A DERIVATIVE OF
ENCYCLOPEDIA OF OCEAN SCIENCES, 2ND EDITION

MARINE ECOLOGICAL PROCESSES

COMPILED BY JOHN H. STEELE

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Editor

JOHN H. STEELE

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MARINE ECOLOGICAL PROCESSES: INTRODUCTION

This is the second of two volumes in this series covering general marine biological and ecological topics. The separation between "biology" and "ecology" is arbitrary since taxonomical and physiological features are determined by environmental patterns and, correspondingly, ecological processes depend on the species mix within communities. In this volume the focus is on ecosystem structure, ecological processes, and the forcing of these systems by external stresses, principally climate and fisheries related.

Given their fluid nature, marine ecosystems are difficult to define in terms of geographical boundaries (see Longhurst, 1998). Thus they are often described by physical processes such as upwelling or ocean gyres. Larger scale systems on the continental shelf may be associated with their fisheries. Many of the smaller ecosystems are determined by special habitats such as coral reefs or hydrothermal vents.

These different kinds of functions can prescribe the distinguishing features of such systems, but their dynamics are a result of their internal food web structure that involves a complicated set of prey-predator and competitive interactions. Study of these food web processes is the dominant impetus for marine ecological research.

Understanding the complex responses of food webs to environmental changes provides a major theme in this research. Some of the most perplexing yet important features are termed regime shifts. These relatively rapid switches in the whole structure of a web have been observed in different oceans in response to physical changes in the environment. These shifts are one example of the more general concern with ecosystem reactions to the increasing stresses imposed by society. The role of the oceans in determining longer period climatic trends is described in other volumes. Outlined here are the responses of major food web components — plankton, marine mammals, seabirds and fish stocks — to climatic change.

The other dominant concern is over-fishing, especially of fish communities on the world's continental shelves. It is now recognized that such fisheries not only affect the targeted fish stocks but also alter the rest of their ecosystem. The articles collected here describe the main types of fisheries and their impacts. Questions relating to management are considered in another volume (*Marine Policy and Economics*).

Mariculture is now the one method of harvesting food from the sea that is still increasing. Salmonid farming demonstrates the economic benefits but also the ecological hazards in terms not only of diseases but also in relation to those ecosystems that must be fished to provide food for the salmonids. Articles in this volume describe the great variety of products that are now farmed. A separate volume (*Marine Policy and Economics*) deals with the economic aspects.

A major limitation on marine research is caused by our inability to sample the oceans adequately. Marine ecosystems, especially, are seriously under-sampled compared with those on land. This is the greatest barrier to improving our understanding of life in the sea. Five articles describe methods for investigating phytoplankton, zooplankton, benthos, fish and marine mammals. Another problem in the open ocean is our inability to conduct controlled experiments at the scale of pelagic ecosystems. As a compromise large containers, called mesocosms, are used to capture parts of planktonic and benthic communities. Two articles discuss the benefits and limitations of this approach.

These problems with sampling and experimenting in the ocean have led to major initiatives to construct numerical models of all aspects of ocean processes. Articles on physical and chemical modeling are in other volumes. Gathered here are a set of articles that describe numerical simulations of ecological processes.

John H. Steele
Editor

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LARGE MARINE ECOSYSTEMS

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Introduction

Coastal waters around the margins of the ocean basins are in a degraded condition. With the exception of Antarctica, they are being degraded from habitat alteration, eutrophication, toxic pollution, aerosol contaminants, emerging diseases, and overfishing. It has also been recently argued by Pauly and his colleagues that the average levels of global primary productivity are limiting the carrying capacity of coastal ocean waters for supporting traditional fish and fisheries and that any further large-scale increases in yields from unmanaged fisheries are likely to be at the lower trophic levels in the marine food web and likely to disrupt marine ecosystem structure.

Large Marine Ecosystems

Approximately 95% of the world's annual fish catches are produced within the geographic boundaries of 50 large marine ecosystems (LMEs) (**Figure 1A**). The LMEs are regions of ocean space encompassing coastal areas from river basins and estuaries out to the seaward boundary of continental shelves, and the outer margins of coastal currents. They are relatively large regions, on the order of 200 000 km^2 or greater, characterized by distinct bathymetry, hydrography, productivity, and trophically dependent populations. The close linkage between global ocean areas of highest primary productivity and the locations of the large marine ecosystems is shown in **Figure 1B**. Primary productivity at the base of marine food webs is a critical factor in the determination of fishery yields. Since the 1960s through the 1990s, significant changes have occurred within the LMEs, attributed in part to the affects of excessive fishing effort on the structure of food webs in LMEs.

Food Webs and Large Marine Ecosystems

Since 1984, a series of LME conferences, workshops, and symposia have been held during the annual meeting of the American Association for the Advancement of Science (AAAS). In the subsequent intervening 15 years, 33 case studies of LMEs were prepared, peer-reviewed, and published (see Further Reading). From the perspective of actual and potential fish yields of the LMEs an 'ECOPATH'-type trophic model, based on the use of a static system of linear equations for different species in the food web, has been developed by Polovina, Pauly and Christensen (eqn [1]).

$$P_i = \mathrm{Ex}_i + \sum B_i(Q/B_i)(\mathrm{DC}_{ji}) + B_i(P/B) - (IEE_i) \quad [1]$$

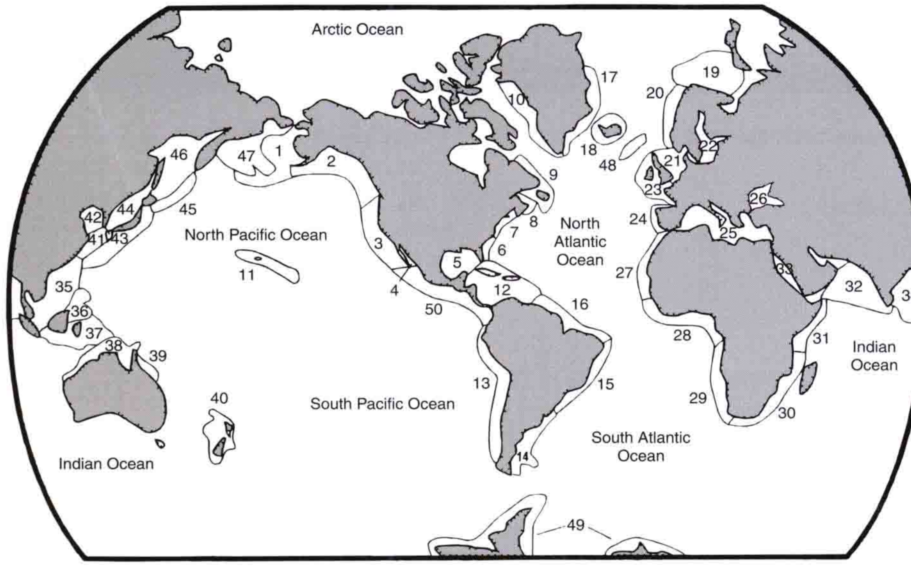
P_i is the production during any normal period (usually one year) of group i; Ex_i represents the exports (fishery catches and emigration) of i; $\sum_i$ represents the summation over all predators of I; B_j and B_i are the biomasses of the predator J and group I, respectively; Q/B_j is the relative food consumption of j; DC_{ji} the fraction that i constitutes of the diet of B_i is the biomass of i and $(\mathrm{I} - \mathrm{EE}_i)$ is the other mortality of I, that is the fraction of i's production that is not consumed within or exported from the system under consideration. A practical consideration of food web dynamics in LMEs is the effect that changes in the structure of marine food webs could have on the long-term sustainability of fish species biomass yields.

Biomass Yields and Food Webs

South China Sea Large Marine Ecosystems

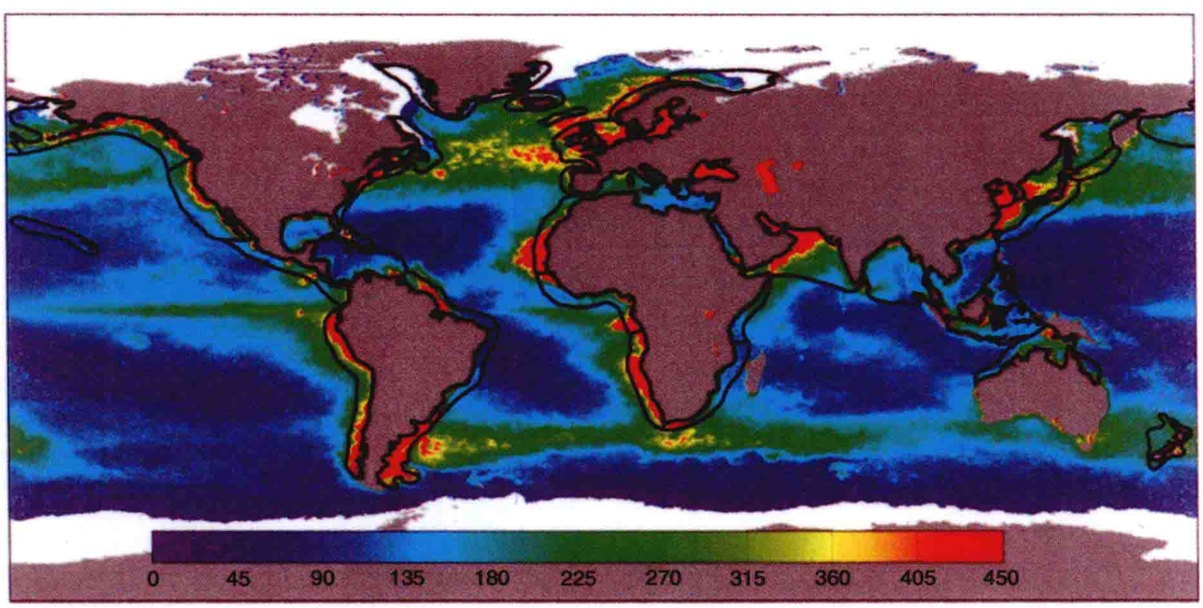
An example of the use of fisheries yield data in constructing estimates of combined prey consumption by trophic levels is depicted in **Figure 2** for shallow waters of the South China Sea (SCS) LME. The trophic transfers up the food web from phytoplankton to apex predators is shown in **Figure 3** for open-ocean areas of the SCS. The differences in fish/fish predation is approximately 50% of the fish production in the shallow-water subsystem and increases to 95% in the open-ocean subsystem.

Application of the ECOPATH model to the SCS LME by Pauly and Christensen produced an initial outcome of an additional 5.8 Mt annually. This is a rate that is nearly double the average annual catch reported for the SCS up through 1993, indicating some flexibility for increasing catches from the ecosystem, but not fully realizing its potential because of technical difficulties in fishing methodologies.



(A)

1. Eastern Bering Sea
2. Gulf of Alaska
3. California Current
4. Gulf of California
5. Gulf of Mexico
6. South-east US Continental Shelf
7. North-east US Continental Shelf
8. Scotian Shelf
9. Newfoundland Shelf
10. West Greenland Shelf
11. Insular Pacific-Hawaiian
12. Caribbean Sea
13. Humboldt Current
14. Patagonian Shelf
15. Brazil Current
16. North-east Brazil Shelf
17. East Greenland Shelf
18. Iceland Shelf
19. Barents Sea
20. Norwegian Shelf
21. North Sea
22. Baltic Sea
23. Celtic-Biscay Shelf
24. Iberian Coastal
25. Mediterranean Sea
26. Black Sea
27. Canary Current
28. Gulf of Guinea
29. Benguela Current
30. Agulhas Current
31. Somali Coastal Current
32. Arabian Sea
33. Red Sea
34. Bay of Bengal
35. South China Sea
36. Sulu-Celebes Seas
37. Indonesian Seas
38. Northern Australian Shelf
39. Great Barrier Reef
40. New Zealand Shelf
41. East China Sea
42. Yellow Sea
43. Kuroshio Current
44. Sea of Japan
45. Oyashio Current
46. Sea of Okhotsk
47. West Bering Sea
48. Faroe Plateau
49. Antarctic
50. Pacific Central American Coastal



(B)

Figure 1 Boundaries of 50 large marine ecosystems (and) (B) SeaWiFS chlorophyll and outlines of LME boundaries.

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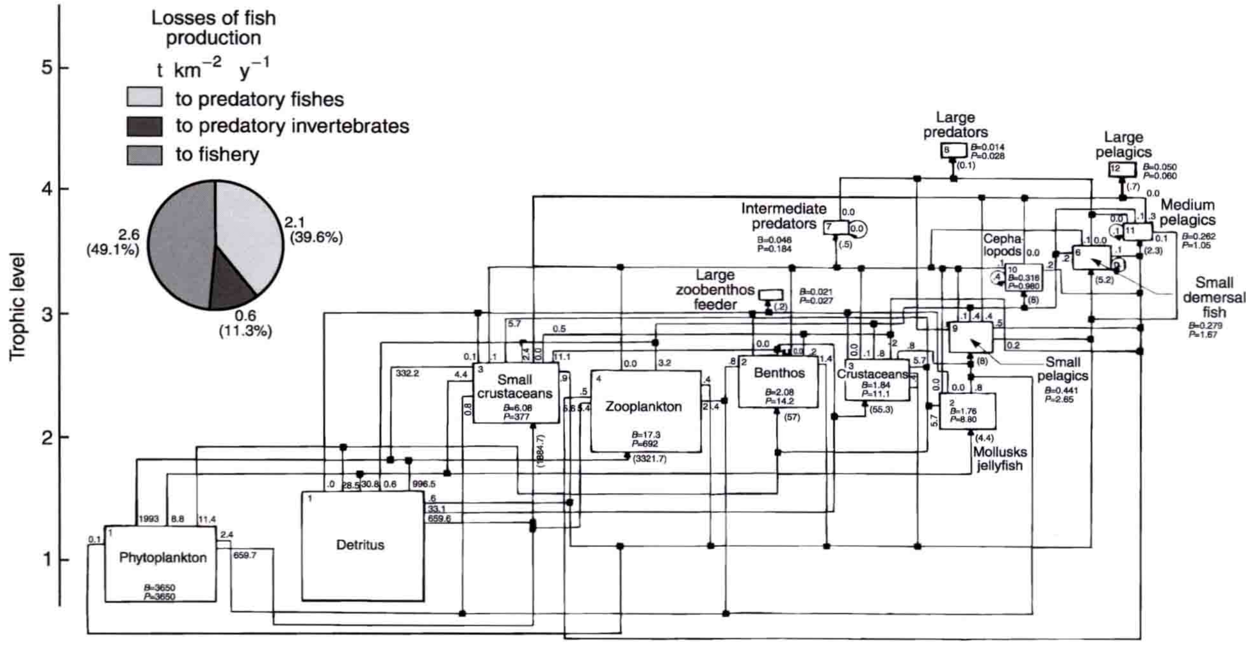

Figure 2 South China Sea shallow-water food web based on the ECOPATH model. (From Pauly and Christensen (1993).)

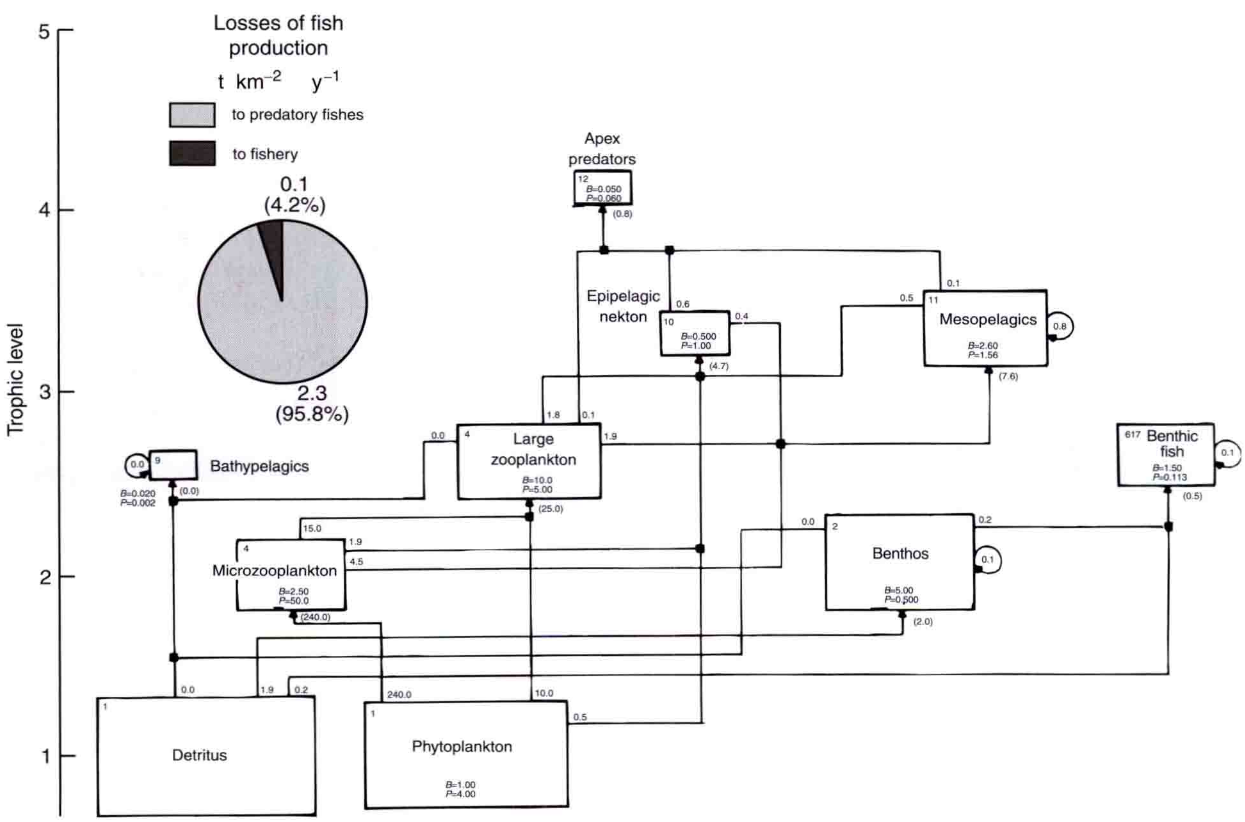

Figure 3 South China Sea open-ocean food web. (From Pauly and Christensen (1993).)

East China Sea Large Marine Ecosystem

Evidence for the negative effects of fishing down the food chain can be found in the report by Chen and Shen for the East China Sea (ECS) LME. For a 30-year period of the early 1960s to the early 1990s, little change was reported in the productivity and community composition of the plankton at the lower end of the food chain of the ECS. However, during the same period major changes were reported for a shift in biomass yields among the 'old traditional' bottom species (yellow croaker) and new species dominated by shrimp, crab, and small pelagic fish species. It appears that the annual catch increase from 0.9 Mt in the 1960s to 5.8 Mt in the early 1990s exceeded the sustainable level of yield for several species. The greatest increases in biomass yield during this period has been in a category designated as 'Other Species.' The species in this category are near the base of the food web. They are relatively small, pelagic, and fast growing, and are not used for human consumption but are used for feeding 'cultured fish or poultry' (**Figure 4**). Collectively, the catches of 'Other Species' provide additional evidence of the effects of 'fishing down the food web.'

Yellow Sea Large Marine Ecosystem

A projection of the Yellow Sea food web is given in **Figure 5**. The decline in the east Asian LMEs of demersal species and what appears to be 'trophic-forcing' down the food web hypothesized by Pauly and Christensen are apparent in the changes that have occurred over 30 years in the Yellow Sea LME (YS LME). The catch statistics indicate a rapid decline of most bottom fish and large pelagic fish from the YS LME from the 1960s through the early 1990s. Recent acoustic survey results indicate that the Japanese anchovy population in the YS LME has significantly increased from an annual catch level of 1000 Mt in the 1960s to an estimated biomass of 4 Mt in the 1990s.

Overfishing has led to major structural changes in the fish community of the YS LME. In the 1950s and 1960s bottom fish were the major target species in China's fisheries. Small yellow croaker was the dominant preferred demersal market species in the late 1950s, constituting about 40% of research vessel trawl catches. By 1986, pelagic fish dominated the catches (~50%) of research vessel surveys suggesting that they may have replaced depleted demersal stocks and are effectively utilizing surplus zooplankton production no longer utilized by the depleted large pelagics and early life-history stages of depleted fish species.

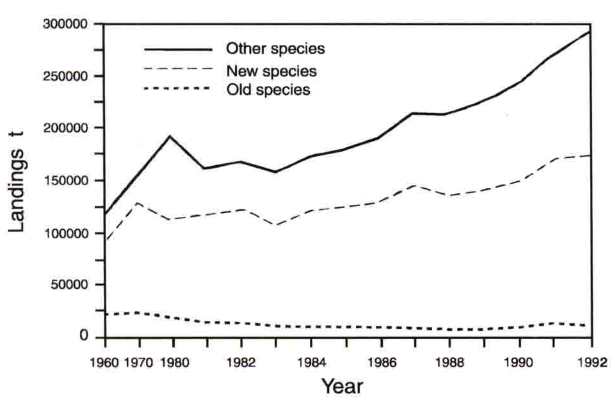

Figure 4 East China Sea fisheries yield 1960s to early 1990s, showing increased annual catches of 'Other Species' used mostly for fish and poultry food. (From Chen and Shen (1999).)

LME Regime Shifts, Food Webs, and Biomass Yields

In the eastern Pacific, large-scale oceanographic regime shifts have been a major cause of changes in food web structure and biomass yields of LMEs.

Gulf of Alaska Large Marine Ecosystem

Evidence of the food web effects from oceanographic forcing was reported for the Gulf of Alaska LME (GA LME). An increase in biomass of zooplankton, approaching a doubling level between two periods 1956–62 and 1980–89 has been linked to favorable oceanographic conditions leading to increases in primary and secondary productivity and subsequent increases in abundance levels of pelagic fish and squid in the GA LME; it is estimated by Brodeur and Ware that total salmon abundance in the GA LME was nearly doubled in the 1980s.

California Current Large Marine Ecosystem

In contrast to the 1980–89 Gulf of Alaska increases in biomass of the zooplankton and fish biomass components of the GA LME, a declining level of zooplankton has been reported for the California Current LME (CC LME) of approximately 70% over a 45-year monitoring period. The cause according to Roemmich and McGowan appears to be an increase in water column stratification due to long-term warming. The clearest food web relationship reported related to the zooplankton biomass reduction was a decrease in the abundance of pelagic sea-birds.

US North-east Shelf Large Marine Ecosystem

The US North-east Shelf LME is an ecosystem with more structured coherence in the lower food web

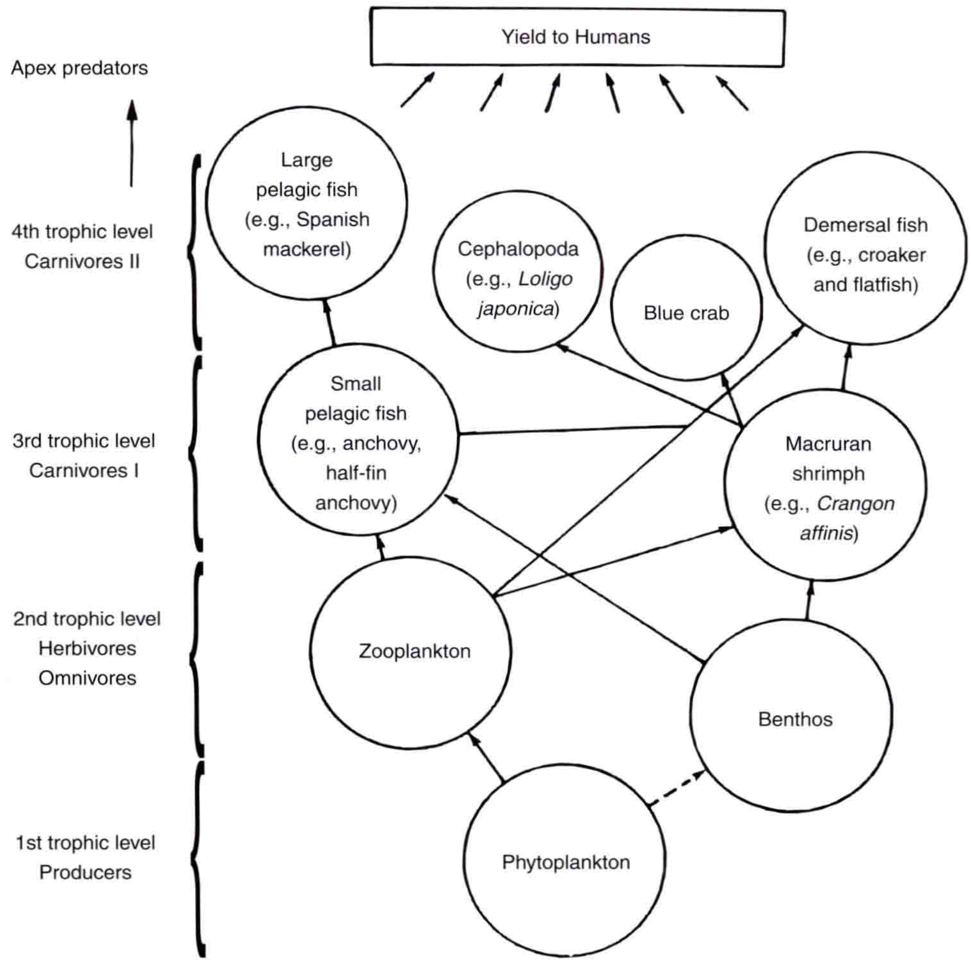

Figure 5 A simplified version of the Yellow Sea food web and trophic structure based on the main resources populations in 1985–1986. (From Tang 1993).)

than in the Gulf of Alaska or California Current systems. Following a decade of overfishing beginning in the mid-1960s, the demersal fish stocks, principally haddock, cod, and yellowtail flounder, declined to historic low levels of spawning biomass. In addition, the herring and mackerel spawning stock levels were reduced in the mid-1970s. By the mid-1980s, the demersal fish biomass had declined to less than 50% of levels in the early 1960s.

Following the 1975 extension of jurisdiction by the United States to 200 miles of the continental shelf, the rebuilding of the spawning stock biomass (SSB) of herring and mackerel commenced. Beginning in 1982 there was a sharp reduction in fishing effort from foreign vessels excluded from the newly designated US Exclusive Economic Zone (EEZ). Within four years the mackerel population recovered from just under 0.5 Mt to 1 Mt in 1986 and an estimated 2 Mt by 1994. Herring recovery was also initiated in the absence of any significant fishing effort from 1982 to 1990 when increases in SSB went from less than 0.2 Mt to 1 Mt. An unprecedented 3.5 Mt level of herring SSB was reached by 1994.

The NOAA-NMFS time-series of zooplankton collected from across the entire North-east Shelf ecosystem from 1977 to 1999 is indicative of an internally coherent structure of the zooplankton component of the North-east Shelf ecosystem. During the mid to late 1990s and the unprecedented abundance levels of SSB of herring and mackerel, the zooplankton component of the ecosystem showed no evidence of significant changes in biomass levels with annual values close to the long-term annual median of 30 ml/100 m^3 for the North-east Shelf ecosystem. In keeping with the robust character of the zooplankton component is the initiation of spawning stock recovery subsequent to reductions in fishing effort for cod, haddock, and yellowtail flounder. Accompanying the recovery of spawning stock biomass is the production of a strong year-class of haddock in 1998 and a strong year-class of yellowtail flounder in 1997. The initial increases in skate and spiny dogfish populations following the declines in cod, haddock, and flounder stocks have been significantly reduced by targeted fisheries on these species. The reductions in abundance of these predators coupled with the robust character at the lower parts of the North-east Shelf food web enhance probability for recovery of the depleted cod, haddock, and yellowtail flounder stocks.

Large Marine Ecosystem Food Web Dynamics and Biomass Yields

Two major sources of long-term changes in biomass near the top of the food web—fishes and pelagic birds—have been observed and reported in the literature. In the case studies of the Yellow Sea and East China Sea, the multidecadal shift in fish community structure resulting from overfishing appeared to promote the production of small pelagic fish species, indicative of 'fishing down the food web' as hypothesized by Pauly and Christensen, as the abundance levels of predator species decline through overfishing. For the South China Sea, estimates from a Pauly and Christensen ECOPATH model suggests that the mean annual biomass yield of fish was not fully utilized. It appears from the case study that a significant percentage of an additional 5 Mt could be fished if managed in a sustainable manner. In the eastern Pacific the results of oceanographic regime shifts had direct impact in increasing zooplankton and fish biomass in the Gulf of Alaska LME, whereas a multidecadal warming trend in the California Current LME lowered productivity at the base of the food web and resulted in a decrease in pelagic bird biomass. The importance of fish and fisheries to the structure of marine food webs is also an important cause of variability in biomass yields. A clear demonstration of this relationship is found in the application of the ECOPATH model to four continental shelf ecosystems, where it was shown that fish preying on other fish was a principal source of fish biomass loss. The level of predation ranged from 3 to 35 times the loss to commercial fisheries.

Fish are keystone components of food webs in marine ecosystems. The worldwide effort to catch fish using highly effective advanced electronics to locate them, and efficient trawling, gill-netting, and longline capture methodologies, has had an impact on the structure of marine food webs. From case studies examined, evidence indicates that the fishing effort of countries bordering on LMEs has resulted in changes in the structure of marine food webs, ranging from significant abundance shifts in the fish component of the ecosystem from overfished demersal stocks to smaller faster-growing pelagic fish and invertebrate species (herrings, anchovies, squids) as fisheries are refocused to species down the food web, predation pressure increases on the plankton component of the ecosystem.

The economic benefits to be derived from the trend in focusing fisheries down the food web to low-priced small pelagic species used, in part, for poultry, mariculture, and hog food are less than from earnings derived from higher-priced groundfish species, raising serious questions regarding objectives of ecosystem-based management integrity of ecosystems and sustainability of fishery resources. These are questions to be addressed in the new millennium with respect to the implementation of management practices. As in the case of the US North-east Shelf LME, overfished species can recover with the application of aggressive management practices, when supported with knowledge that the integrity of the lower parts of the food web remain substantially unchanged during the recovery period. However, under conditions of recent large-scale oceanographic regime shifts in the Pacific, evidence indicates that the biodiversity and biomass yields of the north-east sector of the Pacific in the Gulf of Alaska LME were significantly enhanced from increased productivity through the food web from the base to the zooplankton and on to a doubling of the fish biomass yields close to the top level of the food web. In contrast, in the California Current ecosystem the apparent heating and deepening of the thermocline effectively reduced phytoplankton and zooplankton production over a 40-year period, suggesting that in upwelling regions prediction of oceanographic events effecting food web dynamics require increased commitment to long-term monitoring and assessment practices if forecasts on effects of regime shifts on biomass yields are to be improved.

If ecosystem-based management is to be effective, it will be desirable to refine ECOPATH-type models for estimating the carrying capacity of LMEs in relation to sustainability levels for fishing selected species. It was assumed in the early 1980s by Skud, based on the historic record, that herring and mackerel stocks inhabiting the US North-east Shelf ecosystem could not be supported at high biomass levels simultaneously by the carrying capacity of the ecosystem. However, subsequent events have demonstrated the carrying capacity of the ecosystem is now of sufficient robustness to support an unprecedented almost 5.5 Mt of spawning biomass of both species combined. In addition, the ecosystem in its present state apparently has the carrying capacity to support the growing spawning biomass of recovering haddock and flounder stocks. Evidence of the production of strong year-classes for both species supported by high average levels of primary production of $350\,g\,Cm^2\,y^{-1}$, a robust level of zooplankton biomass, relatively high levels of epibenthic macrofauna, and apparent absence of any large-scale oceanographic regime shift suggests that integrity of the ecosystem food web will enhance the return of the fish component of the ecosystem to the more balanced demersal–pelagic community structure inhabiting the shelf prior to the massive overfishing perturbation of the 1960s to the 1980s.

Prospectus: Food Webs and Large Marine Ecosystem Management

It is clear from the LME studies examined that time-series measurements of physical oceanographic conditions that are coupled with appropriate indicators of food web integrity (e.g., phytoplankton, chlorophyll primary productivity, zooplankton, fish demography) are essential components of a marine science program designed to support the newly emergent concept of ecosystem-based management.

It is important to consider the dynamic state of LMEs and their food webs in considering management protocols, recognizing that they will need to be considered from an adaptive perspective. To assist economically developing countries in taking positive steps toward achieving improved understanding of food web dynamics and their role in contributing to longer-term sustainability of fish biomass yields, reducing and controlling coastal pollution and habitat degradation, and improving oceanographic and resource forecasting systems, the Global Environment Facility (GEF) and its $2 billion trust fund has been opened to universal participation that builds on partnerships with several UN agencies (e.g., World Bank, UNDP, UNEP, UNIDO). The GEF, located within the World Bank, is an organization established to provide financial support to post-Rio Conference actions by developing nations for improving global environmental conditions in accordance with GEF operational guidelines.

See also

Ecosystem Effects of Fishing. Fisheries and Climate. Fisheries Overview. Marine Fishery Resources, Global State of. Network Analysis of Food Webs. Population Dynamics Models. 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 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

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