LARGE MARINE ECOSYSTEMS

K. Sherman, Narragansett Laboratory, Narragansett, RI, USA

doi:10.1006/rwos.2001.0292

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 LMEs

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]).

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

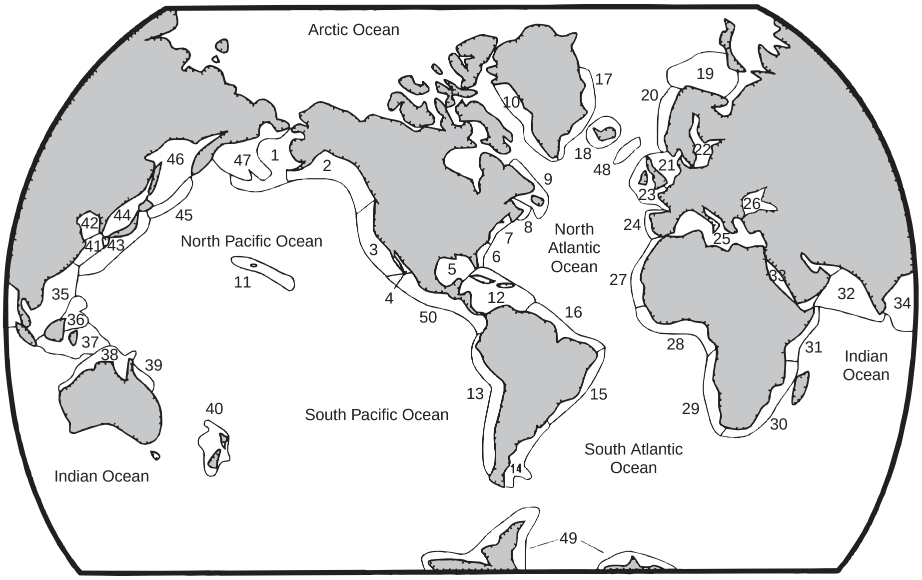
P_i is the production during any normal period (usually one year) of group i; Ex_i represents the exports (fishery catches and emigration) of i; $\sum_j$ represents the summation over all predators of I; B_j and B_i are the biomasses of the predator J and group I, respectively; Q/B_j is the relative food consumption of j; DC_{ji} the fraction that i constitutes of the diet of j; 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 LME

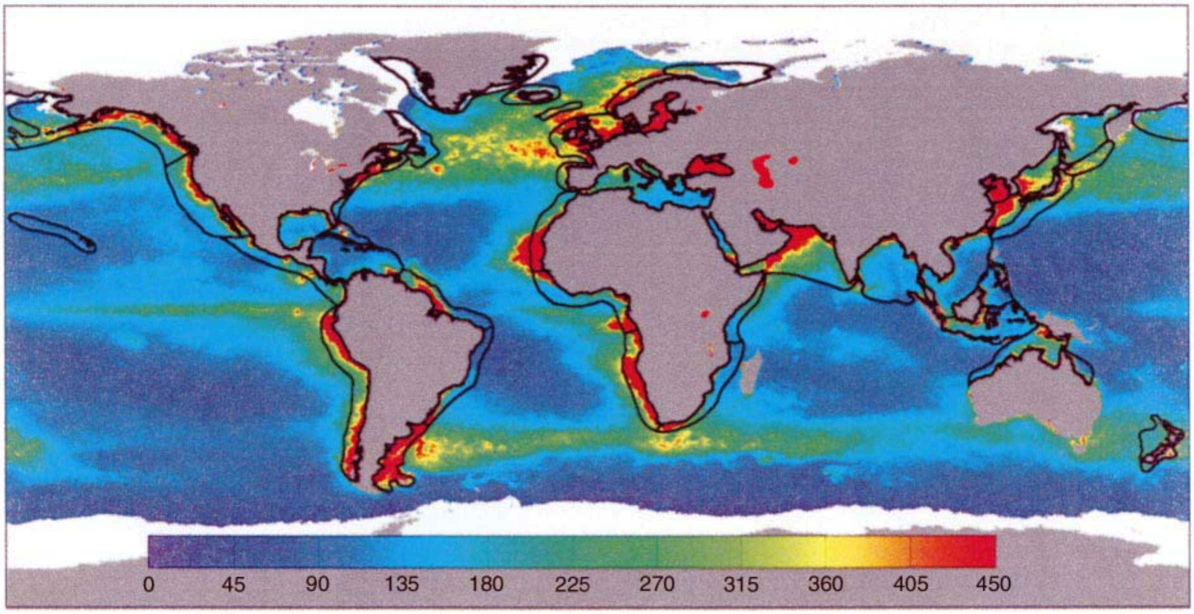
An example of the use of fisheries yield data in constructing estimates of combined prey consumption by trophic levels is depicted in **Figure 2** for shallow waters of the South China Sea (SCS) LME. The trophic transfers up the food web from phytoplankton to apex predators is shown in **Figure 3** for 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 (A) Boundaries of 50 large marine ecosystems (LMEs) and (B) SeaWiFS chlorophyll and outlines of LME boundaries.

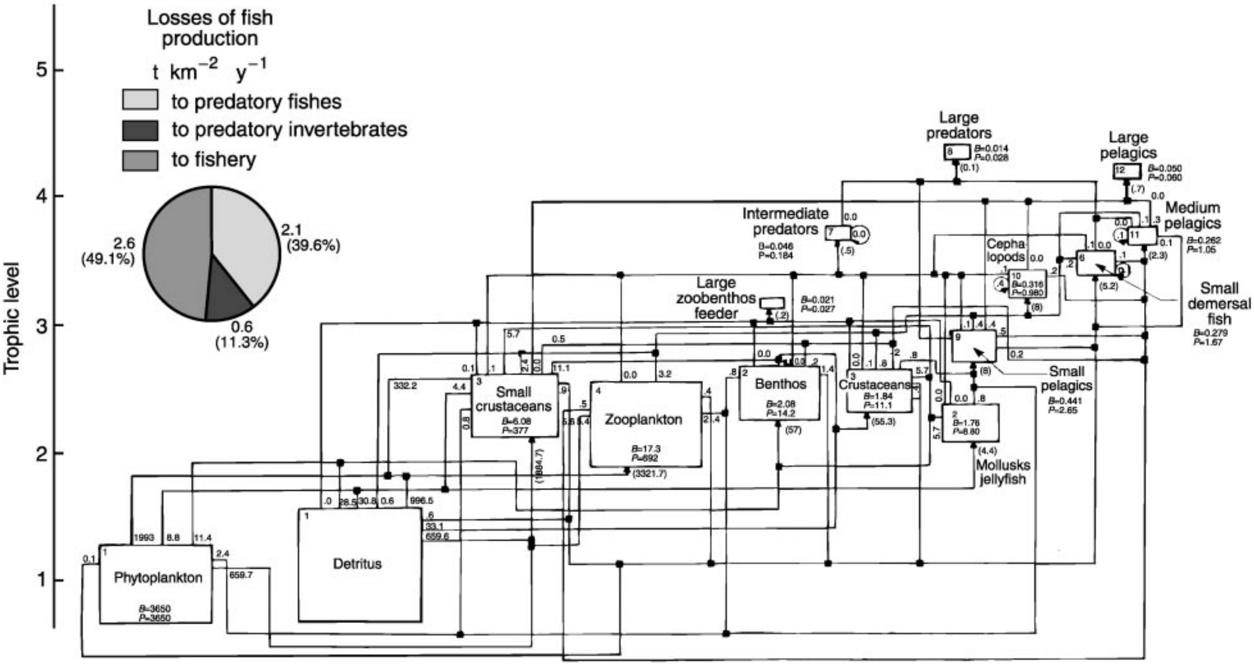


Figure 2 South China Sea shallow-water food web based on the ECOPATH model. (From Pauly and Christensen (1993).)

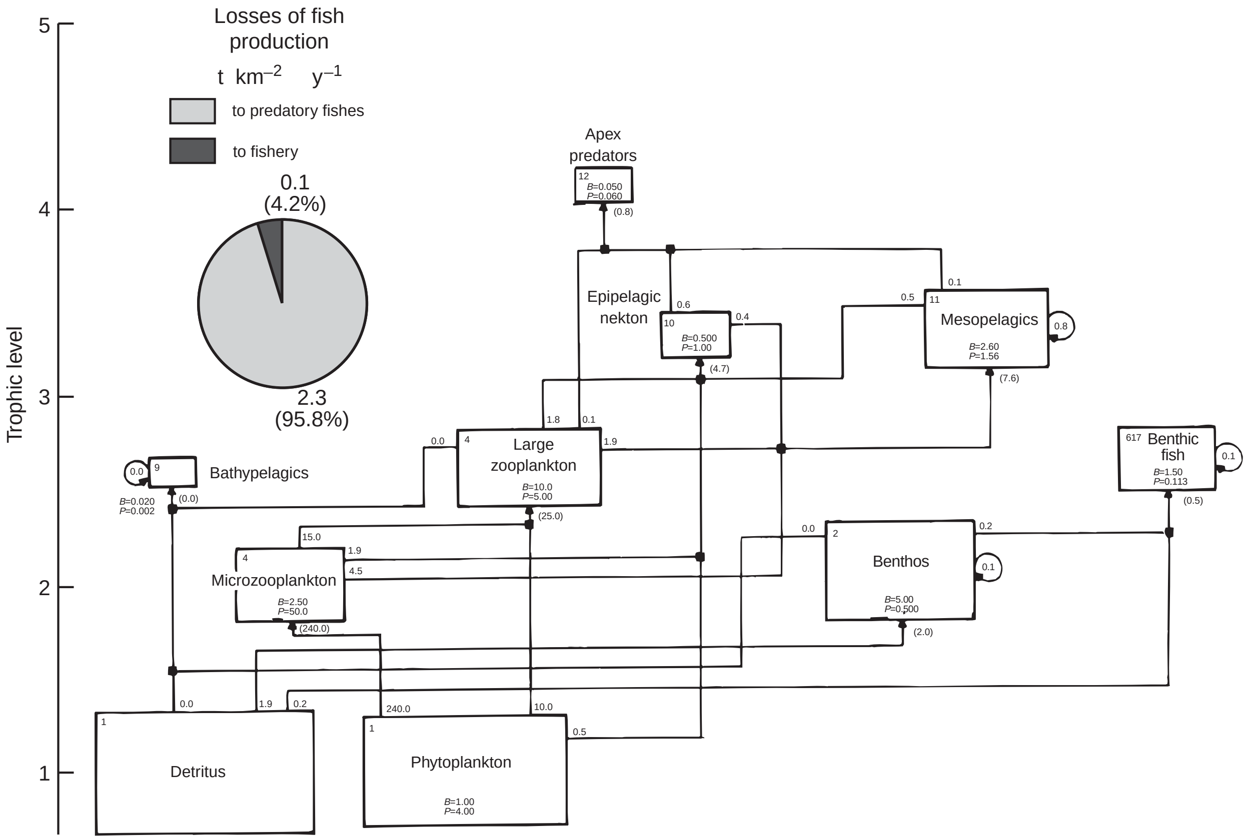


Figure 3 South China Sea open-ocean food web. (From Pauly and Christensen (1993).)

East China Sea LME

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 LME

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.

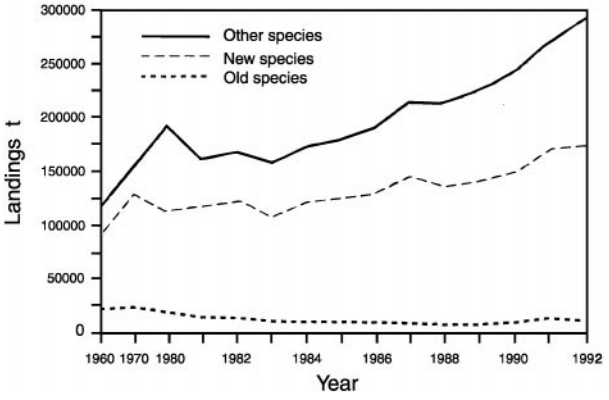


Figure 4 East China Sea fisheries yield 1960s to early 1990s, showing increased annual catches of ‘Other Species’ used mostly for fish and poultry food. (From Chen and Shen (1999).)

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 ($\sim 50\%$) 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.

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 LME

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 LME

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 seabirds.

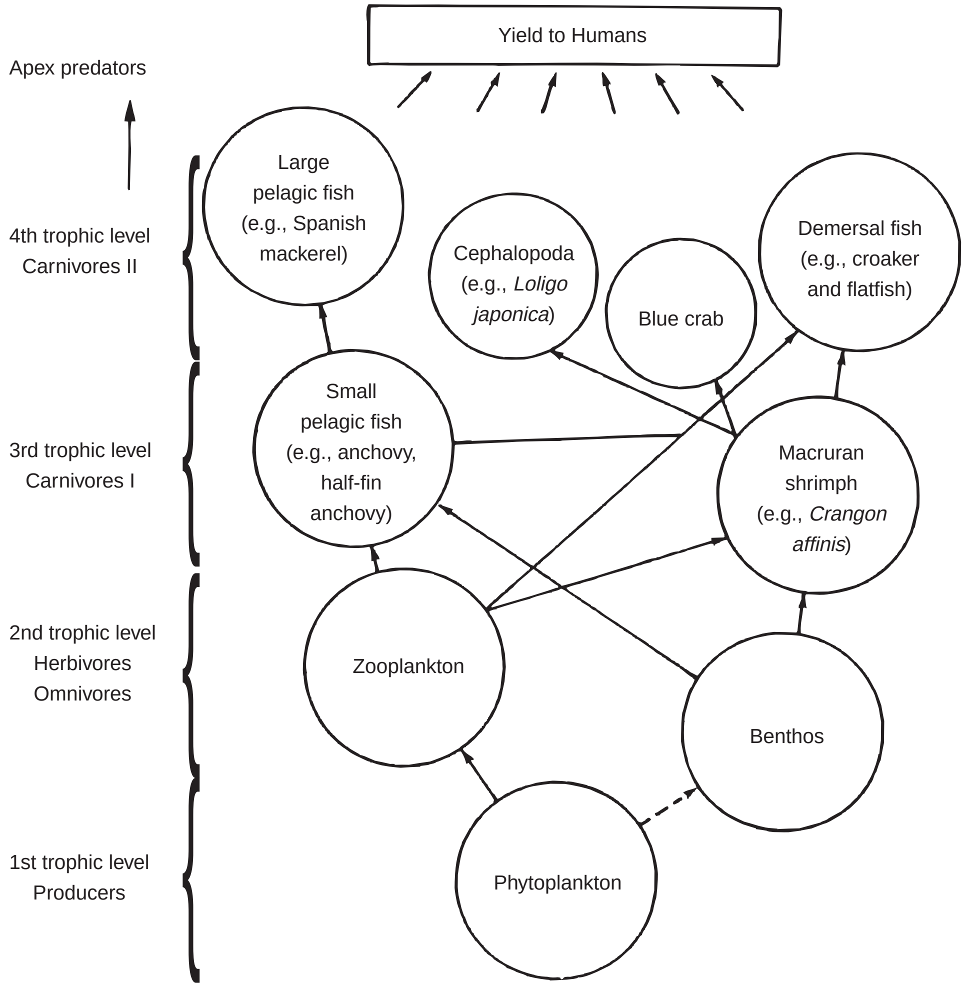


Figure 5 A simplified version of the Yellow Sea food web and trophic structure based on the main resources populations in 1985–1986. (From Tang 1993).)

US North-east Shelf LME

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

LME 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 $350\,\mathrm{g\,C\,m^2\,y^{-1}}$, 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 LME 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

Demersal Fishes. Dynamics of Exploited Marine Fish Populations. Ecosystem Effects of Fishing. Fish Larvae. Fisheries: Multispecies Dynamics. Fisheries and Climate. Fisheries Overview. International Organizations. Marine Fishery Resources, Global State of. Network Analysis of Food Webs. Ocean Color from Satellites. Pelagic Biogeography. Pelagic Fishes. Plankton. Population Dynamics Models. Primary Production Distribution. Seabirds and Fisheries Interactions. Upper Ocean Time and Space Variability. Upwelling Ecosystems.

Further Reading

Chen Y and Shen X (1999) Changes in the biomass of the East China Sea ecosystem. In: Sherman K and Tang Q (eds) *Large Marine Ecosystems of the Pacific Rim: Assessment, Sustainability, and Management*, pp. 221–239. Malden MA: Blackwell Science.

Kumpf H, Stiedinger K and Sherman K (eds) (1999) *The Gulf of Mexico Large Marine Ecosystem: Assessment, Sustainability, and Management*. Malden, MA: Blackwell Science.

Pauly D and Christensen V (1993) Stratified models of large marine ecosystems: a general approach and an application to the South China Sea. In: Sherman K, Alexander LM and Gold BD (eds) *Large Marine Ecosystems: Stress, Mitigation, and Sustainability*, pp. 148–174. Washington DC: AAAS.

Sherman K and Alexander LM (eds) (1986) *Variability and Management of Large Marine Ecosystems*, AAAS Selected Symposium 99. Boulder, CO: Westview Press.

Sherman K and Alexander LM (eds) (1989) *Biomass Yields and Geography of Large Marine Ecosystems*, AAAS Selected Symposium 111. Boulder, CO: Westview Press.

Sherman K, Alexander LM and Gold BD (eds) (1990) *Large Marine Ecosystems: Patterns, Processes, and Yields*, AAAS Symposium, Washington, DC: AAAS.

Sherman K, Alexander LM and Gold BD (eds) (1991) *Food Chains, Yields, Models, and Management of Large Marine Ecosystems*, AAAS Symposium, Boulder, CO: Westview Press.

Sherman K, Alexander LM and Gold BD (eds) (1992) *Large Marine Ecosystems: Stress, Mitigation, and Sustainability*. Washington, DC: AAAS.

Sherman K, Jaworski NA and Smayda TJ (eds) (1996) *The Northeast Shelf Ecosystem: Assessment, Sustainability, and Management*. Cambridge, MA: Blackwell Science.

Sherman K, Okemwa EN and Ntiba MJ (eds) (1998) *Large Marine Ecosystems of the Indian Ocean: Assessment, Sustainability, and Management*. Malden, MA: Blackwell Science.

Sherman K and Tang Q (eds) (1999) *Large Marine Ecosystems of the Pacific Rim: Assessment, Sustainability, and Management*. Malden, MA: Blackwell Science.

Tang Q (1993) Effects of long-term physical and biological perturbations on the contemporary biomass yields of the Yellow Sea ecosystem. In: Sherman K, Alexander LM and Gold BD (eds) *Large Marine Ecosystems: Stress, Mitigation, and Sustainability*. Washington DC, AAAS Press, pp. 79–93.

LARIDAE, STERNIDAE AND RYNCHOPIDAE

J. Burger, Rutgers University, Piscataway, NJ, USA
M. Gochfeld, Environmental and Community Medicine, Piscataway, NJ, USA

doi:10.1006/rwos.2001.0231

Introduction

Gulls belong to the family Laridae and terns to the family Sternidae, although many authorities treat them as subfamilies (Larinae, Sterninae) of a single family, the Laridae. Skimmers belong to the Rynchopidae. Gulls, terns, and skimmers, all members of the order Charadriiformes, are similar in many respects, but they differ significantly in many morphological, behavioral, and ecological ways.

Gulls and terns are generally diurnal species that perform most of their breeding, foraging, and migrating activities during the day, while skimmers are largely nocturnal, and forage and court mostly at night. The only gulls that are primarily nocturnal during the breeding season are the swallow-tailed gull of the Galapagos Islands and the gray gull that breeds in the deserts of northern Chile.

Of all seabirds, gulls are among the least specialized, and occupy a wide variety of habitats from the high Arctic and subAntarctic islands, to tropical sea coasts, and even to interior marshes and deserts. In both breeding and feeding, gulls are generalists, and their overall body shape reflects their lack of specialization to any one foraging method, food type, or nesting habitat. Gulls are highly gregarious birds that breed, roost, feed, and migrate in large colonies or flocks.

Terns and skimmers are more specialized than gulls, both in their breeding habitat and in their foraging behavior, and skimmers have a highly specialized morphology and feeding behavior. While individual species of gulls, such as herring gull, may breed in many different habitats, ranging from dry land to cliffs, species of terns and skimmers breed in fewer habitats, and some are quite stereotypic in their habitat selection. Gulls feed in more different habitats on many different foods, while terns feed mainly over water by plunge-diving or dipping. Skimmers have one of the most unique feeding methods, skimming the water surface.

Taxonomy

The gulls are a worldwide group of about 51 currently recognized species with the main diversity occurring in both north and south temperate latitudes. Terns are also a worldwide group of about 44 species, with the main diversity occurring in tropical as well as temperate latitudes, while each of the three species of skimmers has a more limited distribution, one each in the Americas, Africa, and Asia (scientific names given in **Tables 1** and **2**). There is a tendency for taxonomists working at higher categories to lump genera and families together, where specialists on particular groups are more likely to emphasize differences within the group, by generic splitting – the approach followed here.

Gulls

There are several natural subgroups among the gulls, most of which can be assigned either to the large white-headed or the small dark-hooded tribes. On behavioral grounds, emphasizing the commonality of display patterns, Moynihan treated all gulls in the genus *Larus*. Most taxonomists, however, separate some relatively unique gulls into their own genera, including the swallow-tailed gull (*Creagrus*), of the Galapagos, and several Arctic species, including Ross's gull (*Rhodostethia*), ivory gull (*Pagophila*), kittiwakes (*Rissa*) and Sabine's gull (*Xema*). Less often two south temperate species, the dolphin gull (*Leucophaeus*) and occasionally the Pacific gull (*Gabianus*) are separated as well.

Terns

The main groups of terns include the black-capped terns (mostly in the genus *Sterna*), marsh terns