redistributed throughout the world oceans by the general circulation.

See also

Air–Sea Gas Exchange. Bottom Water Formation. Deep Convection. Ekman Transport and Pumping. Expendable Sensors. Heat and Momentum Fluxes at the Sea Surface. Ocean Subduction. Open Ocean Convection. Penetrating Shortwave Radiation. Thermohaline Circulation. Upper Ocean Heat and Freshwater Budgets. Upper Ocean Mean Horizontal Structure. Upper Ocean Mixing Processes. Upper Ocean Time and Space Variability. Water Types and Water Masses. Wind Driven Circulation. Wind and Buoyancy-forced Upper Ocean.

Further reading

Kraus EB and Businger JA (1994) *Atmosphere–Ocean Interaction*, Oxford Monographs on Geology and Geophysics, 2nd edn. New York: Oxford University Press.

Philips OM (1977) *The Dynamics of the Upper Ocean*, 2nd edn. London and New York: Cambridge University press.

Reid JL (1982) On the use of dissolved oxygen concentration as an indicator of winter convection. *Naval Research Reviews* 3: 28–39.

Warren B and Wunsch W (1981) *Evolution of Physical Oceanography: Scientific Surveys in Honor of Henry Stommel*. Cambridge, MA: MIT Press.

Tomczak M and Godfrey JS (1994) *Regional Oceanography: An Introduction*. Oxford: Pergamon Press.

UPWELLING ECOSYSTEMS

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Introduction

An ecosystem is a natural unit in which physical and biological processes interact to organize the flow of energy, mass, and information. The result of this self-organizing activity is that each kind of ecosystem has a characteristic trophic structure and material cycle, some degree of internal homogeneity, objectively definable boundaries, and predictable patterns of seasonality. Oceanic ecosystems are those ecosystems that exist in the open ocean independently of solid substrates; for example, oceanic ecosystems are fundamentally distinct from coral or intertidal ecosystems.

Upwelling ecosystems are those that occupy regions of the ocean where there is a persistent upward motion of sea water that transports subsurface water with increased inorganic plant nutrients into the sunlit surface layer. The upwelling water is not only rich in nutrients, but also frequently cooler than the surface water it replaces; this results in a variety of atmospheric changes, such as coastal deserts or arid zones. The increased nutrient supply and favorable light regime of upwelling ecosystems, however, distinguish them from other oceanic ecosystems and generate characteristic food webs that are both quantitatively and qualitatively different from those of other oceanic ecosystems.

For persistent upwelling to take place it is necessary for the surface layer to be displaced laterally in a process physical oceanographers call divergence and then for subsurface water to flow upward to replace the displaced water. The physical concept of upwelling is simple in principle but, as with many ocean processes, it becomes surprisingly complex when real examples are studied. To begin with, there are two fundamental kinds of upwelling ecosystems: coastal and oceanic. They differ in the nature of their divergence. In coastal upwelling, the surface layer diverges from the coastline and flows offshore in a shallow layer; subsurface water flows inshore toward the coast, up to the surface layer, then offshore in the surface divergence. In contrast, oceanic upwelling, which occurs in many regions of the ocean, depends on the divergence of one surface layer of water from another. One such oceanic divergence is created when an increasing gradient in wind strength forces one surface layer to move faster, thereby leaving behind, or diverging from, another surface layer. Major regions of this kind of oceanic upwelling are found in high latitudes in the Subpolar gyres of the Northern Hemisphere and the Antarctic divergence in the Southern Ocean. The food webs of polar upwelling ecosystems are described elsewhere in the Encyclopedia and this article will focus on coastal and equatorial upwelling ecosystems that occur in low and mid-latitude regions of the world's oceans.

The physical boundary organizing oceanic divergence in equatorial upwelling is the Coriolis force, which changes sign at the equator, causing the easterly Trade Winds to force a northward divergence north of the Equator and a southward divergence south of the Equator. Both coastal and equatorial upwelling ecosystems have been well studied in recent years, so they are among the best known of oceanic ecosystems. The physical processes of equatorial upwelling are described elsewhere in the Encyclopedia. This article describes the quantitative and qualitative character of the food webs of coastal upwelling ecosystems, focusing especially on how their physical forces and chemical conditions affect the way food webs pass organic material to higher trophic level organisms such as fish, birds, marine mammals, and humans.

Why Are Upwelling Ecosystem Food Webs different?

In low- and mid-latitude oceanic systems where there is annual net positive heat flux, warming of the surface layer produces a density barrier, the pycnocline, that prevents subsurface nutrient-rich water from mixing into the sunlit surface layer. The nutrient-depleted condition of these surface waters severely limits their annual quantity of new primary productivity, and the food webs of these stratified oceanic regions have low phytoplankton biomass, as shown especially clearly in satellite images of ocean color.

In the high-latitude polar regions where there is annual net negative heat flux, the surface waters cool, become unstable, and mix with the underlying nutrient-rich subsurface waters. The concentration of inorganic nutrients in well-mixed high-latitude waters is high during polar fall, winter, and spring during periods of strong winds, heat loss to the atmosphere, short day length, and low sun angle. But during periods of deep convective mixing the phytoplankton population may spend so much time below the euphotic zone that there is no net positive primary production. The primary producers under these conditions are said to be light-limited.

Upwelling is a circulation pattern that overrides both the nutrient limitation of stratified low- and mid-latitude waters and the light limitation of high-latitude polar waters. Upwelling ecosystem food webs are different from those of other oceanic ecosystems because (1) optimal conditions of nutrient supply are provided by the upward flow of cool, nutrient-rich subsurface water into the sunlit surface layer and (2) optimal light conditions are provided for maximal photosynthetic production of new organic matter in the divergent horizontal flow of upwelled water as it gains heat from the sun, producing a well-stabilized, stratified surface flow.

Optimal nutrient conditions are formally defined as having nutrient [$NO_3{}^-$, $PO_4{}^{3-}$, $Si(OH)_4$] concentrations well above those that saturate the phytoplankton cell's nutrient uptake mechanism; i.e., $[N] \gg K_s$, where [N] is nutrient concentration in mole units and K_s in one-half the concentration required for nutrient uptake saturation. Optimal light conditions are formally defined as having a level of irradiance, or photon flux density, in the upper waters that exceeds considerably the irradiance required to saturate the photosynthetic capacity of the phytoplankton assemblage; i.e., $[E] \gg K_E$ where [E] is irradiance in mol photons m^{-2} s^{-1} in surface waters and K_E is irradiance at saturation.

In coastal and equatorial upwelling ecosystems, optimal nutrient and light conditions for high primary production are maintained for several months or longer each year, and in low-latitude Trade Wind regions they persist for the entire year; therefore, the annual quantity of new organic matter generated by primary productivity is much higher in upwelling regions than in other oceanic ecosystems that are nutrient- or light-limited or dependent on one or two seasonal pulses of convective mixing.

The Physical Setting

Upwelling is a response of the ocean to wind-driven divergence of the surface layer. As the wind begins to blow across the surface of the ocean, a thin surface slab of water (25–50 m thick) is set in motion by friction of the wind (**Figure 1**). This wind-driven layer or Ekman layer (named for the Swedish oceanographer who in 1905 worked out how wind drives ocean currents), as a result of the Coriolis force, has a net movement 90° to the right (left) of the wind in the Northern (Southern) Hemisphere. Four of the major coastal upwelling systems are located in the eastern boundary of the ocean basins along the west coasts of the continents where equatorward winds are part of stationary or seasonal mid-ocean high-pressure systems. These four coastal upwelling regions off the west coasts of North America, South America, north-west Africa, and south-west Africa are in the four great eastern boundary current systems, the California Current, Peru Current System, Canary Current, and Benguela Current. The fifth major coastal upwelling region is in a western boundary current, the Somali Current, where strong summer monsoon winds blowing along the coast of the Arabian peninsula set in motion a north-east flow that then diverges from the coast due to Coriolis deflection to the right in the Northern Hemisphere. In all five regions winds blow parallel to the coast for a long enough period

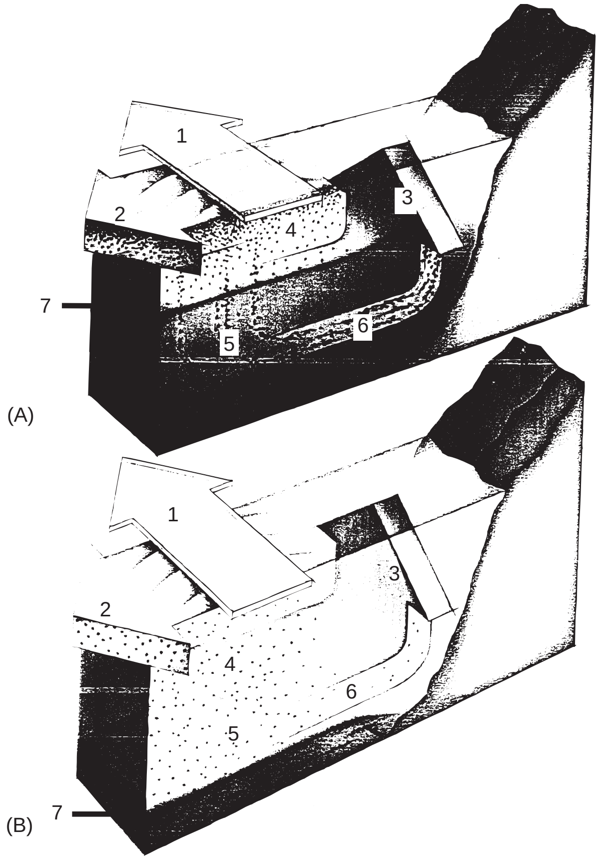

Figure 1 Conceptual diagram of the coastal upwelling ecosystem during (A) normal (cool) conditions and (B) El Niño (warm) conditions. (1) is the alongshore wind blowing toward the Equator; (2) is the wind-driven net offshore surface layer, called the Ekman layer, whose direction of flow is 90° to the left of the wind direction in the Southern Hemisphere because of the Coriolis force; (3) is the upwelling that replaces the water moved offshore in (2); (4) is the euphotic zone where productivity is high relative to other oceanic ecosystems and where high-density blooms of large diatoms accumulate; (5) is the downward flux of ungrazed diatoms and other components of the food web, such as macrozooplankton and fish eggs and larvae; (6) is the subsurface (40–80 m) onshore flow of nutrient-rich water (shown in darker shading) that feeds into the upwelling and recycles material and organisms that sink out of the Ekman layer; (7) is the thermocline and nutricline that separate cool, nutrient-rich subsurface water from the surface layer of warm and nutrient-depleted water. This is an original figure designed by RT Barber in 1983.

of time (months) and over a sufficiently large length of coastline to develop a distinct coastal upwelling ecosystem.

Coastal upwelling is a mesoscale (10–100 km) physical response to a large-scale coastal wind field. The major zone of upwelling is relatively small, extending offshore only 25–50 km from the coast, and the water upwelling to the surface layer is coming from a relatively shallow depth of 40–80 m or just below the pycnocline. Because of a basin-wide tilt in the east/west direction, the pycnocline in the eastern boundary current regions is shallower than in other regions of the ocean basin, making nutrient-rich sub-pycnocline water readily available for entrainment into the upwelling circulation.

The Chemical Environment

The *sine qua non* of coastal upwelling is high concentrations of the new inorganic plant nutrients nitrate ($NO_3{}^-$), phosphate ($PO_4{}^{3-}$), and silicate or silicic acid ($Si[OH]_4$) that are well in excess of the half-saturation concentrations for nutrient uptake. Typical concentrations are as high as 15–20 $\mu mol\,l^{-1}$ of NO_3, with the other macronutrients occurring in appropriate proportional concentrations according to the Redfield ratio. The highest nutrient concentrations and lowest water temperatures are inshore in the most recently upwelled water; there is frequently a strong offshore spatial gradient in nutrient concentration, but the spatial domains of the five great coastal upwelling ecosystems vary remarkably. In the Peruvian upwelling near 15°S latitude the onshore/offshore gradients are steep, with nitrate concentrations decreasing from 20 to 2 $\mu mol\,l^{-1}$ in an offshore distance $\leqslant 50$ km; in the Somali Current off the coast of Oman the initial inshore concentrations are lower, about 10 $\mu mol\,l^{-1}$, but remain elevated for 500–700 km offshore.

The supply of new nutrients advected into the euphotic zone sets up the highly productive character of upwelling ecosystems, but nutrients regenerated or recycled in the euphotic zone are also unusually abundant in coastal upwelling. High-productivity fuels increased heterotrophic consumption by protozoans, crustaceans, and vertebrates, and these consumers, along with heterotrophic bacteria, bring about increased regeneration of nutrients. Regeneration of nutrients from particulate organic matter that sinks out of the offshore surface flow and into the subsurface inshore flow results in nutrient ‘trapping’ that maintains elevated nutrient concentrations in bottom waters of the continental shelf. These regenerated nutrients, together with short-term storage of regenerated nutrients in surficial sediments beneath the upwelling circulation, provide a flywheel to the nutrient supply process that dampens variations in the wind-driven vertical transport of new nutrients from deep water.

An additional important chemical consequence of trapping by the two-layered partitioning of organic particles in coastal upwelling is the generation of zones of intense oxygen depletion. The great oxygen minimum zones of the four eastern boundary currents and the Somali Current are fueled by enhanced productivity in the narrow coastal upwelling zone. In addition to water column oxygen depletion, shelf and slope sediments under coastal upwelling are frequently anoxic and colonized by large anaerobic bacterial mats. These benthic hypoxic and anoxic zones are two sites of intense denitrification, a microbial process by which nitrate is converted to nitrogen gas. Occasionally, oceanographers have found complete denitrification in a midwater anoxic layer beneath upwelling systems; these processes of benthic and water column denitrification may be a major global feedback mechanism involved in the regulation of fixed, or biologically available, nitrogen.

Another important chemical consequence of the reducing conditions generated in anoxic and hypoxic sediments beneath coastal upwelling involves the cycling of iron. Iron is an essential micronutrient for the maintenance of high rates of primary productivity. Studies in the coastal upwelling ecosystem of the California Current System showed that resuspension and dissolution of iron from sediments generated enhanced concentrations of iron in the bottom boundary currents. Subsequent upwelling of this subsurface water during episodes of strong upwelling resulted in elevated iron concentrations in the euphotic layer. Particle sedimentation to anoxic or hypoxic sediments followed by resuspension and dissolution is a positive feedback that enhances the productive potential of coastal upwelling, especially compared to open ocean equatorial upwelling.

A Milestone in Quantifying Food Web Function

The basic food webs of upwelling ecosystems differ in both quantity and quality from those of other oceanic ecosystems. A milestone in understanding these differences was made by John Ryther, who in 1969 provided a quantitative explanation of why fish yields vary by about 200-fold from the richest coastal upwelling ecosystems to the poorest ocean gyres. Variations in productivity are, of course, well known from terrestrial ecosystems, but on land a lack of water from either aridity in deserts or freezing in polar regions is responsible for the productive poverty of the poorest regions. Understanding why the food web of the benign low-latitude gyre ecosystem was so poor in fish production was much more difficult. Part of the explanation was proposed in 1955 by Sverdrup who stated simply that reduced physical supply of nutrients to the euphotic zone is the reason for the low productivity, biomass, and fish yields of stratified oceanic gyre ecosystems. Ryther amplified this simple physical explanation by considering, along with the physics and chemistry, the biological properties of the food web that lead to fish production.

First, Ryther estimated that about half the fish caught in the world are caught in coastal upwelling ecosystems, the smallest of the ocean ecosystems. Why? To begin, Sverdrup was correct: the physical processes of upwelling and subsequent stratification provide optimal nutrients and light to support high primary productivity. However, more is involved. The phytoplankton, especially diatoms, that thrive in coastal upwelling are large – so large that some portion of the diatoms can be eaten directly by fish or other large grazers such as euphausids. This means that in coastal upwelling the food web leading to fish is often very short, involving only one, or at most two, trophic transfers. Ryther estimated that in the Peru upwelling ecosystem half of the diet of the small pelagic clupeid fish such as anchovies is phytoplankton and the other half is composed of crustacean zooplankton such as euphausids. On average, then, the length of the food web from primary producers to fish had 1.5 transfers: large diatoms to anchovies, or large diatoms to euphausids to larger fish such as mackerel. At each ecological transfer, a large portion (80–90%) of the energy of the food is used to support the organism and that portion cannot be passed up the food web. Ryther also noted that in the phytoplankton-rich waters of the spatially small coastal upwelling regions, grazers do not have to work so hard to get food; therefore, the efficiency of transfer through the food web is increased relative to that of a poor environment such as the low-latitude gyre, where grazers have to cover larger distances and filter large volumes of water to get adequate food. Ryther proposed that fish yields are high in the coastal upwelling ecosystem because of (1) high initial primary productivity, (2) large phytoplankton that can be grazed directly, (3) short food webs with few transfers, and finally, (4) increased efficiency at each transfer. These effects multiply and lead to high yields of fish that are 200 times the yield of gyre ecosystems. These high yields are exploited by seabirds, marine mammals and, of course, humans.

Food Web Structure and Function

Coastal upwelling ecosystems are typically dominated by chain-forming and colonial diatoms with individual cell diameters of 5–30 μm. The growth rates of these large cells are surprisingly as fast as those of the much smaller autotrophic pico- and nanoplankton that are the basis of the microbial loop. The larger diatoms are more effective than pico- or nanoplankton at taking up high concentrations of new nutrients; this property, together with their more favorable photosynthesis/respiration ratio, makes diatoms considerably more efficient at new production.

New production uses nutrients carried into the system by upwelling, while regenerated production is based on nutrients recycled in the euphotic zone. The *f*-ratio measures the proportion of new production; *f*-ratios of coastal upwelling are as high as any in the oceans, with values ranging from 0.3 to 0.8 and 0.5 being a representative value. Primary productivity values in the most productive portion of the upwelling ecosystem range from 1.0 to $6.0\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$. Representative inshore values for the California Current System are 1.0–$3.0\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$; for the Peru Current System 2.0–$6.0\,\mathrm{mg\,C\,m^{-2}\,d^{-1}}$; for the Canary Current 1.0–$3.0\,\mathrm{mg\ C\ m^{-2}\ d^{-1}}$; and for the Somali Current 1.0–$2.0\,\mathrm{mg\ C\,m^{-2}\,d^{-1}}$. High *f*-ratios and high primary productivity indicate that more organic material can be exported via the food web to higher trophic levels such as fish, birds, and marine mammals or exported vertically as particle flux to deep water or sediments.

A second element in Ryther's hypothesis was that large diatoms could be grazed directly by clupeid fishes. Why are the phytoplankton in coastal upwelling large? One explanation comes from a model study of diatom sinking and circulation in the Peruvian upwelling region. Small phytoplankton that sank slowly or maintained themselves in the euphotic zone were consistently carried in the surface Ekman layer to the oligotrophic offshore waters; large diatoms that sank rapidly fell into the subsurface onshore circulation and were carried back into the upwelling cycle (**Figure 1A**). Large size that confers fast sinking is an adaptation that keeps diatoms in the highly productive upwelling habitat for several growth cycles. In addition, newly upwelled water contains large numbers of diatom resting spores, indicating that diatoms sink to sediment, remain there in a resting stage, then become resuspended and transported into the euphotic zone by episodes of strong upwelling. Large size confers rapid sinking, which enhances both recirculation and resuspension, but it also makes the large diatoms efficient prey for fish and large zooplankton like euphausids.

The biomass of larger phytoplankton such as diatoms is more variable in time and space than the biomass of pico- and nanophytoplankton. The abundance of small phytoplankton is efficiently controlled by their fast-growing protozoan microzooplankton grazers. The micrograzers can grow as rapidly as their prey, so there is no opportunity for uncoupling of prey and predator abundance; pico- and nanoplankton, therefore, rarely form blooms. In contrast, diatoms are grazed by larger organisms with longer reproductive cycles, such as clupeid fish with a 1-year cycle or copepods and euphausids with a cycle of 10–40 days or longer. Clearly, the zooplankton or fish cannot reproduce fast enough to keep up their abundance in pace with a diatom bloom; at times, therefore, large diatoms can accumulate in dense blooms with low initial grazing losses. While fish and zooplankton cannot match growth rates with diatoms, they do have mobility and behavior that enable them to find and move into patches of abundant food. In practice, however, coupling of the growth rates of diatoms and their animal grazers frequently breaks down, and when this happens high biomass blooms become evident in the ocean color satellite images in upwelling regions.

Phytoplankton cells, especially large cells that are not grazed or consumed by heterotrophic microorganisms, rapidly sink out of the water column when ungrazed biomass accumulates in a dense bloom (**Figure 1A**). If nutrients are depleted by the high-biomass bloom, phytoplankton lose the ability to regulate their buoyancy and sink rapidly at rates as high as $100\,\mathrm{m\,d^{-1}}$. Sediments under coastal upwelling ecosystems are characterized by the highest rate of organic deposition found in the ocean. These high deposition rates indicate that the large diatom/large grazer food path is relatively more important to the throughput of material than the microbial or picophytoplankton/nanophytoplankton/protozoan grazer path. The microbial path is always present in the two-path upwelling food web and it does increase in absolute productivity during increased upwelling; however, the huge increase in biomass and productivity of the large diatom/large grazer food path dominates export of new organic material. The large diatom food path does not replace the picophytoplankton/nanophytoplankton path, but it becomes so numerically overwhelming that it appears as though there is a shift in the character of the food web.

In coastal upwelling ecosystems there is enough time and space constancy in the physical response that macrozooplankton and shoaling pelagic fish have been able to evolve adaptations that enable them to exploit this rich but small habitat, and these adaptations affect the efficiency of transfer of primary production to higher trophic levels.

Zooplankton such as copepods and euphausids have limited ability to swim against onshore–offshore currents, but they have considerable ability to migrate up and down rapidly. Some upwelling zooplankton species have evolved behavior that causes them, when saturated with food in the offshore flow, to migrate down into the onshore flow, which then carries them back into the upwelling circulation for another cycle. Other species remain in the food-rich habitat by having eggs or juvenile life stages that sink into the subsurface onshore flow. The adaptations of macrozooplankton to the physics of upwelling are remarkable examples of how the evolution of upwelling organisms differs from the evolution of organisms of other oceanic ecosystems. Parallel adaptations are present in the shoaling pelagic fish that dominate the fish biomass of coastal upwelling ecosystems. These behavioral adaptations have optimized feeding, reproduction, and growth for the sardines, anchovies, and mackerel that make up the bulk of the fish harvested from coastal upwelling ecosystems.

Climatic Forcing and Food Web Responses

Adaptations to the specific upwelling circulation pattern confer great fitness advantage to phytoplankton, zooplankton, fish, birds, and marine mammals when the upwelling pattern is prevalent, but the coastal upwelling ecosystems are buffeted by strong interannual and interdecadal climate variability. The El Niño–Southern Oscillation (ENSO) phenomenon is the best-known example of large-scale, climate-driven biological variability. El Niño is defined by the appearance and persistence, for 6–18 months, of anomalously warm water in the coastal and equatorial ocean off Peru and Ecuador. The anomalous ocean conditions of El Niño are accompanied by large reductions of plankton, fish, and sea birds in the normally rich upwelling region. To understand how this climate variability causes these large decreases in abundance, consider how El Niño temporarily alters the physical pattern of the upwelling circulation. One discovery of recent decades is that during El Niño events the coastal winds that drive coastal upwelling do not stop entirely (**Figure 1B**). In fact, coastal winds sometimes intensify during El Niño because of increased thermal differences between land and sea. Therefore, coastal upwelling as a physical process continues, but because the ENSO process has depressed the thermocline and nutricline to a depth below the depth at which water is entrained into the upwelling circulation (40–80 m), the water upwelled is warm and low in nutrients. As a result, during El Niño the upwelling circulation transports only warm, nutrient-depleted water to the surface layer. The physics of upwelling continues, but the chemistry of upwelling stops very dramatically.

This conceptual model of El Niño forcing and food web response, shown in **Figure 1B**, indicates that El Niño affects the upwelling ecosystem by decreasing the nutrients supplied to the euphotic layer, which causes primary production to decrease proportionally. In this manner the supply of nutrients is reduced as El Niño strengthens in intensity, and the decrease in new primary production available to fuel the food web causes proportional reductions in the growth and reproductive success of fish, birds, and marine mammals. Obviously, temperature, nutrients, primary productivity and higher trophic level productivity are tightly linked in coastal upwelling ecosystems, but by far the most dramatic link is the climate variability/fish variability link. That is, the most impressive biological consequence of El Niño is its effect on the abundance and catch of Peruvian anchovy (*Engraulis ringens*), the basis of the world's largest single-species fishery. **Figure 2** shows the covariation of thermal conditions and anchovy harvest from the 1950s to the present. This relationship is causal in the sense that temperature is a proxy for nutrients, and nutrient decreases (temperature increases) are always accompanied by reduction in the productivity of the food web including the catch of anchovies. Note that the temperature/nutrient variability works in both directions. Each local minimum in catch is associated with a warm anomaly and each local maximum is associated with cool, nutrient-rich conditions. The period of very low catch from 1976 to 1985 is often cited as an example of the destruction of a fishery by overfishing, but **Figure 2** indicates that the anchovy stock failed to recover from 1972 and 1976 El Niño events because there was little upwelling of cool, nutrient-rich waters during that decade. The coastal winds were normal or even stronger than normal during this decade, but the increased heat storage in the upper ocean apparently kept the thermocline and nutricline anomalously deep from 1976 to 1985.

The extreme variability of anchovy abundance sends shock waves into the global economy, because fishmeal from upwelling ecosystems is a commodity that is necessary for a variety of animal production processes. The social hardship of this climate-driven variability affects many people, but the upwelling ecosystem is not in the least damaged by ENSO variability. The food web has evolved to exploit the

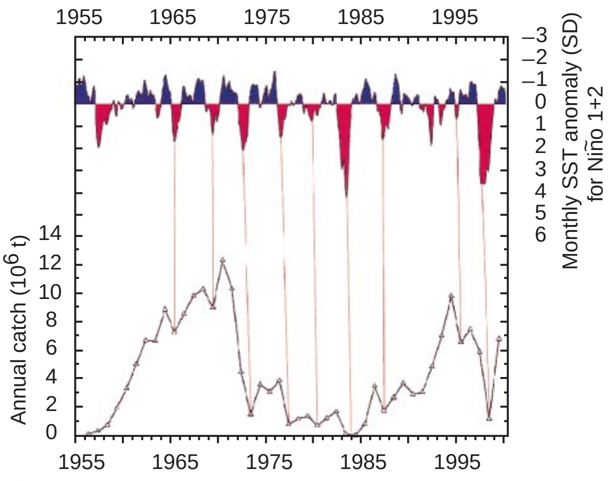

Figure 2 The association of sea surface temperature (SST) anomaly along the coast of Peru and Ecuador with the annual catch of Peruvian anchovy, showing that each minimum of catch is associated with a period of anomalously warm water. Note that the SST anomaly scale is inverted, with red showing the warm anomalies. The anomaly is calculated from SST in the Peru coastal area (Niño 1) and the eastern equatorial Pacific (Niño 2). Warmer water at the sea surface means that warmer water is being entrained into the upwelling cell because the thermocline has deepened owing to large-scale, basin-wide responses to changes in Trade Winds. The nutricline also deepens, so that the warmer water is also lower in nutrient concentration. Temperature is a proxy in this figure for nutrient concentration. The close association of SST anomaly and anchovy catch suggests that natural thermal and nutrient variability, not overfishing, is the process controlling the interannual variability of this particular fish stock.

productive phase of the ENSO cycle and persist through the unproductive phase. **Figure 2** shows that as long as a period of cool, high-nutrient conditions follows the warm event, the coastal upwelling system recovers to its previous high productivity. The climate process that appears to have the potential to alter or disrupt this ecosystem is the lower-frequency, decadal anomaly that prevailed from 1976 to 1985 and again in the mid-1990s. A decadal anomaly that causes relative nutrient poverty appears to have greater long-term food web consequences than short periods of extreme nutrient depletion during El Niño events.

How is the character of the coastal upwelling ecosystem altered during a strong El Niño? When the group of equatorially and coastally trapped waves excited during onset of an ENSO event forces the nutricline below the depth where upwelling entrains water, the coastal system rapidly develops a typical assemblage of tropical plankton. Dense blooms of diatoms are missing, but the tropical pico- and nanophytoplankton-based food web is healthy and has productivity levels typical of tropical waters. The diversity of phytoplankton, zooplankton, and fish is high – as would be expected in tropical waters. The response of the upwelling food web to climate variability emphasizes the resilience of oceanic ecosystems to strong transient perturbations; their resilience to the effects of persistent change, however, is unknown.

Glossary

Antarctic divergence The zone of upwelling driven by the Antarctic Circumpolar Current (ACC).

Convective mixing Vertical mixing produced by the increasing density of a fluid in the upper layer, especially during winter in temperate and polar regions.

Denitrification A microbial process that takes place under anoxic conditions, converting nitrate to N_2 gas.

Diatom A taxonomic group of phytoplankton that are nonmotile, have silicon frustules, and are capable of rapid growth.

Ecosystem A natural unit in which physical and biological processes interact to organize the flow of energy, mass, and information.

Ekman layer The surface layer of the ocean that responds directly to the wind.

Euphotic zone The surface layer of the ocean where there is adequate sunlight for net positive photosynthesis.

Nutrients Dissolved mineral salts necessary for primary productivity and phytoplankton growth; macronutrients are phosphate, nitrate, and silicate; micronutrients are iron, zinc, manganese, and other trace metals.

Oxygen minimum zone A mid-water layer along the eastern boundary regions of the oceans in which oxygen concentrations are significantly reduced relative to the layers above and below it.

Phytoplankton Photosynthetic single-called plants or bacteria that drift with ocean currents and are the major primary producers for oceanic food webs; very small phytoplankton are called picoplankton and small phytoplankton are called nanoplankton; all of these are $< 2\,\mu m$ in diameter.

Primary productivity The use of chemical or radiant energy to synthesize new organic matter from inorganic precursors.

Pycnocline The layer where density changes most rapidly with depth and separates the surface mixed layer from deeper ocean waters.

Southern Ocean The circumpolar ocean in the Southern Hemisphere between the Subtropical Front and the continent of Antarctica.

Stratification The formation of distinct layers with different densities (see 'pycnocline' above); stratification inhibits mixing or exchange between the nutrient-rich deeper water and the sunlit surface layer.

Subpolar gyres Large cyclonic water masses in the Northern Hemisphere between the subtropical front and the polar front.

Tropical Pertaining to the regions that, under the influence of the Trade Winds, are permanently stratified.

Upwelling Upward vertical movement of water into the surface mixed layer produced by divergence of the surface waters.

Zooplankton Animals that float or drift with ocean currents; microzooplankton are protozoan plankton that graze on small phytoplankton; mesozooplankton are crustaceans that graze on larger phytoplankton such as diatoms.

See also

Antarctic Circumpolar Current. California and Alaska Currents. Canary and Portugal Currents. Ekman Transport and Pumping. El Niño Southern Oscillation (ENSO). El Niño Southern Oscillation (ENSO) Models. Fisheries and Climate. Iron Fertilization. Microbial Loops. Network Analysis of Food Webs. Nitrogen Cycle. Ocean Color from Satellites. Ocean Gyre Ecosystems. Pacific Ocean Equatorial Currents. Pelagic Biogeography. Pelagic Fishes. Plankton. Plankton and Climate. Polar Ecosystems. Primary Production Distribution. Primary Production Processes. Redfield Ratio. Small Pelagic Species Fisheries. Somali Current.

Further Reading

Bakun A (1990) Global climate change and intensification of coastal ocean upwelling. *Science* 247: 198–201.

Barber RT and Chavez FP (1983) Biological consequences of El Niño. *Science* 222: 1203–1210.

Barber RT and Smith RL (1981) Coastal upwelling ecosystems. In: Longhurst A (ed.) *Analysis of Marine Ecosystems*, pp. 31–68. New York: Academic Press.

Longhurst A (1998) *Ecological Geography of the Sea*. San Diego: Academic Press.

Pauly D and Christensen V (1995) Primary production required to sustain global fisheries. *Nature* 374: 255–257.

Richards FA (ed.) (1981) *Coastal Upwelling*. Washington, DC: American Geophysical Union.

Ryther JH (1969) Photosynthesis and fish production in the sea. *Science* 166: 72–76.

Smith RL (1992) Coastal upwelling in the modern ocean. In: Summerhayes CP, Prell WL and Emeis K-C (eds) *Upwelling Systems: Evolution Since the Early Miocene*, Geological Society Special Publication 64, pp. 9–28. London: The Geological Society.

Summerhayes CP, Emeis, K-C, Angel MV, Smith RL and Zeitschel B (eds) *Upwelling in the Ocean Modern Processes and Ancient Records*. Chichester: Wiley.

Sverdrup HU (1955) The place of physical oceanography in oceanographic research. *Journal of Marine Research* 14: 287.

URANIUM–THORIUM DECAY SERIES IN THE OCEANS OVERVIEW

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Introduction

Natural radioactivity provides tracers in a wide range of characteristic timescales and reactivities, which can be used as tools to study the rate of reaction and transport processes in the ocean. Apart from cosmogenic nuclides and the long-lived radioisotope K-40, the natural radioactivity in the ocean is primarily derived from the decay series of three radionuclides that were produced in the period of nucleosynthesis preceding the birth of our solar system: Uranium-238, Thorium-232, and Uranium-235 (a fourth series, including Uranium-233, has already decayed away). The remaining activity of these so-called primordial nuclides in the Earth's crust, and the range of half-lives and reactivities of the elements in their decay schemes, control the present distribution of U-series nuclides in the ocean.

The Distribution of Radionuclides of the Uranium Thorium Series in the Ocean

Distribution of ^{238}U, ^{235}U, ^{234}U, and ^{232}Th (*see* Uranium–Thorium Series Isotopes in Ocean Profiles)

Uranium is supplied to the ocean by rivers. In sea water it is stabilized by a strong complexation as