Pacific.

The northeast Pacific may be the most studied area in terms of regime shifts. During El Viejo from the late 1970s to the early 1990s, zooplankton and salmon declined off Oregon and Washington but increased off Alaska. The flip-flop between ecosystems in the Gulf of Alaska and the California Current is one of the conundrums

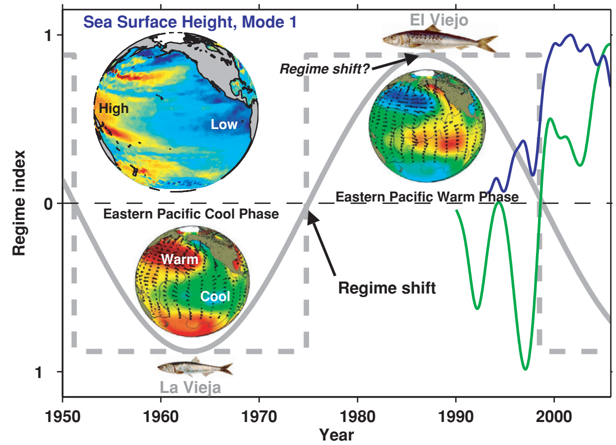

FIGURE 1 Hypothetical oscillation of a regime index with a period of 50 years. From the early 1950s to about 1975, the Pacific was cooler than average and anchovies dominated. The cool phase is referred to as La Vieja. From about 1975 to the late 1990s, the Pacific was warmer and the sardines dominated. The warm phase is referred to as El Viejo. The large-scale spatial pattern of sea surface temperature (SST) and atmospheric circulation anomalies are shown for each regime. The spatial pattern shows that warming or cooling is not uniform and the eastern Pacific is out of phase with the central North and South Pacific. Some indices suggest that the shifts are rapid (dashed) whereas others suggest a more gradual shift (solid). Regime shifts are commonly associated with a change in index sign, but populations may also exhibit changes in abundance when the index stops increasing or decreasing. The first empirical orthogonal function (EOF) of global TOPEX sea surface height (SSH) is shown above the cool, La Vieja regime. Low SSH implies a shallow thermocline/nutricline when the coefficient (blue line) is positive. The coefficient is shown in blue together with surface chlorophyll anomalies (mg m^{-3}) for the eastern margin of the California Current system from 1989 to 2005. Note the high chlorophyll after 1997–1998, consistent with the shallow thermocline of the eastern Pacific. Modified from Chavez *et al.* (2003). <AUQ1>

associated with these longer-term cycles. During El Niño the California Current and the Gulf of Alaska seem to be in phase in that productivity decreases in both locations. The El Niño changes are associated with thermocline depth, which decreases in both cases lowering nutrient supply and primary production. Spring mixed-layer depths, on the other hand, decrease in the Gulf of Alaska while they increase in the California Current during the positive or El Viejo phase of the PDO. It is surmised that mixed-layer decreases may favor primary production in the North Pacific by reducing light limitation. In the California Current the deeper mixed layers are associated with a deeper thermocline and lower primary production. A possible explanation for the different responses of the California Current and the Gulf of Alaska to El Niño and El Viejo might be that (1) during strong El Niños thermocline displacements dominate in both systems, reducing productivity at both locations, and (2) weaker thermocline anomalies during El Viejo reduce productivity in the California Current, but these effects are counteracted in the Gulf of Alaska by changes in mixed-layer depth resulting in increases in productivity at this location. This suggests fundamental differences between low-latitude stratified oceans, where thermocline displacements and upwelling regulate, and high-latitude environments, where mixing is the dominant process.

Seabird populations decrease off California and Peru during El Viejo. The California Current weakens and moves shoreward during the warm phases, and the subarctic gyre intensifies. Warmer temperature and lower salinity near the California coast support the weakening of the California Current. A stronger and broader California Current, brought about during the cool La Vieja regime, is associated with a shallower coastal thermocline from California to British Columbia, leading to enhanced primary production. It should be noted that the multidecadal changes in the circulation of the California Current system are not fully resolved and some argue that regime-shift changes in the position rather than the intensity of the currents are the primary mechanism for some of the observed patterns. What is very clear is that the boundaries of warm-water species move poleward during the warm regimes, and the boundaries of cold-water species move equatorward during cool regimes. In the southeastern Pacific biological variability is similar to that observed in the northeast Pacific albeit much less well documented.

In the northwest Pacific off Japan, the depth of the thermocline, nutricline, sea surface temperatures, and the winter mixed layer have shown changes on multidecadal time scales. During the El Viejo regime, sea surface temperatures cooled, sea level dropped, the thermocline and nutricline shoaled, and mixed layers deepened. Transport by the Kuroshio Current weakened. Primary production increased and sardine populations expanded from coastal waters eastward across the North Pacific to beyond the International Date Line. It remains unclear why sardines increase off Japan when local waters cool and become more productive, whereas they increase off California and Peru when those regions warm and become less productive.

In the warm pools of the western and northeastern tropical Pacific, physical variability has been harder to elucidate, partly because temperatures are warm and homogenous there. However, there is evidence of lower recruitment of yellow fin tuna during the cool La Vieja regime. The northeastern tropical Pacific is surrounded by regions with strong multidecadal fluctuations (California Current, Peru Current, equatorial Pacific, subtropical gyre). Tuna in the warm waters of the western Pacific seem to be similarly affected. Populations of yellow fin tuna in the western Pacific may have increased during the cool regimes. Highly mobile organisms such as the blue fin tuna migrate on basin scales, spending significant periods in areas altered by these large-scale climate and ocean changes. These organisms must respond in complex ways to regime shifts.

Episode-to-episode differences for El Viejo and La Vieja are just beginning to emerge. This should come as no surprise. After several iterations of El Niño it became clear that no two El Niños were alike. In 1982 the development of a canonical El Niño in the tropical Pacific was described for data from the 1950s to the 1970s. Following this description (and the 1976 regime shift) no El Niño resembled the development of the canonical El Niño. It will be interesting if after the regime shift in the mid- to late 1990s, El Niño development once again follows the canonical El Niño; the first one, the moderate 2002–2003 event, has apparently not.

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FURTHER READING

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VERTEBRATES, TERRESTRIAL

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A surprisingly diverse community of terrestrial vertebrates, which includes baboons, porcupines, rats and even bears, forage on wave-swept rocky shores, consuming marine invertebrates and fish on all continents except Antarctica.

DIVERSITY OF TERRESTRIAL VERTEBRATES ON ROCKY SHORES

The phenomenon of terrestrial vertebrates as consumers and agents of energy transfer on wave-swept rocky shores is underreported and poorly understood. This lack of understanding is primarily due to the fact that the subject matter falls in the gap between marine and terrestrial science, resulting in the majority of information being presented in anecdotal form. To date, in excess of 35 species of mammal, reptile, and amphibian have been recorded using wave–swept rocky shores as feeding grounds, and as scientific scrutiny of this phenomenon increases, this number is likely to increase.

Primates

In South Africa, Chacma baboons (*Papio ursinus*) consume limpets, mussels, crabs, and shark egg cases, whereas on Koshima Island off Japan, macaques (*Macaca fuscata*) prize barnacles and limpets from rocks and enter shallow water to capture small octopuses.

Rodentia and Lagomorpha

Porcupines (*Hystrix africaeaustralis*) along Namibia's coast and European rabbits (*Oryctolagus cuniculus*) on South African sea-bird islands graze on seaweeds. In Chile Norway rats (*Rattus norvegicus*) consume more than 40 species of intertidal organisms, with keyhole limpets being the most frequently consumed marine prey.

Carnivora

In North America, raccoons (*Procyon lotor*) feed on crabs, sea urchins, gastropods and small fishes. Arctic foxes (*Alopex lagopus*) from Iceland, Greenland, and Alaska also consume a wide variety of intertidal species ranging from polychaetes and mussels to starfish and kelp. Coyotes (*Canis latrans*, Fig. 1) in Baja California, Mexico, feed on

FIGURE 1 The coyote *(Canis latrans)* is ordinarily regarded as a creature of the desert rather than the seacoast but feeds on rocky-shore invertebrates in Baja California. Photograph by. <AUQ2>