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From Anchovies to Sardines and Back: Multidecadal Change in the Pacific Ocean

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In the Pacific Ocean, air and ocean temperatures, atmospheric carbon dioxide, landings of anchovies and sardines, and the productivity of coastal and open ocean ecosystems have varied over periods of about 50 years. In the mid-1970s, the Pacific changed from a cool "anchovy regime" to a warm "sardine regime." A shift back to an anchovy regime occurred in the middle to late 1990s. These large-scale, naturally occurring variations must be taken into account when considering human-induced climate change and the management of ocean living resources.

Landings of sardines show synchronous variations off Japan, California, Peru, and Chile (1). Populations flourished for 20 to 30 years and then practically disappeared for similar periods. Periods of low sardine abundance have been marked by dramatic increases in anchovy populations (2–5). Several important conclusions can be drawn from this. First, the mechanism responsible for the variability must have been similar in all cases and, some argue, relatively simple and direct (6). Second, the variability is difficult to explain on the basis of fishing pressure. Third, the variability must be linked to large-scale atmospheric or oceanic forcing.

The discovery of these so-called biological regime shifts preceded the description of the underlying physical variability. A decade or more after the observations of sardine variations (1), scientists discovered fluctuations in air temperatures, atmospheric circulation and carbon dioxide (7–9), and ocean temperatures (10) that were remarkably similar in phase and duration to the biological records (Fig. 1). As a result, it has been suggested (11) that a regime or climate shift may even be best determined by monitoring marine organisms rather than climate. Recent theoretical work supports the idea that complex food webs can undergo substantial changes in response to subtle physical forcing (12). Here, we review physical and biological fluctuations with periods of about 50 years that are particularly prominent in the Pacific Ocean. We also highlight the evidence for a change in the middle to late 1990s.

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Climate Indices and Regime Shifts

The sardine and anchovy fluctuations are associated with large-scale changes in ocean temperatures (Fig. 2); for 25 years, the Pacific is warmer than average (the warm, sardine regime) and then switches to cooler than average for the next 25 years (the cool, anchovy regime). Instrumental data provide evidence for two full cycles: cool phases from about 1900 to 1925 and 1950 to 1975 and warm phases from about 1925 to 1950 and 1975 to the mid-1990s (Fig. 1). A wide range of physical and biological time series in the Pacific Ocean basin show systematic variations on this same time scale. Anomalies, representing deviations from the mean value, were negative from about 1950 to 1975 and positive from about 1975 to the middle to late 1990s (Fig. 1). Because each index or parameter is influenced by forcings that act on multiple time scales, differences are expected in the timing of index sign changes and in the duration of the negative and positive phases. The mid-1970s change has been widely recognized in a myriad of North Pacific climatic (13) and biological (11, 14) time series and has been referred to as the 1976–1977 regime shift (15, 16), even though its precise timing is difficult to assess. Some indices suggest that the shift occurred rapidly whereas others suggest a more gradual change, though all indicate a shift in the 1970s.

The "sardine regime" of the 1930s and 1940s (Fig. 1E) (5) was most notable for the sardine fishery off California and its collapse, the subject of a memorable novel by Steinbeck (17). From the 1950s through the early 1970s, an "anchovy regime" led to the establishment of the largest single-species fishery in the world, the Peruvian anchoveta fishery (18). To extend the southeastern Pacific anchoveta time series, we constructed an ecosystem index (Fig. 1F) from seabird abun-

dance data (19) and anchovy and sardine landings off Peru (Fig. 1G). The seabird record, compiled from guano harvest and direct bird counts, extends back to the early 1900s. The seabirds are represented primarily by a single species, the cormorant (*Phalacrocorax bougainvillii*), which feeds almost exclusively on anchoveta (the anchovy, *Engraulis ringens*). The ecosystem index suggests a regime shift in the mid-1990s (Fig. 1F); the sardine catch decreased from 4 million metric tons in the late 1980s to 40,000 metric tons in 2001. At the same time, anchovy populations recovered (Fig. 1G).

The Big Picture

In a simplified conceptual view of the Pacific, the trade winds set up a basin-wide slope in sea level, thermal structure, and, importantly for biology, nutrient structure (Fig. 2). The shallow thermocline in the eastern Pacific leads to enhanced nutrient supply and productivity (20). Higher sea level in the western Pacific leads to a deep thermocline and nutrient structure and to lower productivity. These basin-scale east-west gradients are disrupted by large-scale climatic phenomena like El Niño and its counterpart, La Niña (20), which affect not only eastern boundary systems but also the western boundaries, subtropical gyres, and equatorial upwelling systems, leading to the concept of a "basin-wide ecosystem" (21).

The multidecadal fluctuations have basin-wide effects on sea surface temperature (SST) and thermocline slope that are similar to El Niño and La Niña but on longer time scales; El Niño occurs more frequently, once every 3 to 7 years. During the cool eastern boundary anchovy regime, the basin-scale sea level slope is accentuated (lower in the eastern Pacific, higher in the western Pacific). A 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 SST, 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 a few of many biological perturbations associated with regime shifts (Fig. 3), and these are reflected around the entire Pacific.

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Northeast Pacific. The northeast Pacific may be the most studied area in terms of regime shifts (10, 11, 13, 14). Only a few of the most notable changes are highlighted here. An important change for this region is an intensification (sardine) or relaxation (anchovy) of the Aleutian Low (15). During the sardine regime from the late 1970s to the early 1990s, zooplankton and salmon declined off Oregon and Washington but increased off Alaska (11, 14). Seabird popula-

tions decreased off California (22) and Peru. The California Current weakened and moved shoreward at this time, as evidenced by warmer temperature and lower salinity near the coast (23). A stronger and broader California Current, brought about during the anchovy regime, is associated with a shallower coastal thermocline from California to British Columbia, leading to enhanced primary production (Fig. 2). Off Peru, biological variability is similar to that observed off California.

Equatorial Pacific. El Niño dominates the conditions in the upper ocean of the equatorial Pacific. During El Niño, the surface waters of the central and eastern equatorial Pacific warm, and upwelling and primary productivity decrease (24). However, recent evidence suggests that the equatorial Pacific is also subject to multidecadal fluctuations in upwelling and water mass transport (25) that are superimposed on the higher frequency El Niño pattern. The meridional overturning circulation associated with equatorial upwelling has slowed by about 25% since the 1970s (Table 1).

The equatorial Pacific is a strong natural source of carbon dioxide (CO₂) to the atmosphere because of upwelling of high-CO₂ waters from depth (26). A reduction in upwelling during the sardine regime would decrease the flux of CO₂ to the atmosphere from this region (25, 27). Data collected in the equatorial Pacific since 1981 show a strong correlation between surface nitrate content, supplied by upwelling, and chlorophyll ($r = 0.86, P < 0.001$); both of these properties decreased between the 1980s and 1990s in concert with the meridional overturning and upwelling (Table 1). The circulation patterns (Fig. 3) are consistent with a mechanism recently proposed to explain multidecadal fluctuations in ocean temperatures (28). Further similarities to El Niño are the strong ocean-atmosphere interactions; multidecadal changes in circulation are intimately tied to changes in the wind field (25).

North Pacific subtropical gyre. The depths of the thermocline and mixed layer in the North Pacific subtropical gyre change on a multidecadal scale. The thermocline is shallower and the mixed layer deeper during the sardine regime, resulting in increases in primary production. Karl and co-workers (29) suggested that phytoplankton biomass and primary productivity in the north Pacific subtropical gyre were lower before the mid-1970s than during the 1980s and 1990s. They also suggested that

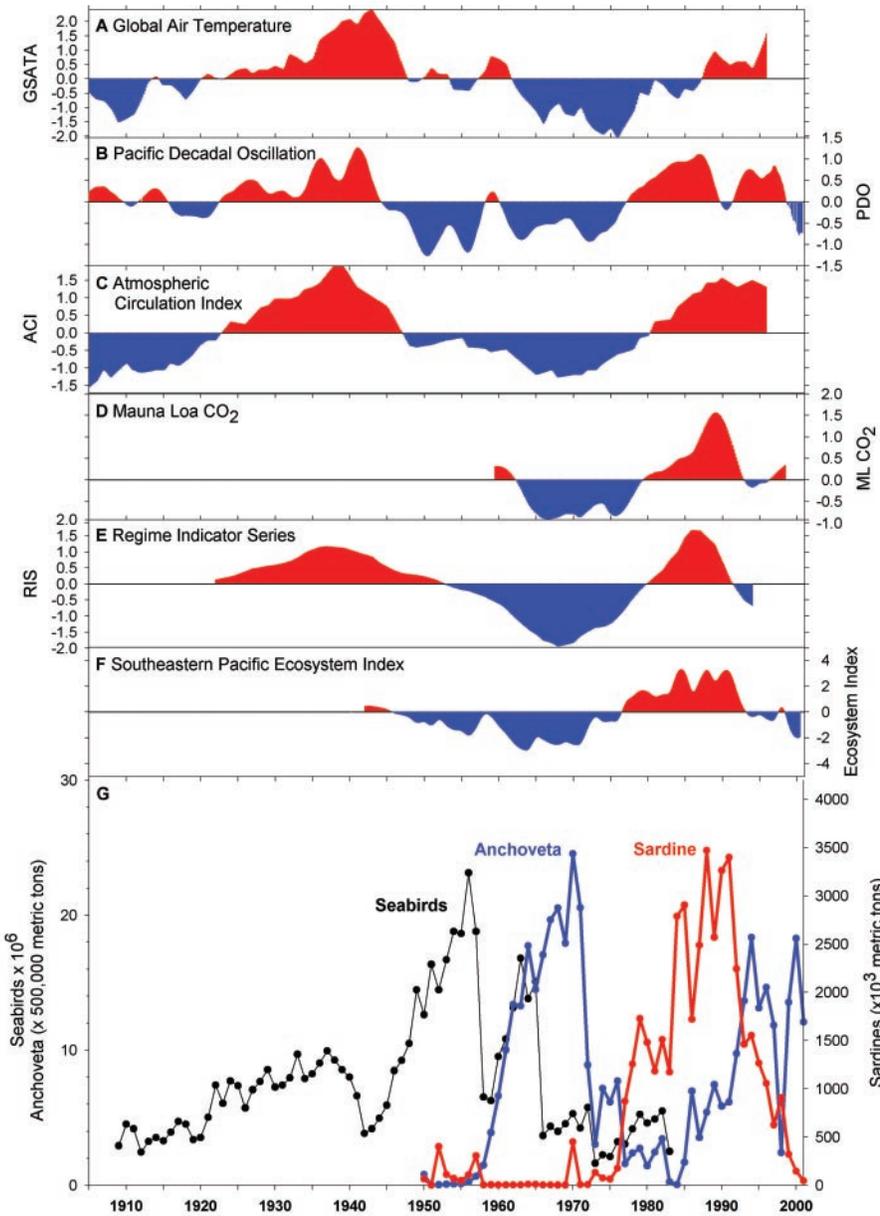


Fig. 1. Anomalies of (A) global air temperature, with the long-term increase removed (8); (B) the Pacific decadal oscillation (PDO) index (°C), derived from principal component analysis of North Pacific SST (10); (C) the atmospheric circulation index (ACI), which describes the relative dominance of zonal or meridional atmospheric transport in the Atlantic-Eurasian region (9); (D) atmospheric CO₂ measured at Mauna Loa (parts per million) with the long-term anthropogenic increase removed (7); (E) the regime indicator series (RIS) that integrates global sardine and anchovy fluctuations (5); and (F) a southeastern tropical Pacific ecosystem index based (19) on (G) seabird abundance and anchovy and sardine landings from Peru. All series have been smoothed with a 3-year running mean.

Table 1. Comparison of upwelling (sverdrup) (25), transport convergence (sverdrup) (25), surface nitrate (μM), and chlorophyll (from 5°N to 5°S and from 95°W to 140°W) (μg L⁻¹) for the equatorial Pacific. The means and standard errors are shown for two 10-year periods.

	1980–1989	1990–1999	Ratio
Equatorial upwelling	42.1 ± 4.2	35.4 ± 4.8	0.84
Transport convergence	20.5 ± 1.6	14.0 ± 1.5	0.68
Surface nitrate	5.41 ± 0.10	3.76 ± 0.34	0.70
Surface chlorophyll	0.22 ± 0.003	0.16 ± 0.005	0.73

community structure shifted and that the cyanobacteria *Prochlorococcus* increased in particular. The concentration of dissolved phosphorus in the surface ocean also declined gradually in the late 1980s and early 1990s, possibly as a result of utilization by nitrogen-fixing organisms. Because denitrification along the eastern boundary increases phosphorus relative to nitrate, phosphorus supply to the subtropical gyre may increase during the cool, anchovy regime as a result of spillover from more vigorous eastern Pacific upwelling (30). The transition-zone chlorophyll front (TZCF) marks the boundary between the subtropical gyre, where productivity is low, and the high-latitude ecosystems, where increased productivity is driven by deep winter mixing (31). Variations in the position of the TZCF can have important ecological

consequences because many fish and marine mammals forage along the front. The position of the TZCF changes during El Niño and may also vary on multidecadal time scales (31).

Northwest Pacific. In the northwest Pacific off Japan, the depths of the thermocline, the nutricline, and the winter mixed layer have followed changes similar to those in the subtropical gyre (15). During the sardine regime, sea level dropped, the thermocline and nutricline shoaled, mixed layers deepened (Figs. 2 and 3), and the Kuroshio Current weakened (32). Primary production increased, and sardine populations expanded from coastal waters eastward across the North Pacific to beyond the International Date Line (33). 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 (34).

Warm pools of the tropical Pacific. In the open ocean waters of the northeastern tropical Pacific, physical variability is harder to elucidate, partly because temperatures are warm and homogeneous there. However, there is evidence of lower recruitment of yellow-fin tuna during the anchovy regime (35). The area is surrounded by regions with strong multidecadal fluctuations (California Current, Peru Current, equatorial Pacific, and subtropical gyre). Tuna in the warm waters of the western Pacific must be similarly affected. Populations of yellow-fin tuna in the western Pacific may have increased during the cool regimes (36). Highly mobile organisms like the bluefin tuna migrate on basin scales, spending periods in areas altered by these large-scale climate and ocean changes. These organisms must respond in complex ways to regime shifts.

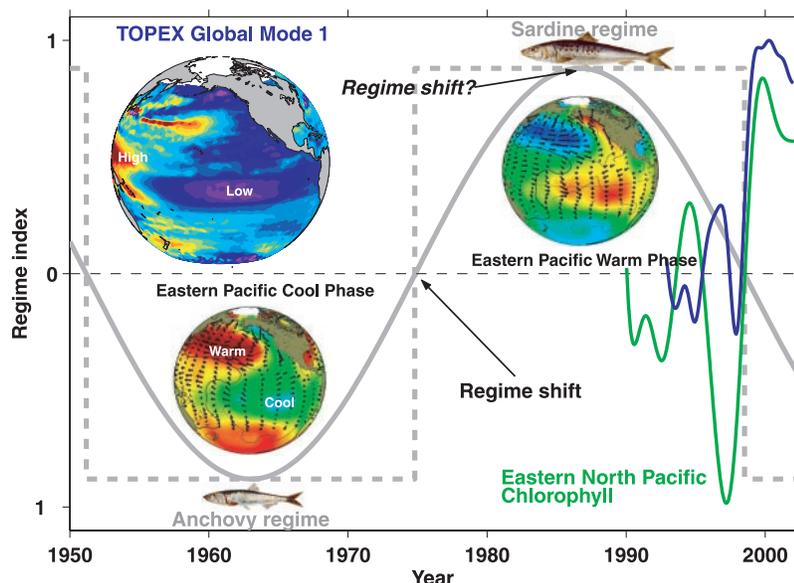


Fig. 2. Hypothetical oscillation of a regime index with a period of 50 years. From the early 1950s to about 1975, the Pacific was cooler than average, and anchovies dominated. From about 1975 to the late 1990s, the Pacific was warmer, and sardines dominated. The spatial patterns of SST and atmospheric circulation anomalies are shown for each regime (10). The spatial pattern shows that warming and cooling are not uniform and that 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, anchovy regime. It accounts for 31% of the variance in 18-month low-pass filtered SSH from 1993 through 2001. Low SSH implies a shallow thermocline and 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 2001 (45), also low-pass filtered. The high chlorophyll after 1997–98 is consistent with the shallow thermocline of the eastern Pacific. Changes in the circulation of the subtropical gyre and its boundary currents are also indicated by the first EOF. This basin-scale anticyclonic (clockwise spinning in the northern hemisphere) gyre maintains a positive gradient in SSH from its center to its periphery. The changes described by the first EOF after 1997–98 can be interpreted as (i) stronger positive gradients in SSH between the gyre center and its eastern and southern boundaries that would be associated with stronger anticyclonic flow (stronger southward flow along the eastern gyre boundary and stronger westward flow along the southern gyre boundary) and (ii) weaker positive gradients in SSH between the gyre center and its western and northern boundaries that would be associated with weaker anticyclonic flow (weaker northward flow along the western gyre boundary and weaker eastward flow along the northern gyre boundary). Thus, after the recent shift evident after 1997–98, a stronger California Current and a weaker Kuroshio Current are indicated.

Atmospheric CO₂

In the previous sections, we focused primarily on ecological consequences of multidecadal variability, but there must be carbon cycle effects associated with the fluctuations in nutrients, primary production, and ecosystem structure as well. Atmospheric CO₂ measurements have been made at Mauna Loa since 1958. This record also shows evidence for multidecadal fluctuations, with CO₂ accumulating more slowly in the atmosphere during the anchovy than during the sardine regime (Fig. 1). This is at odds with the expectation of a stronger CO₂ flux to the atmosphere due to enhanced equatorial upwelling (25, 27) during the cool, anchovy regime. Perhaps the slower growth in atmospheric CO₂ is associated with an enhanced coastal and equatorial biological pump of carbon into the ocean interior. If a stronger biological pump is implicated, then there must be an imbalance between carbon and other nutrients supplied by upwelling and those exported by the biological pump. A small deviation from the Redfield ratio (106 C:16 N:1 P) could account for the variability shown in Fig. 1 (37). Terrestrial biota may also be implicated in long-term fluctuations of atmospheric CO₂. A North American carbon sink, presumably resulting from changes in land use, has recently been suggested (38). The terrestrial uptake is of similar magnitude to the fluctuations shown in Fig. 1. Determining what drives multidecadal fluctuations in atmospheric CO₂ will necessarily require an interdisciplinary approach.

A Recent Regime Shift?

Satellites have recorded an increase in the basin-wide sea-level slope after the 1997–98 El Niño that was coincident with a dramatic

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increase in ocean chlorophyll off California (Fig. 2). These results are consistent with a return to a cool, anchovy regime (11, 39). The changes occurred about 25 years after the regime shift in the mid-1970s. Along with the physical and primary productivity changes, dramatic increases in baitfish (including northern anchovy) and salmon abundance off Oregon and Washington have been reported since 1999 (40, 41). Concurrently there have been increases in zooplankton abundance and changes in community structure from California to Oregon and British Columbia (42, 43), with dramatic increases in northern or cooler species. Recent changes off Peru are similar, with species that are normally restricted to the cooler Chilean coasts now commonly found off Peru (44).

The changes in fish abundance off Peru (Fig. 1G) are perhaps the most convincing evidence for a long-term, late-1990s regime shift. Sardine abundance off Japan and California displays similar changes (9). As during the mid-1970s shift, it appears as though the coast of Peru leads changes in the North Pacific. Does the southeastern Pacific really lead, or did the 1997–98 El Niño obscure changes in the northeastern Pacific? Reports off Oregon (45) and California (46) seemed to indicate that the warm anomalies in SST during 1997–98 were just as strong as during the 1982–83 El Niño but that the biological responses were not, as though the biological effects of El Niño were dampened by the onset of an anchovy regime. A change in the composition and abundance of organisms in

the eastern North Pacific in 1989 has also been reported (11, 14). It is uncertain whether the 1989 shift is related to the 1925, 1950, 1976, and late-1990s shifts, but, curiously, 1989 is the approximate midpoint of a regime that began in 1976 and ended in the late 1990s (Fig. 2).

The Future

The longest instrumental series (rather than reconstructions based on proxies) cover the past ~140 years (6); many are shorter than a century. These series are often used in climate change projections (47). They are, however, strongly influenced by multidecadal variability of the sort described here, creating an interpretive problem that is amplified for biological time series (which rarely span more than a few

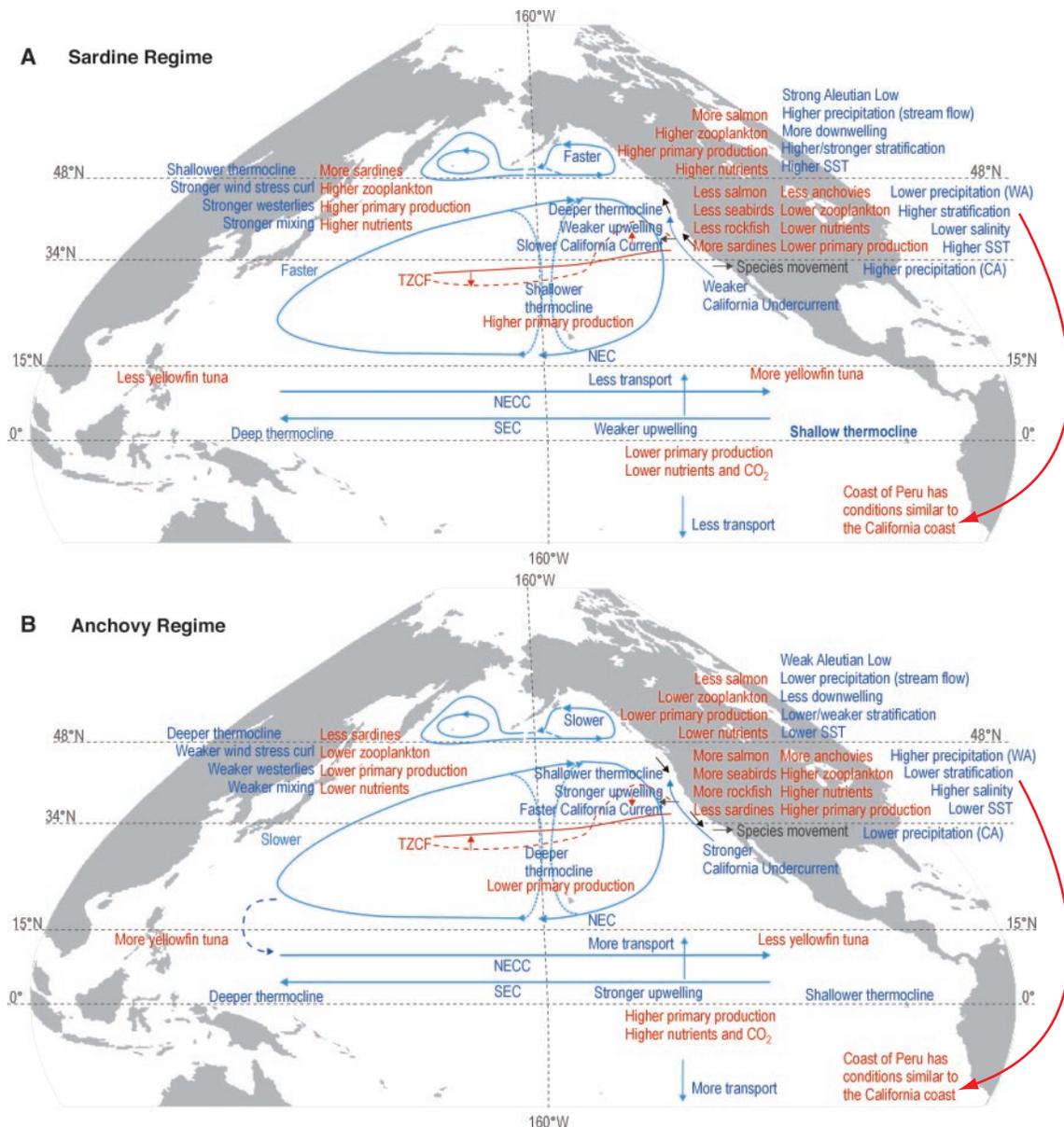


Fig. 3. Synthesis of Pacific conditions during the (A) sardine and (B) anchovy regimes. Physical changes are in blue, and biological and chemical changes are in red.

decades). Studies of anthropogenic effects and management of ocean resources must consider these natural, multidecadal oscillations. Anthropogenic influences may in turn influence the character of regime shifts. For example, overfishing or global warming may alter the response of populations to natural multidecadal change.

It took well over a decade to determine that a regime shift had occurred in the mid-1970s. If a regime shift is confirmed for the late 1990s, it will have been identified much earlier. However, identifying a regime shift is much easier than understanding the process determining it. Unraveling the processes behind multidecadal variability and how they affect ocean ecosystems and biogeochemical cycling will require a concerted and integrated observational and modeling effort. Such efforts are under way for developed countries (48), but they must be expanded to global scales. Measurement networks, analogous to those established by meteorologists, will be required for ocean physics, ecology, and biogeochemistry.

As longer time series are collected and integrated into a basin-scale or global view, longer period fluctuations may be uncovered. These time series will help answer many of the fundamental questions associated with regime shifts. For example, what is the underlying physical forcing behind these shifts? How do they influence fish populations—through changes in nutrient supply or through more direct climate links? Do the shifts between regimes occur rapidly, gradually, or both? How are they related to El Niño and La Niña (49)? Because of the similarity to El Niño and La Niña, the use of El Viejo (the old man) for the warm eastern boundary “sardine regime” and La Vieja (the old woman) for its counterpart are suggested.

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