

technique could work. However, to advance the state of the art to a degree of sophistication and accuracy required for global change research, many improvements in satellite sensor technology, atmospheric and oceanic radiative transfer modeling, field observation methodologies, calibration metrology, and other areas have been necessary and are continuing to evolve. As these develop, new products and applications will become feasible. It is the intention of the international ocean science community, working with the various space agencies, to develop a continuous long-term global-time series of highly accurate and well-documented satellite ocean color observations which will enable periodic reprocessing of the time series and an unambiguous interpretation of the results.

See also

Aircraft Remote Sensing. Bio-optical Models. Carbon Cycle. El Niño Southern Oscillation (ENSO). Inherent Optical Properties and Irradiance. Iron Fertilization. Large Marine Ecosystems. Ocean Color from Satellites. Ocean Gyre Ecosystems. Pacific Ocean Equatorial Currents. Patch Dynamics. Pelagic Biogeography. Penetrating Shortwave Radiation. Phytoplankton Blooms. Plankton and Climate. Radiative Transfer in the Ocean. Satellite Oceanography, History and Introductory Concepts. Satellite Remote Sensing of Sea Surface Temperatures. Upper Ocean Time and Space Variability. Upwelling Ecosystems.

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OCEAN GYRE ECOSYSTEMS

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The Generalized Open-Ocean Food Web

Food webs, simply put, describe all of the trophic relationships and energy flow between and among the component species of a community or ecosystem. A food chain depicts a single pathway up the food web. The first trophic level of a simple food chain in the open ocean begins with the phytoplankton, the autotrophic primary producers, which build organic materials from inorganic elements. Herbivorous zooplankton that feed directly on the

phytoplankton are the primary consumers and make up the second trophic level. Subsequent trophic levels are formed by the carnivorous species of zooplankton that feed on herbivorous species and by the carnivores that feed on smaller carnivores, and so on up to the highest trophic level occupied by those adult animals that have no predators of their own other than humans; these top-level predators may include sharks, fish, squid, and mammals.

In ocean gyres, the dominant phytoplankton, especially in oligotrophic waters, are composed of very small forms, marine protozoans such as zooflagellates and ciliates become important intermediary links, and the food chain is lengthened. There are thus typically about five or six trophic levels in these ecosystems. In contrast, large diatoms dominate in nutrient-rich upwelling regions, resulting in shorter food chains of three or four trophic levels since large zooplankton or fish can feed directly on

the larger primary producers. Production of larger flagellates/diatoms in specialized habitats of the open ocean may lead to shortened energy paths. As there are seldom simple linear food chains in the sea, a food web with multiple and shifting interactions between the organisms involved portrays more accurately the trophic dynamics of a given ecosystem. Examples of food webs are presented for the North Pacific Subarctic and Subtropical gyres in Figures 1 and 2, respectively. The place a particular species occupies in the ecosystem food web is not necessarily constant, since feeding requirements change as organisms grow. Some species change diets (and trophic levels) as they grow or as the relative abundance and availability of different food items change. In some species, cannibalism of their own young may be important.

Before proceeding, we need to recognize that in ocean gyre ecosystems, very large percentages of organic matter are cycled through microbes before entering the linear arrangement of the classic food web. The role of viruses, bacteria, heterotrophic nanoflagellates, nano- and microplanktonic protozoans, and the microbial loop in the open ocean ecosystem is discussed in detail elsewhere in the Encyclopedia and we only note here that if several

trophic steps are involved in a microbial food web, there must be a significant loss of carbon at each transfer and therefore little transfer of carbon from microbial to classic planktonic food webs.

The Ocean Gyre Ecosystem

In each of the major ocean basins, surface winds drive currents that form the large anticyclonic subtropical gyres as well as the smaller, cyclonic subarctic gyres. The details of both vertical structure and trophic links in the ocean gyre food web differ regionally and seasonally; opportunism is generally the rule of prey selection and is driven by regional and seasonal differences in vertical physical structure of the upper water column.

The surface waters in the warm subtropical gyres away from seasonal meridional frontal systems tend to be highly stratified, with a permanent thermocline that limits vertical enrichment of the euphotic zone throughout the year. In this nutrient depleted environment, recycled nitrogen (primarily in the form of ammonia and urea) excreted by the zooplankton or released by the microbial community provides the primary nitrogen for a continued low level of phytoplankton 'regenerated' production that

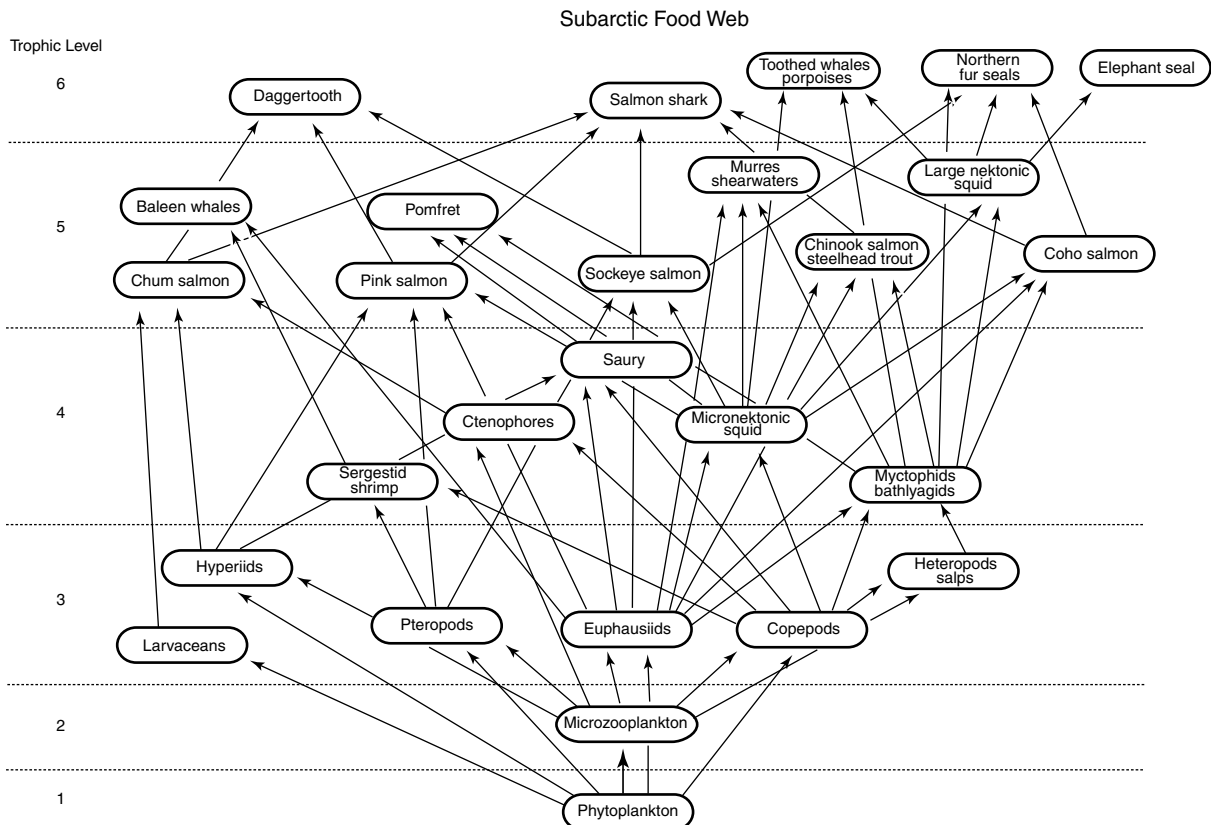


Figure 1 Food web of the Subarctic North Pacific oceanic ecosystem; arrows point in the direction of energy flow. (Adapted from Brodeur *et al.* (1999).)

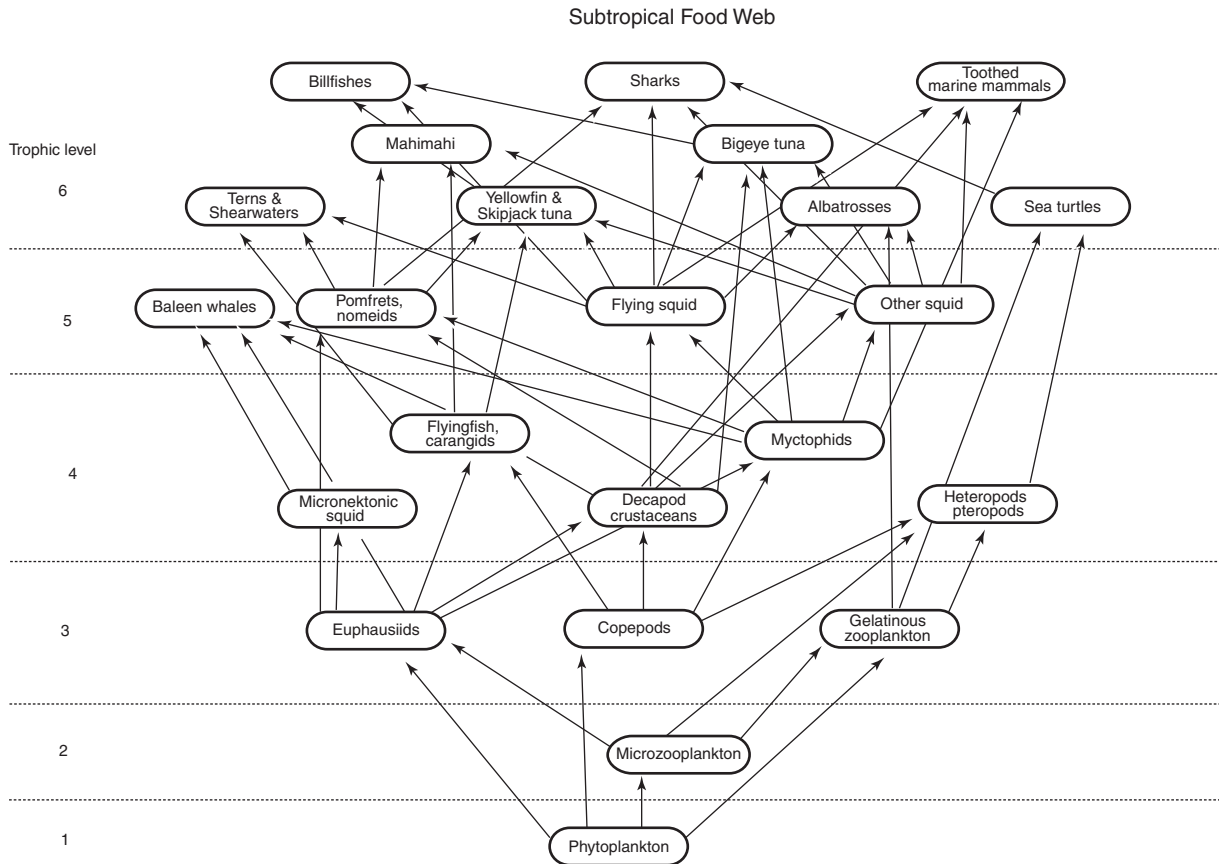


Figure 2 Food web of the Subtropical North Pacific oceanic ecosystem; arrows point in the direction of energy flow.

remains in approximate balance by zooplankton grazing. These oligotrophic waters are characteristically recognized as some of the least productive waters in the world's oceans. Alternatively, 'new' primary production based on the input of new nitrogen (primarily nitrate) into the euphotic zone occurs at much lower levels through oceanographic physical forcing, atmospheric input, or nitrogen fixation. As in most other ocean systems, a deep chlorophyll maximum (DCM) is present, but this will vary spatially and temporally with consequent changes in the depth of the thermocline, nutrient flux, and the maximum primary production rate.

In contrast, subarctic oceans benefit from alternating periods of summer stratification and winter mixing, so that there is a seasonal injection of nutrients into surface waters. In the North Atlantic the trophic framework is set up by the classic temperate bloom cycle; i.e., a 'spring bloom' followed by a 'crash', a 'stable state summer equilibrium', a smaller 'fall bloom', and a 'winter decline'. Winter storms create deeper well-mixed conditions including the presence of high nitrate levels. With the onset of spring comes an increase in solar irradiation and water column stability. Phytoplankton

(normally diatoms) 'blooms' with nutrient injection. Slightly lagging behind the phytoplankton bloom is a bloom of zooplankton that feeds on the increased phytoplankton. As the increased phytoplankton population exhausts the nitrate supply and zooplankton grazing overshoots phytoplankton growth, a 'crash' occurs, returning nitrate, phytoplankton, and zooplankton to low, stable levels. During the summer months, water is well stratified with balanced processes (i.e., phytoplankton growth (limited by lower levels of available nitrate) is balanced by zooplankton grazing). During fall, early episodic storms induce some mixing and hence phytoplankton blooms followed by periods of stability. The onset of increased winter storm activity mixes nutrients in surface waters; however, available light energy decreases, limiting phytoplankton production. Thus the low phytoplankton production periods are light limited during the winter and nutrient-limited during the summer.

In the subarctic North Pacific there is virtually no bloom, diatoms populations are low, and high abundances of microzooplankton graze the small phytoplankton, keeping the abundance down. The subarctic North Pacific waters are thus high in

nutrients (nitrogen) but low in chlorophyll (HNLC), similar to those ecosystems found near the equator and in the Antarctic. Modest winter mixing in the subarctic Pacific results in a more favorable light regime and a continued modest level of biological production throughout the year and reduced biomass accumulation that is less strongly pulsed than that occurring in the Atlantic. The constant planktonic biomass in the Pacific favors pelagic fish production in contrast to the Atlantic, where much of the plankton biomass is lost to sinking without being grazed, thereby supporting more benthic resources.

The Intermediate Trophic Levels

The animals occupying the intermediate trophic levels that link the primary producers and consumers with the top of the food web include all of the zooplankton and micronekton (smaller organisms 10–100 cm in length) large enough to swim in inertial conditions. Two groups of animals in particular play a key role in the ocean gyre food web: those that compose the vertically migrating deep scattering layer (DSL) and the small pelagic ‘forage fishes’.

As night approaches, myriads of animals make an ascent from various depths to grazing or hunting grounds near the surface. Before daybreak, the DSL organisms descend back to their deeper, daytime residence. These migrations range 200–700 m in vertical extent and are confined to the epipelagic and mesopelagic zones. With the diel DSL migration, concentrations of food near the surface are much greater (a hundredfold increase in population numbers) at night than during day, establishing a forage base for larger, aggressive, nocturnally active carnivores; e.g., dolphins and pelagic squid. In the tropics, large filter-feeding organisms such as whale sharks, baleen whales, and megamouth sharks probably also utilize these high-density layers of plankton and micronekton. Diel vertical movements of bigeye tuna (*Thunnus obesus*) exhibit high correlation with the migration of the DSL and their associated prey species. The DSL micronekton, which includes fishes (e.g., myctophids, gonostomids), squid, and crustaceans (especially euphausiids and sergestid shrimps) are likely the primary zooplanktivores in the open ocean.

A large component of the DSL faunal composition is the gelatinous zooplankton (combjellies, pelagic tunicates, medusae, ctenophores, siphonophores, etc.). Despite their ubiquitous and abundant nature, the significance of these zooplankton in the pelagic food web has been and still is somewhat equivocal. These gelatinous animals had been thought to represent an ecological dead end. Because

of their low food value, energy taken up through their phytoplankton grazing was not passed up to higher trophic levels. From the growing list of fish, sea turtle, and seabird species identified as habitually feeding on gelatinous prey, there is strong evidence that this resource plays more of a key role in the gyre food web than previously believed.

In the open ocean, small pelagic ‘forage fishes’ are the keystone prey species among apex predators. By definition, forage fishes are ‘... abundant, schooling fishes (and squid) preyed upon by many species of seabirds, marine mammals, and other fish species’ according to A. M. Springer and S. G. Speckman. These animals are generally short-lived, highly fecund, and heavily preyed on as juveniles as well as adults. In the subtropical gyre, loose aggregations of flying squid, pomfret, saury, or mackerel, and in temperate waters tighter schools of anchovies, sardines, or herring, are representative of this guild. From a trophic standpoint, the importance of pelagic ommastrephid squids in the gyre ecosystems cannot be understated. These forage animals have rapid population turnover rates and can dominate the epipelagic nektonic biomass, as is the case with the red flying squid *Ommastrephes bartramii* at the summer Subarctic Boundary. Throughout the gyre food webs, ommastrephids often dominate the diets of toothed cetaceans, pinnipeds, fishes, and seabirds, as well as of tropical seabirds and marine mammals.

The Higher Trophic Levels

The faunal compositions of epipelagic nekton communities tend to be more diverse and more complex in the subtropics than those found in the temperate subarctic. At the top levels of the epipelagic (0–400 m) food web (and particularly within the 0–100 m euphotic zone) are the fast-swimming predators such as sharks, billfishes, and large tunas as well as some of the marine mammals and surface-feeding seabirds that feed at the fourth and fifth trophic levels. Generally, most of these breed in warmer tropical fall/winter waters, some seabirds notwithstanding, but make major excursions to the northern subtropics–subarctic during spring/summer to feed; all are opportunistic predators within their respective niches.

Large pelagic fishes are the most abundant and diversified of the apex predators but are nevertheless still highly dispersed, with typical population densities of only one fish per square kilometer integrated over the upper mixed layer. Blue sharks (*Prionace glauca*) are by far the most abundant shark species in the ocean gyres and in subtropical waters; frequent encounters with fishing gear make them seem

ubiquitous. Dominant prey items for blue shark include the abundant ommastrephid squids and forage fishes. Billfishes, including the marlins (*Makaira* spp. and *Tetrapturus* spp.) and swordfish (*Xiphias gladius*), are capable of extensive vertical excursions of several hundred meters but concentrate feeding at the surface on smaller fishes and, in the case of swordfish, exhibit a particular predilection for pelagic squid. Tunas (Scombridae) are diurnal predators and feed from the surface down to about 400 m. With the exception of bigeye tuna, tunas feed almost solely on small surface dwelling fauna – i.e., they rarely feed on the vertically migrating DSL. Juvenile and postlarval crustaceans, cephalopods, and oceanic- (Bramidae, Nomeidae, etc.) and shore-fishes (Mullidae, Chaetodontidae, etc.) dominate the tuna diet. Insular-based prey are likely artifacts of the inherent bias introduced from land-based fishing operations that underlie our present perception of oceanic predatory fish diets; these diminish in importance to the food web with distance from land.

Among marine mammals, baleen whales are filter feeders of large zooplankton and hence feed at the third trophic level. Toothed whales and delphinids all feed at the fifth or sixth trophic level on pelagic cephalopods and, depending on the respective species' distributional range, on epipelagic and mesopelagic fish. In the North Pacific, only two species of pinnipeds, the northern fur seal and northern elephant seal use the open ocean regions of the gyres to any extent. For these mammals, stomach contents suggest that oceanic squid are the key food web link.

Most seabirds foraging in the high seas of the ocean gyres are Procellariiformes, namely the albatrosses, shearwaters, petrels, and fulmars. These seabirds are opportunistic surface feeders on small 'forage fishes'. In the oligotrophic subtropics close to nesting colonies, a feeding guild of shearwaters and terns represents numerically the most abundant among breeding seabird species, relying on predatory fish such as tuna to drive schools of small pelagics to the ocean surface, thereby facilitating feeding.

Enhanced Feeding Habitats

The pelagic zone of the open ocean gyre is often perceived as the most monotonous living space of our planet, with few visual cues to maintain spatial orientation, and spatial heterogeneity effectively restricted to vertical gradients of light, temperature, and abundance of organisms. However, regions of horizontal oceanographic variability abound throughout the gyre ecosystem in the form of large-

scale frontal systems and mesoscale dynamic features where productivity is enhanced and trophic transfer facilitated. A discussion of the gyre food web would not be complete without highlighting these dynamic features where so much of the ecosystem energy is mobilized.

Large-scale fronts and associated frontal zones in the open ocean have profound effects on the distribution and movement patterns of pelagic animals. Generally, the distribution of pelagic animals tends to be coupled with preferred thermal habitats, a response to forage accumulation (enhanced forage opportunity), migration cues, and/or energetic gains from riding currents. On one hand, these basin-scale features form the boundaries that divide some of the large, core pelagic biogeographic provinces; on the other, the fronts are recognized as regions of convergence where life-forms on all trophic levels are concentrated and so support feeding and spawning aggregations. In the North Pacific, these thermohaline fronts mark the bounds for many of the Transition Zone keystone species, including the Pacific pomfret (*Brama japonica*), the red flying squid, and blue shark, which undergo extensive seasonal migrations northward during summer to feed along the Subarctic Boundary convergence and southward during the winter and spring to spawn in the subtropics. The aggregation of all trophic levels at the Subarctic Boundary results in a complex but trophically rich community where considerable energy is transferred. During the winter–spring, shoaling of the thermocline at the North Pacific Subtropical Front is believed to elevate the nutricline into the euphotic zone, resulting in enhanced local productivity, particularly at the depth of the DCM, as well as physically concentrating loose aggregations of prey closer to the ocean surface for predation. A basin-wide surface chlorophyll front, the Transition Zone Chlorophyll Front, is also manifested in the surface waters of the North Pacific. This biological front lies at the boundary between the low-chlorophyll subtropical and high-chlorophyll subarctic gyres. Recently, neuston-feeding loggerhead sea turtles, *Caretta caretta*, have been found to exhibit strong affinities for this specialized habitat.

Mesoscale variability on spatial scales of 10–100 km –the 'weather' of the ocean – includes high-gradient dynamic features such as frontal meanders, eddies, and jets. These features often give rise to localized regions of higher productivity, leading to aggregation and development of a forage base while physical gradients provide cues for predators to locate prey or more directly aggregate or concentrate food items. In stratified, oligotrophic waters of the large ocean gyres, recycling of nutrients between

the grazers and the phytoplankton typically maintains primary production at uniformly low levels. Transient episodes of upwelled nutrient-rich water from mesoscale events, particularly strong cyclonic eddies and meanders, have been shown to induce 'new' production, thus providing a mechanism to shorten the trophic pathway and facilitate energy transfer. The injection of nutrients at these features increases the biomass of phytoplankton through the contribution of larger eukaryotic phytoplankton, notably diatoms and dinoflagellates, over the recycled-nutrient-based picophytoplankton (e.g., photosynthesizing cyanobacteria species) that normally typify the system.

Seamounts, also known as submarine rises or table mounts, can have a strong influence on adjacent open-ocean food webs in a variety of ways, particularly those that rise within the upper few hundred meters of the surface. Waters overlying seamounts are often characterized by high standing stocks of plankton and, at some locations, concentrate and transfer energy not only among the pelagic community but also to the demersal resident ecosystems. Several phenomena contribute to the maintenance and enhancement of the unique seamount communities. For one, some seamount ecosystems possess midwater micronekton communities that include both a unique resident assemblage as well as a DSL component advected from adjacent waters. At shallower seamounts, the members of the DSL community rise in the water column at night, are advected over the seamount, and are subsequently trapped on the summit as they descend at dawn, creating an enhanced feeding regime during the morning hours. The resident faunal assemblages are analogous to the land-associated mesopelagic boundary communities identified on larger island and shelf slopes. Seamounts are also hypothesized to benefit from the development of Taylor columns, or semistationary eddies located above the seamount, that would help retain planktonic populations and enhance productivity.

Food Web Dynamics

Food webs of ocean gyres are altered by a range of factors, including fishing and variations in physical forcing resulting from climate fluctuations. The relationship between climate variation and ecosystem dynamics has been a focus of considerable research. Changes in abundance of organisms at many trophic levels have been documented to vary coherently with various atmospheric indices, including the Aleutian Low in the Pacific and the North Atlantic Oscillation in the Atlantic. For example, in the

North Pacific subarctic gyre, changes in the fishery catches of all species of salmon vary on timescales of decades, coherent with the intensity of the Aleutian Low Pressure System. While the link between the atmosphere and salmon productivity has not been resolved, a number of hypotheses suggest that changes in salmon carrying capacity result from changes in physical forcing that impact productivity at the bottom of the food web and propagate up the food web to salmon. A change in the energy flow through the food web from the bottom up in response to climate variation is typical of many relationships described between climate and food web dynamics in ocean gyres.

Fisheries in ocean gyres typically impact food webs through removals at top or mid-trophic levels. For example, longline or troll fisheries target apex predators including tunas, swordfish, marlins, and salmon, although some mid-trophic level species including squid can also be the target species. Bycatch and incidental catches in ocean gyre fisheries also include apex species including sharks and protected species such as seabirds, marine mammals, and sea turtles. Data on the responses of oceanic gyre food webs to fishing are generally limited to harvested species, so the food web impacts at lower trophic levels are not documented. However, a dynamic ecosystem model has been used to investigate possible impacts and has found no evidence that the removal of any single high trophic level species significantly altered the food web. The lack of a keystone species appears to be due to a high degree of diet overlap among the high trophic level species. Fisheries in oceanic gyres alter the food web by reducing biomass at the top of the food web. When this reduction becomes substantial, it may result in some increase in biomass at mid-trophic levels.

See also

Ecosystem Effects of Fishing. Fish Feeding and Foraging. Fish Migration, Vertical. Fish Predation and Mortality. Large Marine Ecosystems. Marine Mammal Trophic Levels and Interactions. Mesopelagic Fishes. Ocean Gyre Ecosystems. Pelagic Fishes. Seabird Foraging Ecology.

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OCEAN MARGIN SEDIMENTS

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Introduction

Ocean margin sediments are largely detrital deposits of terrestrial origin that extend from the shoreline to the foot of the continental rise. Indeed, about 80% of the world's sediment is stored within margin systems, which cover about 14% of the Earth's surface (Table 1; Figure 1). Margin deposits typically consist of sand, silt, and clay-sized particles, the characteristics of which reflect the geology and climate of the adjacent continent. Some of the signals relevant to terrestrial conditions include sediment size, mineralogy, geochemistry, and isotopic signature. Upon entering the marine realm, however, sediments take on new characteristics indicative of coastal ocean processes that include waves, tides, currents, sea level, and biological productivity. Given that these numerous terrestrial and marine processes impart a signature to the sediments, ocean margins preserve an important record of Earth history, providing insights into past atmospheric, terrestrial, and marine conditions. Beyond their significance as environmental recorders ocean

margin sediments support major petroleum and mineral resources. Currently, over 50% of the world's oil is recovered along ocean margins, and much of the remaining fraction is held within ancient margin deposits.

In the 1950s, early investigations of ocean margins focused on tectonic structure and how overlying sedimentary sequences developed on timescales of 10^5 – 10^7 years. Originally aimed at understanding plate tectonics and the nature of ocean–continent boundaries, these large-scale studies continued through the 1960s with specific interest in petroleum resources. Such efforts culminated in the publication of large scientific volumes such as Burk and Drake's *Geology of Continental Margins* (1974). At the time of these summary publications, new models of sedimentary margin systems were already being developed, notably the approach of seismic stratigraphy established at the Exxon Production Research Company. Growing out of this approach was the more general model of sequence stratigraphy, which helped establish that margin strata could be grouped into discrete packages reflecting cycles of sea-level rise and fall. These concepts represent a general approach that has been applied to stratigraphic development and margin evolution in most of the world's ancient and modern sedimentary systems. Sequence stratigraphic data has also been mated with lithologic, magnetic, and biostratigraphic