

Biological Consequences of El Niño

Richard T. Barber and Francisco P. Chavez

El Niño is defined by the appearance and persistence, for 6 to 18 months, of anomalously warm water in the coastal and equatorial ocean off Peru and Ecuador. However, the anomaly in the eastern tropical Pacific Ocean is only one facet of a large-scale phenomenon involving the global atmosphere and the entire tropical Pacific. In addition to major ecological and agricultural consequences in Asia and the Americas (1), the anomalous ocean conditions of El Niño are accompanied by large reductions in plankton, fish, and seabirds in the normally rich waters of the eastern equatorial Pacific. To understand how the ocean changes affect the biology, it is necessary to describe the unique character of this region.

The eastern equatorial Pacific over a wide band along the coast and equator normally is remarkably cool (2). In August 1982, for example, a swimmer on a beach at 5°S near Paita, Peru (Fig. 1), would have encountered water that was 17°C despite continuous heating by the equatorial sun. This August 1982 condition was close to normal [mean August temperature is 16.5°C (3)] and demonstrates that ocean processes must continuously export from the region a portion of the solar heat received. By October 1982, however, sea-surface temperature (SST) had risen 5°C (Fig. 2), sea level had risen, the surface mixed layer had deepened, and the thermocline had been depressed by 50 m or more (4).

The region's normal cool conditions result from a dynamic balance of heat transfer between ocean and atmosphere and between different parts of the ocean. El Niño is what results when the normal balance is upset. Wyrtki (5) suggested that El Niño, in addition to transporting extra heat into the eastern equatorial Pacific, also interrupts the normal export of heat.

Cool SST's are accompanied by three other correlates of reduced heat storage in the upper layer of the ocean: a low sea level, a shallow surface mixed layer, and a shallow thermocline (6). Of these four characteristics of the eastern boundary region of the Pacific, sea level does not

have direct biological sequelae, but the cool SST's, shallow surface mixed layer, and shallow thermocline result in high annual productivity at all trophic levels of the ecosystem (7). Upwelling ecosystems appear not to differ qualitatively from other marine ecosystems, but they differ quantitatively. It is this high productivity that El Niño disrupts.

Summary. Observations of the 1982–1983 El Niño make it possible to relate the anomalous ocean conditions to specific biological responses. In October 1982 upwelling ecosystems in the eastern equatorial Pacific began a series of transitions from the normal highly productive condition to greatly reduced productivity. The highly productive condition had returned by July 1983. Nutrients, phytoplankton biomass, and primary productivity are clearly regulated by the physical changes of El Niño. Evidence from 1982 and 1983 also suggests effects on higher organisms such as fish, seabirds, and marine mammals, but several more years of observation are required to accurately determine the magnitude of the consequences on these higher trophic levels.

There is ample evidence for year-to-year variations in biological production along the Peru coast (7, 8), but the environmental changes responsible for these variations are not known. During the equatorial warming event of 1975 (9), anomalously warm water west of the Galápagos Islands at 95°W was nutrient-rich (10), but primary productivity was reduced about tenfold from values in the 1960's at the same location and season. At the onset of the 1976 El Niño a sudden bloom of the dinoflagellate phytoplankton *Gymnodinium splendens* took place in the coastal waters along Peru when a sudden warming of the nutrient-rich surface layer increased the static stability. Interest in the causality of changes in biological productivity during thermal anomalies in the coastal and equatorial ocean led to a program in which the environment of plankton was studied in terms of both day-to-day and year-to-year changes. Anecdotal accounts from 1972 and 1976 suggested that biological consequences of El Niño showed up almost simultaneously along the entire Peru coast, persisted for months, and then rapidly disappeared. The program, begun in early 1982, was designed to adequately evaluate such an

event. During 1982 and 1983 triweekly observations were made at shore stations in Paita and on the equator at the Galápagos Islands. In addition, ship-board observations were made quarterly along the five transects shown in Fig. 1.

Conceptual Framework

There is a clear theoretical basis for a decrease in biological productivity during El Niño. The theory has two causal aspects, one dealing with inorganic plant nutrients such as nitrate, phosphate, or silicate and the other with the supply of light for photosynthesis. The major inorganic nutrient reservoir of the ocean is water below the thermocline (11); any process that depresses the thermocline away from the surface layer, where there

is enough light for photosynthesis, will necessarily reduce productivity. Because light decreases exponentially as a function of depth, the depth of the surface mixed layer in which phytoplankton are homogeneously distributed determines the quantity of light that can be captured by the phytoplankton (12). If the mixed layer is deep, phytoplankton spend a greater proportion of time in the dark and water molecules, not phytoplankton, absorb most of the light. Note that we have invoked two of the correlates of ocean thermal dynamics, thermocline depth and mixed layer depth, whose variability is an integral part of El Niño (6). Regions of the ocean, such as the eastern tropical Pacific, having a thermocline near the surface and a very shallow mixed layer are biologically richer than other regions of the ocean (13) because large-scale thermal structure provides the opportunity for enhanced simultaneous capture of light and nutrients. This enhanced primary production is reflected in all levels of the ecosystem

Richard T. Barber is professor in the Department of Zoology and the Department of Botany and Francisco P. Chavez is a graduate student in the Department of Botany, Duke University, Beaufort, North Carolina 28516.

as well as in the geochemistry of sediments (7).

Large-scale trade winds blowing across the Pacific from east to west set up the tilt in the thermocline that brings its middle (the 20°C isotherm) to a favorable, shallow depth of 40 m or less in the eastern boundary (1, 14). Mixed layer thinning in the eastern boundary current is also a consequence of the large-scale zonal winds (6). Exploitation of the large-scale thermal structure involves a set of smaller scale physical processes that act within the favorable, basin-wide thermal structure of the Pacific but are somewhat independent of it. These mesoscale physical processes are set in motion by meridional winds blowing toward the equator along the coasts. The meridional winds drive coastal upwelling; this phenomenon, which takes place within 50 km of the shore, transports water from depths of 40 to 80 m to the surface (15). In a narrow band along the equator, wind-driven equatorial upwelling (16) provides the same final advective link between the thermocline and the surface layer. Vertical mixing in the wake of islands, shelf break upwelling, and geostrophic upwelling resulting from current shear all play ecological roles analogous to those of coastal and equatorial upwelling by providing local vertical transport

or mixing that can connect the nutrient pool with the light supply. But these local processes can enhance biological processes only if the large-scale thermal structure is favorable in the sense that nutrient-rich water is close to the surface.

In a 1974 description of El Niño, Wooster and Guillen (17) said that coastal upwelling ceased or weakened during the events. This was a reasonable interpretation of the data at the time because cool SST's were the major signature of coastal upwelling and this signature disappeared during El Niño. When coastal wind data became available it became clear that in previous El Niño events (18) and the 1982–1983 event (19) the coastal winds driving coastal upwelling did not weaken. In fact, coastal winds may intensify during El Niño because of increased thermal differences between land and sea (18). During El Niño it appears that coastal upwelling continues but that the water entrained is warmer and poorer in nutrients. As the thermocline is progressively depressed toward and below the depth of entrainment (40 to 80 m), coastal upwelling (as well as the other mechanisms of local vertical flux mentioned above) transports smaller and smaller quantities of nutrients to the surface.

This conceptual model suggests that El Niño affects the ecosystem by decreasing the quantity of nutrients transported to the surface, which in turn causes primary production of organic material to decrease proportionally. In addition, the amount of light available to a phytoplankton population for the synthesis of organic material is decreased by a deepened mixed layer. In this manner the supply of both nutrients and light is reduced as El Niño strengthens in intensity and the decrease in new primary production available to the food chain after some period of time causes proportional reductions in the growth and reproductive success of zooplankton, fish, birds, and marine mammals. Because temperature, nutrients, productivity, and food are tightly linked in upwelling ecosystems, fish, seabirds, and marine mammals (20) have evolved behavioral adaptations that enable them to use temperature as an environmental cue to find areas of abundant food. Such behavior, of course, is disrupted by El Niño, so the short-term biological response of higher organisms to the productivity anomaly of El Niño may be mediated through behavior responding to the thermal anomaly. Examples of both temperatures and food responses are evident in observations of the 1982–1983 El Niño.

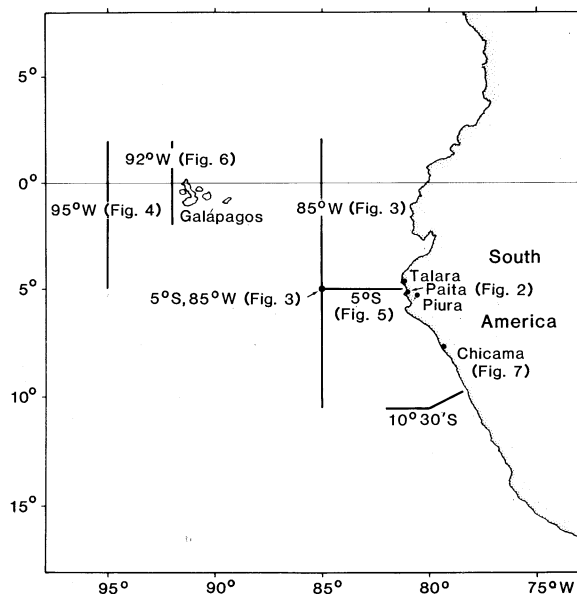
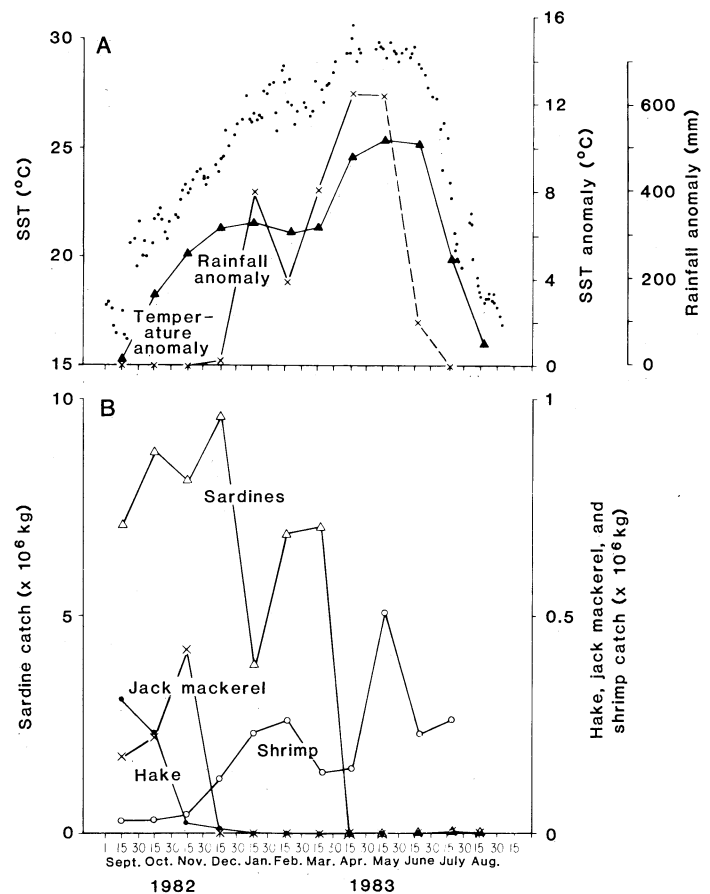


Fig. 1 (left). Chart of the eastern equatorial Pacific, showing the location of the transects and observation stations. Fig. 2 (right). (A) Triweekly SST measurements made 8 km offshore at the 100-m isobath at Paita (5°04'S, 81°15'W), temperature anomalies calculated by comparing the monthly averages of triweekly temperatures to the Talara (4°35'S, 81°17'W) 26-year monthly mean temperatures (1955 to 1981), and monthly rainfall anomaly at Piura (5°18'S, 80°35'W) calculated with the 26-year monthly mean rainfall (1955 to 1981). (B) Monthly catch of sardines, hake, jack mackerel, and shrimp along the northern coast of Peru (reported at Paita).



Development of the 1982–1983 El Niño

The anomaly arrived at Paita (Fig. 1) during the last week of September 1982 as a 4°C SST increase in one 24-hour period (Fig. 2). The SST at the Paita ocean station, which is 8 km offshore over the 100-m isobath, and at the pier where the historic Paita temperature record is obtained (3), showed the same rapid change. About 400 km offshore (5°S, 85°W), the mixed layer deepened dramatically in the first week of October 1982 without a very large change in SST (Fig. 3B). Comparison of October 1982 with November 1981 shows the magnitude of the mixed layer deepening that took place in 1982 in the absence of a significant change in coastal winds (19). The October 1982 profile shows that the largest temperature anomaly associated with onset of El Niño is 40 m below the surface; this explains why the anomaly appears first at the coast (1), where local upwelling entrains the anomalously warm subsurface water and transports it to the surface.

The mixed layer deepening seen in the October 1982 profile could have decreased primary productivity in the region, but nutrients remained favorable for phytoplankton growth, with nitrate concentrations over 4 μM . The relation between phytoplankton growth and ambient nutrient concentration is complex (21). Here it is sufficient to know that water with nitrate concentration of 4 μM or more is nutrient-rich; that is, the uptake versus concentration relation is saturated (21). Conversely, water with a nitrate concentration of 0.1 μM or less is nutrient-poor. Nitrate, silicate, and phosphate, the major inorganic nutrient anions (7), covary in the upper 100 m of the eastern equatorial Pacific, so nitrate is used as an index of the nutrient abundance of all the major nutrient anions. The difference in the nitrate concentration in the water column between November 1981 and October 1982 shows that the processes normally keeping the surface layer nutrient-rich were reduced in the first week of October 1982 but that the surface layer was not depleted of nitrate.

It is tempting to speculate that the October 1982 to November 1982 progression shows the interplay of remote and local processes. That is, a propagated Kelvin wave transiting from the equatorial wave guide to the coastal wave guide (19) deepened the mixed layer by October 1982; in the following month local heating increased the temperature of the upper 100 m and phytoplankton uptake stripped nutrients from the surface layer

of the water column that was now isolated from the nutrient-rich water of the thermocline. The trouble with this scenario is that it neglects large-scale horizontal water movements that were occurring around 5°S and 85°W in October and November 1982. Drogued surface buoys (4) showed episodes of strong flow to the southeast in this region, and the surface layer had salinities of less than 34 parts per thousand, suggesting that the surface water originated north of the equator and flowed into the region between October and November 1982 (22). Further evidence of southward overflow of the Equatorial Front along 85°W can be seen by comparing November 1981 to November 1982 in Fig. 3A. The Equatorial Front was 2°S in November 1981, separating the cooler, nutrient-rich waters of the Peru Current from the nutrient-depleted surface waters to the north.

In November 1982 the front, as indicated by the 24°C and 4 μM nitrate isopleths, was in the vicinity of 10°S, 800 to 900 km south of the normal November location. On the basis of the October and November 1982 observations we calculate that the Equatorial Front progressed southward at 16 km/day. The change from October to November along 85°W probably resulted from a combination of a propagating Kelvin wave (19), large-scale southward flow (4), and, to a lesser degree, local heating and nutrient uptake. Figure 3 shows that, regardless of the processes involved, the ocean along 85°W changed in October and November 1982 from a nutrient-rich eastern boundary current condition to a nutrient-depleted condition typical of a central ocean gyre (23).

Along the cross-equatorial transect at 95°W (Fig. 4), the initial change caused

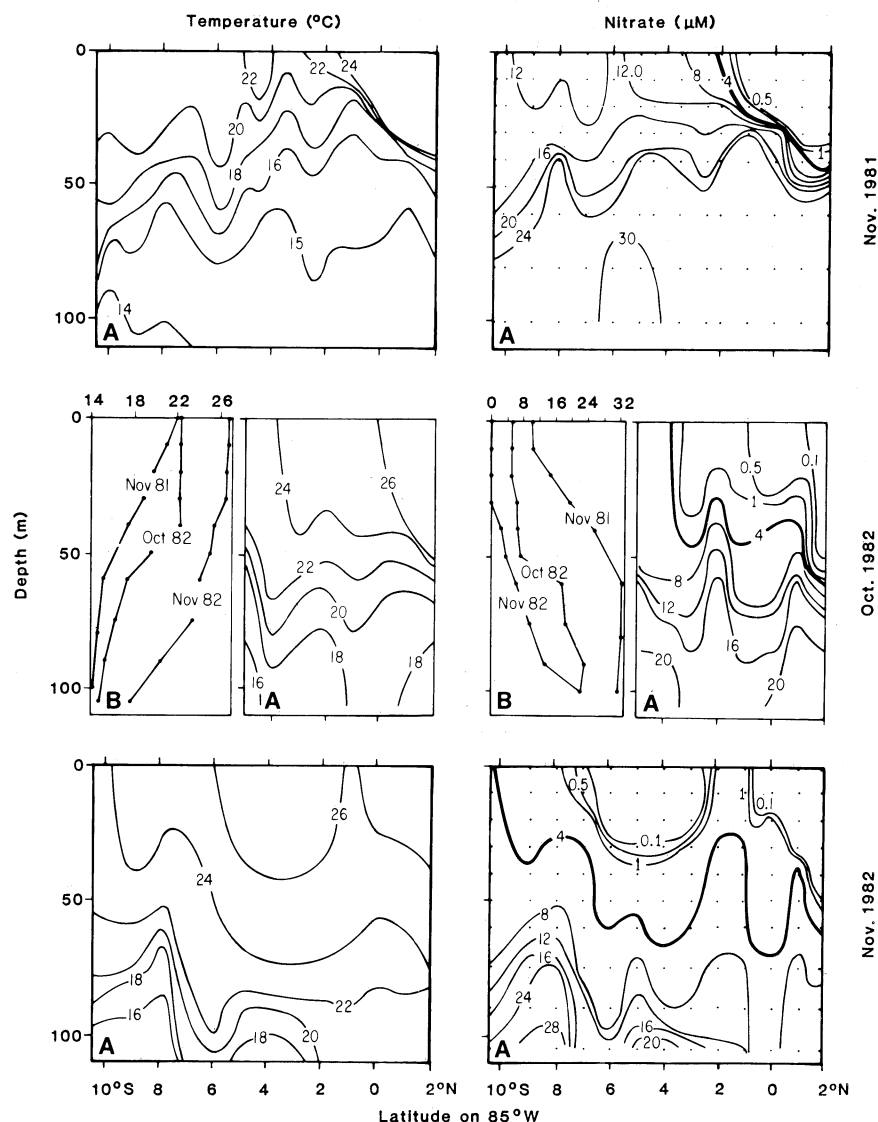


Fig. 3. (A) Cross-equatorial profiles of temperature and nitrate along a transect at 85°W from 2°N to 10°S. November 1981 shows normal conditions; October, onset of the anomaly. (B) Vertical temperature and nitrate profiles measured at 5°S, 85°W during November 1981, October 1982, and November 1982.

by the onset of El Niño is clear; profiles from November 1979 and April 1982 show presumably normal conditions during the cool season (October and November) and the warm season (March and April) (24). During both seasons, and indeed throughout the annual cycle, the equatorial region at 95°W provides phytoplankton with optimum nutrient and mixed layer conditions in that nitrate concentrations are over 4 μM and thermal stratification is strong in the upper 50 m (that is, there is a very shallow or nonexistent mixed layer). The position of the Equatorial Front at 95°W is shown by the 24°C isotherm in November and the 26°C isotherm in April 1982. In November 1982, after the onset of the anomaly, thermal stratification was absent in the upper 75 m and the equatorial band from 1°N to 4°S was nutrient-rich (less than 8 μM but greater than 4 μM nitrate) and relatively warm (less than

26°C but greater than 24°C). The chlorophyll profiles in Fig. 4 show that phytoplankton biomass was low in November 1982. A deepened mixed layer would reduce primary production, but the large decrease in static stability of the layer also may have enhanced diffusive and sinking losses of nonmotile phytoplankton such as diatoms. By March 1983 the anomaly was peaking; no surface signature of equatorial upwelling was present along the 95°W transect. The region at 95°W showed nutrient depletion and reductions in specific photosynthetic activity and the absolute quantity of primary productivity (Table 1). While the transect along 95°W showed a fivefold reduction in absolute productivity, a cross-equatorial transect along 92°W (Fig. 1) close to the Galápagos Islands showed a 20-fold decrease (Fig. 5 and Table 1) in March 1983 at the peak of the 1982–1983 El Niño. Ocean waters around islands

and coasts have inherently higher productivity than waters far removed from land, so the proportional reduction by El Niño was greater in the island (92°W transect) and coastal (5°S transect) waters (Fig. 5 and Table 1). The phytoplankton species (25) showed surprisingly little taxonomic change between normal (26) and El Niño conditions on the 92°W transect, but there were fewer diatoms and more microflagellates during the peak of the anomaly.

The cross-equatorial transect at 95°W shows onset of the event in November 1982 (depressed thermocline, deepened mixed layer, nutrient richness) and peak conditions (29°C SST, relatively strong stratification, nutrient depletion) in March 1983, but we do not know whether the change from onset to peak was rapid or gradual. Along the coast, development of the anomaly had a 5-month maturation phase between onset in October 1982 and the peak in May 1983. Figure 2 illustrates development of the SST anomaly: a rapid rise in late September, a slower but steady increase from October through March from 22°C to 28°C, and a plateau at 29°C. The sequence of transects along 5°S normal to the coastline (Fig. 6) shows the temporal and spatial development at the offshore and equatorward anomaly progressively moves inshore and poleward.

In November 1982 there was deepening of the thermocline and the appearance of a layer of warm, low-salinity, low-nutrient, and low-chlorophyll water at 40 m along the transect from 85°W to a position at about 82°W, or 150 km off the coast (Fig. 6). Coastal upwelling continued to supply nutrients to the surface layer in a band next to the coast, but the narrow 30- to 50-km band of enrichment in November 1982 contrasts sharply to the 400-km-wide region of high nutrients and chlorophyll present in November 1981. During November 1982 chlorophyll concentrations all across the transect were lower than in November 1981; however, stations within 30 km of the coast during November 1982 measured 1 to 10 μg of chlorophyll per liter in a bloom dominated by a diatom typical of coastal upwelling, *Asterionella japonica* (26).

Conditions in March 1983 were like those in November 1982 except for warmer SST's and a still narrower band of coastal enrichment (Fig. 6). These increases, which are also evident in the Paita ocean station time series (Fig. 2), had begun in late September 1982. In March 1983 coastal upwelling still supplied a narrow inshore band with nutrients, and this band remained rich in phytoplankton, as shown by cross-shelf

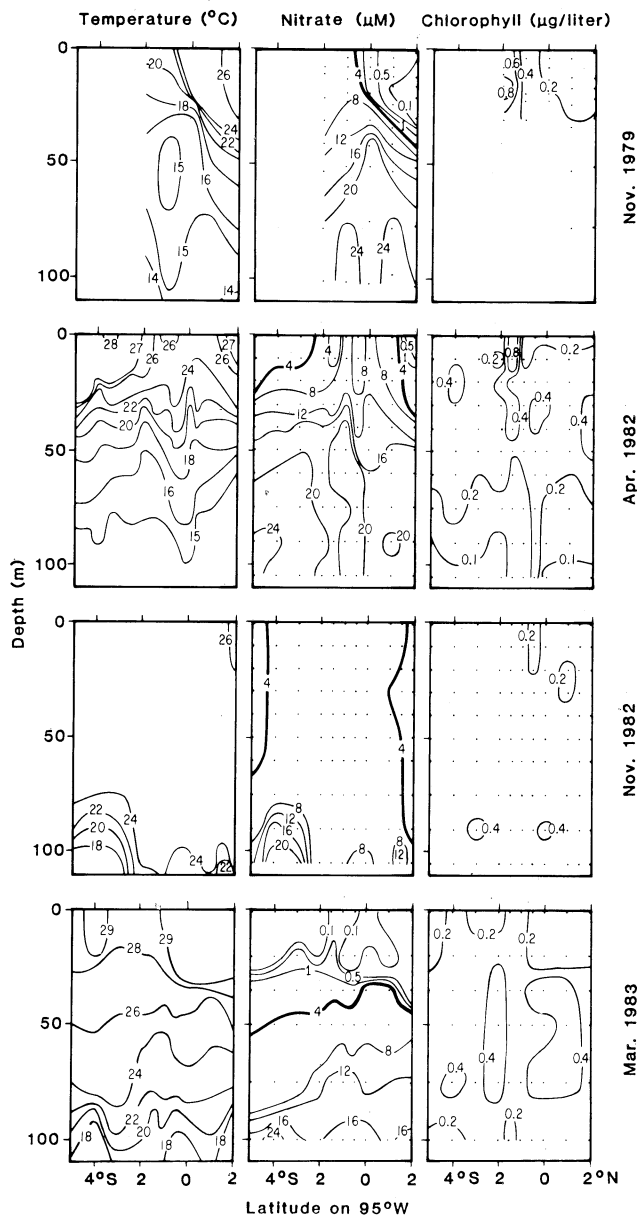


Fig. 4. Cross-equatorial profiles of temperature, nitrate, and chlorophyll along a transect at 95°W from 2°N to 5°S. November 1979 and April 1982 show normal conditions for those months. November 1982 is during onset of the anomaly at 95°W and March 1983 is during the peak of the anomaly. In all profiles temperature was measured as a continuous vertical record; discrete nitrate and chlorophyll observations were made at the depths shown by the dots.

profiles of chlorophyll. The coherence of the nitrate and chlorophyll profiles in Fig. 6 shows that, to a first approximation, the spatial distribution of phytoplankton biomass in this ecosystem is determined by advective supply of new nutrients to the surface layer. A progressive decrease in the area of productive inshore habitat started in November 1982 and continued through March 1983, but as the size of the productive habitat decreased the concentration of phytoplankton biomass, as reflected by chlorophyll concentration, remained remarkably high. Figure 6 shows that chlorophyll in the extreme inshore area in March 1983 ranged from 1 to 6 $\mu\text{g}/\text{liter}$, concentrations that characterize the coastal upwelling habitat during normal conditions (7, 8).

The May 1983 profiles in Fig. 6 show a 50-m-deep layer of 29°C, nutrient-depleted water against the coast and maximum expression of the physical and biological anomalies of the 1982–1983 El Niño. The thermocline is deep with the 20°C isotherm at 150 m, isotherms tilt down toward the coast, and a 50-m-deep mixed layer has very low nutrient concentrations, low phytoplankton biomass, and low productivity (Fig. 5 and Table 1).

Transects farther south along 10°30'S indicated that the anomalous conditions were delayed and somewhat reduced in intensity off central Peru compared with the northern coast around 5°S. In November 1982 water characteristic of the region north of the Equatorial Front had not progressed southward to 10°30'S; surface layer concentrations of nitrate were between 4 and 8 μM . By March 1983 the anomaly was present at 10°30'S and reached to within 50 km of the coast. Comparison of these results with those from 5°S establishes that the anomaly was less intense farther from the equator. This supports the concept that in an oceanographic sense El Niño is an equatorial phenomenon that propagates poleward and progressively weakens along the coast (5, 14, 19, 27).

Recovery from the 1982–1983 anomaly started at the Paita ocean station early in July 1983 (Fig. 2). By 15 July 1983 the temperature had decreased to 20°C; a transect along 5°S (Fig. 6) showed a simultaneous return to normal conditions in a 200-km-wide band next to the coast. Figure 5 shows that the 200-km band contained nitrate concentrations of 4 to 16 μM and chlorophyll concentrations of 1 to 20 $\mu\text{g}/\text{liter}$. The speed (Fig. 2), spatial extent (Fig. 6), and intensity (Fig. 5) of the recovery in nutrient levels, phytoplankton biomass, and primary production along the 5°S transect was unexpected. During July and August

Table 1. Mean surface nitrate, chlorophyll, and primary productivity during normal and El Niño conditions on transects at 95°W, 92°W, and 5°S (Fig. 1). Values were calculated by integrating the values along the three transects (the space under the curves of Fig. 6) and dividing by the length of the transect.

Transect	Date	Nitrate (mmole/ m^3)	Chloro- phyll a (mg/m^3)	Primary productivity (milli- grams of carbon per cubic meter per day)	Assimi- lation (milli- grams of carbon per milli- gram of chloro- phyll per hour)
Equator at 95°W; 2°N to 2°S	April 1982 (normal)	5.3	0.22	15.6	7.0
	March 1983 (El Niño)	0.1	0.16	3.0	1.8
	Ratio (April 1982 to March 1983)	53.0	1.4	5.2	3.9
Equator at 92°W; 2°N to 2°S	April 1966 (normal)	7.8	0.57	77.8	13.6
	March 1983 (El Niño)	0.1	0.17	3.9	2.3
	Ratio (April 1966 to March 1983)	78.0	3.4	20.0	5.9
Coast at 5°S; 81°15'W to 85°W	July 1983 (normal)	3.0	4.44	219.3	4.9
	May 1983 (El Niño)	0.1	0.21	10.3	4.9
	Ratio (July 1983 to May 1983)	30.0	20.9	21.3	1.0

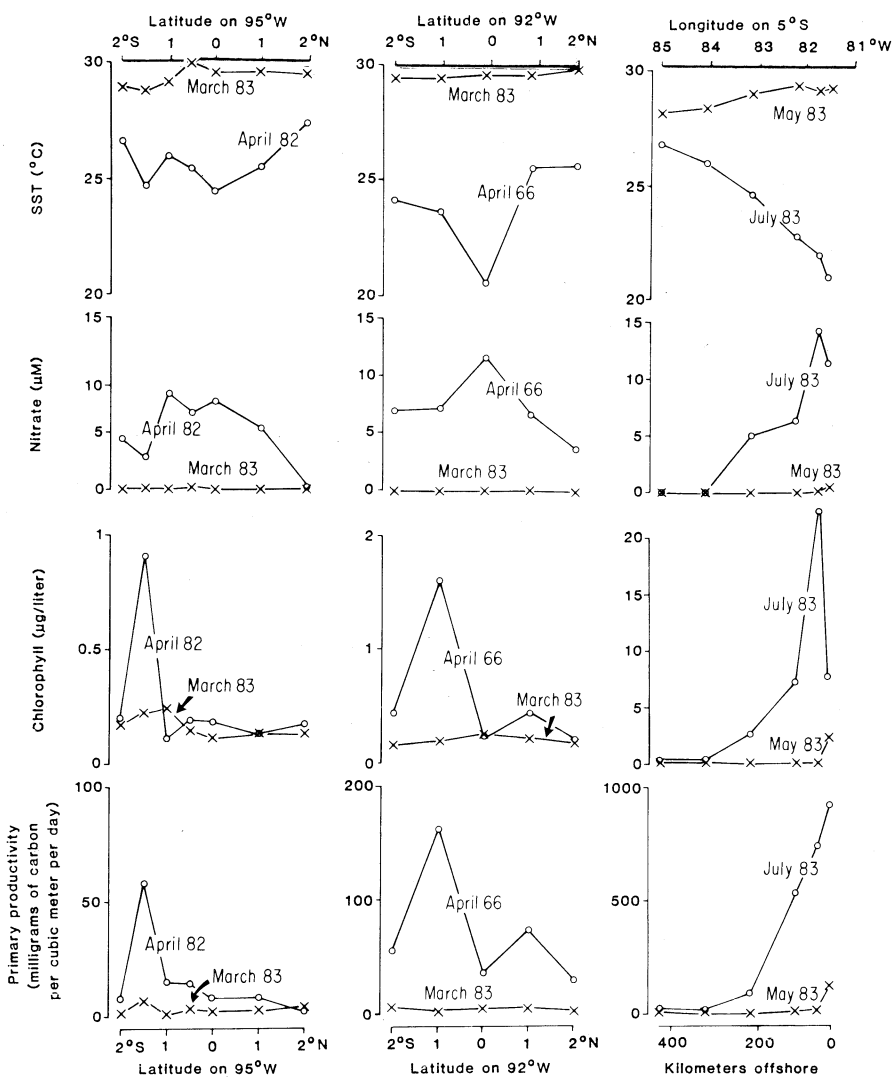


Fig. 5. Comparison of SST, nitrate, chlorophyll a, and primary production along the 95°W, 92°W, and 5°S transects during normal conditions and during the peak of the anomaly when biological productivity was affected most.

1983 the offshore water beyond 200 km remained anomalously warm, nutrient-depleted, and low in productivity. Recovery of the upwelling ecosystem started next to the coast and progressed offshore. Still, even the nutrient-rich and highly productive water in the 200-km band along the coast remained anomalously warm in July and August; satellite observations of the large-scale temperature field off the coast of Peru and Ecuador for those months (28) gave no indication of the large-scale recovery in primary productivity that was taking place.

Effects on Higher Trophic Levels

Interannual variability in SST along the coasts of Ecuador and Peru and in the Galápagos Islands is well known because of the association of warm anomalies with reductions in fish (Fig. 7). Most investigators of the effects of El Niño on fish, particularly Peruvian scientists most familiar with the phenomenon (8, 29), believe that reductions in fish abundance are caused by decreases in primary productivity that affect the entire food web. Evidence for a causal

relation between primary productivity and changes in anchovy abundance has been fragmentary because a complete cycle of productivity changes during El Niño was not observed along with the consequences of the perturbation at higher trophic levels. What was missing before 1982 were time series of nutrients and productivity to compare with the excellent time series of temperature, fish catch, and seabird abundance obtained in the past (29).

There have been other views on how El Niño affects fish. For example, a decade ago it was suggested that the Peruvian anchovy (*Engraulis ringens*) simply swam to deeper, cooler water and that the missing fish would return in full abundance after the warm anomaly passed (30). In the 1970's, however, multi-ship acoustic surveys of Peruvian coastal waters showed convincingly that spatial redistribution does not explain how El Niño affects the anchovy (31). For most species of the higher trophic levels we believe that the major effect of the 1982–1983 El Niño was an absolute decrease in growth and reproductive success caused by disruption of the normal food web. The specific change was a 5- to 20-fold reduction of primary productivity (Table 1) as this normally eutrophic region changed to one with an oligotrophic character typical of a central ocean gyre (23).

To our knowledge the first report of a biological response to the 1982–1983 El Niño was the reproductive failure of seabirds on Christmas Island (2°N, 157°W). In June the nesting of the blue-faced booby (*Sula dactylatra*) was proceeding normally with many adult birds, nestlings, and eggs present on the island; by November 1982 Schreiber and Schreiber (32) found only three adult birds and one underweight nestling. Equally large reproductive failures were observed for most of the species of sea birds that nest on Christmas Island. For example, the number of great frigate birds (*Fregata minor*) declined from 20,000 in June 1982 to fewer than 100 in November 1982. Rains and flooding may have killed some nestlings, but Schreiber and Schreiber stated that disappearance of small fish and squid caused the adult birds to abandon the island. Such abandonment of nests and young at the onset of El Niño was observed frequently in the 1982–1983 event as well as in earlier events (33). The spatial extent of this behavior in 1982–1983 was from the central Pacific to 15°S on the Peru coast. Nest abandonment and widespread dispersal from the nest sites is appropriate evolutionary behavior for these relatively long-lived

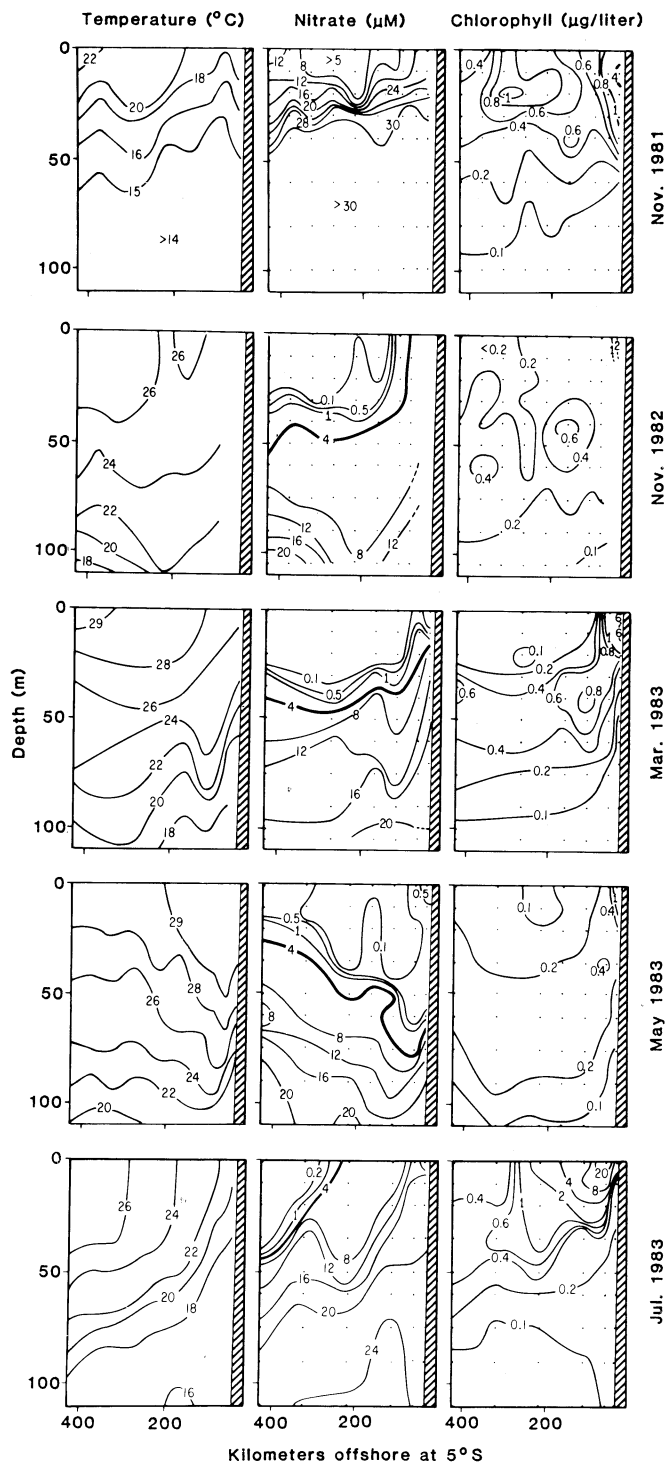


Fig. 6. Cross-shelf profiles of temperature, nitrate, and chlorophyll a along a 5°S transect from 85°W to Paita. November 1981 shows the normal conditions; November 1982 is during onset; March 1983 is during maturation; May 1983 is during the peak of the anomaly; and July 1983 shows recovery of normal conditions in the nearshore upwelling cell and persistence of the anomaly farther offshore.

birds because it allows the adults to use available food for survival rather than reproduction. Adult seabirds along the coast of Peru survived through March 1983 without detectable mortality, but by April there were reports of many dead adults on beaches throughout the region. It appears that, in addition to causing failure of the class of 1982, the event significantly reduced the adult population because of its intensity and duration.

Seabirds responded rapidly to altered conditions, but marine mammals (34) provide the clearest evidence for the food stress that accompanies El Niño. In 1982 and 1983 the Galápagos fur seal (*Arctocephalus galapagoensis*) and the California sea lion (*Zalophus californianus*) were studied in the Galápagos Islands and the South American fur seal (*Arctocephalus australis*) and sea lion (*Otaria byronia*) were studied at Punta San Juan near 15°S on the southern coast of Peru. Limberger *et al.* (34) reported that all the Galápagos fur seal pups born in 1982 had died by March 1983 and that many of the pups and some of the adults of the other three species had died. The pup mortality may have resulted from lack of foraging success by the adult females (34); females stayed at sea for an average of 5 days rather than the typical 1.5 days, and when they returned to shore they were unable to provide enough milk to prevent pups from starving. Apparently the fish and squid that these marine mammals require were not available in adequate numbers between November 1982 and March 1983, either near the Galápagos or off Peru. In addition to the loss of the individuals born in 1982, it appears that the adult population has been reduced (34).

Figure 2B shows changes in the catch of several commercially important species in the northern Peru region. Catch is not synonymous with abundance, but, according to the fisheries biologists who provided the data, it accurately reflects the presence or absence of these species because from November 1982 to August 1983 the fishing fleet continuously tried a variety of techniques at locations throughout the region to catch whatever they could. Changes in catch were closely related to the timing and intensity of environmental changes in the different habitats of hake, shrimp, mackerel, and sardines. The first species to respond was hake (*Merluccius gayi*). Apparently, these relatively large and motile bottom-dwelling fish moved down the continental slope, staying with the cool water to which they are adapted. In November 1982, when the 18°C isotherm moved

down the shelf to below 100 m and subsurface warming was observed in the moored current meter array (19), the hake catch slowly decreased to zero (Fig. 2); when 18°C water returned to the shelf break in July 1983 a few fish reappeared in the catch.

The increase in shrimp catches at Paita shown in Fig. 2 is consistent with the idea that the altered currents of El Niño redistributed shrimp throughout the region (35). The catch of the three major species of shrimp (*Xiphopenaeus riueti*, *Penaeus occidentalis*, and *Trachypenaeus byesi*) was normal on the Pacific Coast of Colombia from January 1982 to September 1982, then decreased sharply in the last quarter of 1982. The shrimp catch along Ecuador was normal through February 1983, while the catch off northern Peru, which is usually very low, increased as the temperature increased from November 1982 to February 1983 (Fig. 2). The southward shift of shrimp abundance reflects the somewhat planktonic character of these organisms; they were carried southward by the inshore, southward-flowing warm current characteristic of El Niño (6). Shrimp and hake had no observed mortality in connection with the anomaly, but not all demersal species avoided mortality. Between December 1982 and February 1983 large numbers of dead corbina (*Cynoscion xanthulus*) were found floating off northern Peru (35). Cross-shelf temperature profiles (Fig. 6) show that by March 1983 the habitat of this demersal species had increased in temperature from about 16° to 24°C.

The sardine (*Sardinops sagax*) is in the

1980's an important resource for Ecuador, Peru, and Chile; Fig. 7 shows the increase in this fishery in the past few years in Peru to an annual catch of over 1 million metric tons. In January 1983 sardines disappeared from the Ecuadorian coast, did not change in abundance along the Peru coast, and greatly increased along the coast of Chile. Maintenance of the sardine catch off northern Peru through March 1983 (Fig. 2) can be accounted for by the cross-shelf profiles from 5°S (Fig. 6). From November 1982 to March 1983 sardines remained in the dwindling band along the coast where chlorophyll concentrations were over 1 µg/liter. Chlorophyll is an index of phytoplankton abundance but not of zooplankton, the major food of sardines. However, because phytoplankton are the major food of zooplankton, chlorophyll concentration does delimit the habitat of sardines. As adult sardines concentrated in the nearshore region they were extremely vulnerable to fishermen, and their physiological condition was deteriorating, as shown by the decrease of their oil content to less than 1 percent by weight (35). In mid-April 1983 (Fig. 2) sardines disappeared from the northern Peru catch; in confirmation, the May 1983 profiles in Fig. 6 show that the rich habitat containing more than 1 µg of chlorophyll per liter was virtually eliminated from the region.

Jack mackerel (*Trachurus symmetricus*) disappeared from the catch in December 1982 (Fig. 2), between the times when hake and sardines left the coastal region. This timing is in accordance with the alteration of the habitat of the three

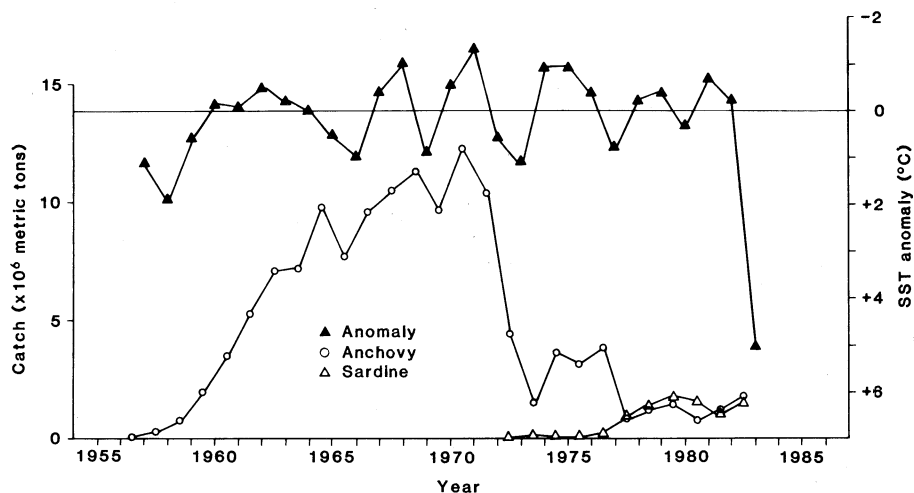


Fig. 7. Association of annual SST anomalies with annual catch of anchovies and sardines off Peru. The anomaly temperature scale is inverted: upwards indicates cooler temperatures; downwards indicates warmer temperatures—that is, El Niño. The annual temperature anomaly is relative to the 26-year mean temperature of 16.9°C at Chicama; it is calculated for the thermal year from July to June spanning half of two calendar years, and the value is plotted in the middle of the thermal year at January. The fish catch for each calendar year is plotted in the middle of the calendar year at July.

species by El Niño. The subsurface warming (19) and thermocline depression (4) of the onset forced hake to move first. Jack mackerel occupy the offshore boundary of upwelling circulation, where their euphausiid food is most abundant (7). The warm, nutrient-poor, phytoplankton-poor water seen offshore in the November 1982 profiles is a habitat in which jack mackerel cannot survive, so this species was crowded into the inner 30-km band by the offshore-to-onshore progression of anomalous conditions. At this time predatory species that eat jack mackerel—bonito (*Sarda chiliensis*), dorado (*Coryphaena hippurus*), and yellowfin tuna (*Thunnus albacores*)—became more abundant close to the coast (35). Increasingly predation by these oceanic species, which are tolerant of warm temperatures, on the concentrated jack mackerel may have contributed to its disappearance in December 1982.

The most impressive biological consequence of El Niño is the effect on the Peruvian anchovy (*Engraulis ringens*), once the basis of the world's largest fishery (29). Figure 7 shows the covariation of thermal conditions and anchovy harvest. We believe that this relation is causal and that the causality depends on increased heat storage depressing the thermocline and increasing the depth of the mixed layer. As shown in Figs. 3, 4, and 6 and Table 1, thermocline depression and mixed layer deepening are always accompanied by reductions in the productivity and biomass of phytoplankton. The 20-fold decrease in phytoplankton biomass and productivity that took place along the coastal transect in 1983 will decrease the growth, survival, and particularly reproductive fitness of the adult anchovy. Because larval survival is especially dependent on the availability of phytoplankton (36), the reproductive success of the species will be impaired. In combination these processes will reduce the anchovy stock to a record low level.

The coastal region around Paita was closed to anchovy fishing in 1982, so there is no information on the catch of this species to relate to the local changes in physical conditions and productivity on the 5°S transect. Observations made by the Instituto del Mar del Peru (35) confirm that the anomaly has had an effect. During December 1982 to February 1983 anchovy schools were concentrated in small pockets next to the coast and numerous dead adult anchovies were seen on the surface at several locations. This observation is significant because mortality of adults was not observed during the 1972 or 1976 El Niño events (35). It appears that for the anchovy, as for seabirds and marine mammals, the 1982–1983 El Niño profoundly affected both reproduction and adult survival.

References and Notes

1. E. M. Rasmusson and J. M. Wallace, *Science* **222**, 1195 (1983).
2. S. Zuta and W. Urquiza, *Bol. Inst. Mar Peru* **8**, 461 (1972).
3. F. Vasquez and C. Raul Castillo, *Estud. Reg. Fenóm. El Niño Bol.* **3**, 9 (1983) (available from Comisión Permanente del Pacífico Sur, Quito, Ecuador).
4. D. Halpern, S. P. Hayes, A. Leetmaa, D. V. Hansen, S. G. H. Philander, *Science* **221**, 1173 (1983).
5. K. Wyrtki, *J. Phys. Oceanogr.* **5**, 572 (1975); *ibid.* **9**, 1223 (1979); *Mar. Technol. Soc. J.* **16**, 3 (1982). (The last of these is a nontechnical discussion of El Niño with figures showing the effect of large-scale winds on sea level, thermocline tilt, and mixed layer thickness.)
6. M. A. Cane, *Science* **222**, 1189 (1983).
7. R. T. Barber and R. L. Smith, in *Analysis of Marine Ecosystems*, A. R. Longhurst, Ed. (Academic Press, New York, 1981), p. 31.
8. O. Guillen, in *Fertility of the Sea*, J. D. Costlow, Ed. (Gordon & Breach, New York, 1971), p. 187; — and R. Z. Calienes, in *Resource Management and Environmental Uncertainty: Lessons from Coastal Upwelling Fisheries*, M. H. Glantz and J. D. Thompson, Eds. (Wiley, New York, 1981), p. 255.
9. K. Wyrtki, E. Stroup, W. Patzert, R. Williams, W. Quinn, *Science* **191**, 343 (1976).
10. T. J. Cowles, R. T. Barber, O. Guillen, *ibid.* **195**, 285 (1977).
11. A. C. Redfield, *Am. Sci.* **46**, 205 (1958); R. C. Dugdale, *Limnol. Oceanogr.* **12**, 685 (1967).
12. H. U. Sverdrup, *J. Cons. Cons. Int. Explor. Mer.* **18**, 287 (1953).
13. J. H. Ryther, *Science* **166**, 72 (1969); R. C. Dugdale, *Geoforum* **11**, 42 (1972).
14. A. J. Busalacchi, K. Takenchi, J. J. O'Brien, in *Hydrodynamics of the Equatorial Ocean*, J. C. J. Nihoul, Ed. (Elsevier, New York, 1983), p. 155.
15. Figure 5 of R. T. Barber and R. L. Smith (7) shows the depth of entrainment in three coastal upwelling ecosystems, as determined by dense vertical arrays of current meters.
16. M. Vinogradov, in *Analysis of Marine Ecosystems*, A. R. Longhurst, Ed. (Academic Press, New York, 1981), p. 69.
17. W. S. Wooster and O. Guillen, *J. Mar. Res.* **32**, 387 (1974).
18. D. B. Enfield, *J. Geophys. Res.* **86**, 2005 (1981).
19. R. L. Smith, *Science* **221**, 1397 (1983).
20. J. J. Walsh, *ibid.* **176**, 969 (1972).
21. J. J. McCarthy and J. C. Goldman [*ibid.* **203**, 670 (1979)]; R. C. Dugdale, B. H. Jones, Jr., J. J. MacIsaac, and J. J. Goering [*Can. Bull. Fish. Aquat. Sci.* **211**, 234 (1981)] and R. W. Eppley [*ibid.*, p. 251] provide entrée to the topic of nutrient regulation of phytoplankton growth.
22. W. S. Wooster, *Deep-Sea Res.* **16**, 407 (1969).
23. M. Blackburn, in *Analysis of Marine Ecosystems*, A. R. Longhurst, Ed. (Academic Press, New York, 1981), p. 1.
24. R. T. Barber, S. Zuta, J. Kogelschatz, F. Chavez, *Trop. Ocean-Atmos. Newsl. No. 16* (1983), p. 15.
25. Phytoplankton were identified and counted by T. Arcos of Instituto Nacional de Pesca, Guayaquil, Ecuador, for 1983 and by E. Hulbert of Woods Hole Oceanographic Institution, Woods Hole, Mass., for 1966.
26. R. Jimenez [in *Coastal Upwelling*, F. A. Richards, Ed. (American Geophysical Union, Washington, D.C., 1981), p. 327] and B. Rojas de Mendiola [*ibid.*, p. 328] describe the phytoplankton species normally found in Ecuadorian and Peruvian waters.
27. D. B. Enfield and J. S. Allen, *J. Phys. Oceanogr.* **10**, 557 (1980).
28. R. A. Kerr, *Science* **221**, 940 (1983).
29. O. Guillen, R. Z. Calienes, R. I. de Rondon, *Bol. Inst. Mar Peru* **2**, 49 (1969); G. J. E. Valdivia, *Rapp. P. V. Reun. Cons. Int. Explor. Mer.* **197**, 196 (1978); D. H. Cushing, in *Upwelling Ecosystems*, F. A. Richards, Ed. (American Geophysical Union, Washington, D.C., 1981), p. 449; S. Zuta and O. Guillen, *Bol. Inst. Mar Peru* **2**, 157 (1970); A. Bakun and R. H. Parrish, *Calif. Coop. Oceanic Fish. Invest. Rep.* **23**, 99 (1982).
30. G. Murphy, *Geoforum* **11**, 63 (1972).
31. K. Johannesson and R. Vilchez, in *Meeting on Hydroacoustical Methods for the Estimation of Marine Fish Populations*, J. B. Suomala, Ed. (Charles Stark Draper Laboratory, Inc., Cambridge, Mass., 1981), p. 765.
32. R. W. Schreiber and E. A. Schreiber, *Trop. Ocean-Atmos. Newsl. No. 16* (1983), p. 10.
33. P. D. Boersma, *Science* **200**, 1481 (1978); R. C. Murphy, *Oceanic Birds of South America* (American Museum of Natural History, New York, 1936), p. 1210.
34. D. Limberger, F. Trillmich, G. L. Kooyman, P. Majluf, *Trop. Ocean-Atmos. Newsl. No. 21* (1983), p. 16.
35. J. Valdivia, R. Jimenez, S. Avaria, O. Mora, *Informe de la Tercera Reunión del Comité Científico del Estudio Regional del Fenómeno El Niño* (Comisión Permanente del Pacífico Sur, Quito, Ecuador, 1983), p. 11.
36. R. Lasker, *Rapp. P. V. Reun. Cons. Int. Explor. Mer.* **174**, 212 (1978).
37. Shiptime was provided by the Equatorial Pacific Ocean Climate Study of the National Oceanographic and Atmospheric Administration and by the National Science Foundation. Research support was provided by NSF grant OCE-8110702. The authors acknowledge the generous support provided by the governments of Peru and Ecuador for this work and the valuable assistance of the staff of the Paita laboratory of Instituto del Mar del Peru. We thank J. E. Kogelschatz, V. Thayer, and J. C. Ramus for their contributions.