4

Ecosystems

Patterns, Processes, and Paradigms

As part of the celebration of its seventy-fifth anniversary, the British Ecological Society conducted a survey of members in which individuals were asked to list the 10 most important ideas in ecology (Cherrett 1989). At the top of the ranked list was "The Ecosystem," and nearly 70% of the respondents included it somewhere on their lists. This is indeed appropriate because the ecosystem is at the foundation of ecology (e.g., McIntosh 1985, Anderson and Kikkawa 1986, Waring 1989, Real and Brown 1991, Toft and Mangel 1991, Hagen 1992, Likens 1992, Golly 1993).

Our goal in this chapter is to consider how one can think about ecosystems and the marine mammals that are part of them. We focus discussion on different ways of thinking about ecosystems, in terms of patterns, processes, and paradigms. We accomplish the task by considering a number of factors exemplified by real ecosystems described in the literature. Various characteristics of ecosystems emerge to form concepts of crucial practical importance. We consider elements of variability in time and space, and the complexity and intensity of interactions among species that also differ in time and space. The concepts we describe are often interrelated and apply to all ecosystems. We begin with what ecosystems are, consider the various concepts, and end with discussion and examples of practical application.

Defining the Ecosystem

The ecosystem is the community of organisms, the physical environment, and the interactions between and among organisms and abiotic environments. This definition avoids a description of the physical boundaries of the ecosystem. For the practical questions regarding marine mammals, the boundaries will perforce be vague and determined to some extent by the kinds of questions being asked. This definition leads to two crucial questions: what is a community and what is the nature of the interactions?

There is still disagreement about the meaning of a community of organisms (e.g., Price et al. 1984, Diamond and Case 1986). Here we adopt Fager's (1963:415) concept that communities are "recurrent organized systems of organisms with similar structure in terms of species presence and abundances." In other words, communities consist of mixtures of organisms. A given mixture can vary over time and space, but there is consistent pattern to the mixture, even if

it can only be described in terms of probabilities (Fager 1957, 1963; Hubalek 1982).

There are alternative definitions. For example, Stenseth (1985:61) defined a community on the basis of systemic integrity or stability as "being such that neither a mutant strategy of an existing species nor any new species can invade." This is a fundamentally static viewpoint, whereas Fager's concept is fundamentally dynamic.

It is difficult to study communities at any large scale in a fully experimental manner (Hairston 1981). We must rely on good thinking, clever experiments (when possible), use of opportunities provided by natural perturbations ("natural experiments"), and thoughtful interpretation of data to discern relationships. Because we are far from having a science that is as sophisticated as ecosystem organization, we need to alternate our thinking between the particular and the general. Thus, it is important to know a few systems thoroughly, but to think broadly. We must adopt a pluralistic approach to understanding communities and ecosystems, which means "using a diversity of methodologies to obtain data, and a diversity of models to interpret data" (Diamond and Case 1986).

Large Marine Ecosystems, Fisheries Resources, and Marine Mammals

Many marine mammals are found in large marine ecosystems (LMEs) (Sherman 1990, 1991) that are located around the margins of the ocean basins and are characterized by distinct physical and biological features. About 95% of the annual production in the world's oceans is found in such areas (Bardach 1990). We use recent reviews of LMEs (Sherman and Alexander 1986; Sherman et al. 1990, 1991; Sherman 1994) to help identify some of the main concepts for thinking about ecosystems, particularly coastal upwelling areas.

Coastal upwellings are caused by winds blowing warm surface waters offshore so that cold bottom water containing nutrients rises to the surface. The five major coastal upwelling areas in the world are the California, Peru, Canary, Benguela, and Somalia Currents. These upwelling areas support a mix of species and generally contain the world's most productive fisheries. Other important upwelling areas are off the coasts of India, Java, and Costa Rica. Although upwelling areas constitute only 0.1% of the ocean surface, they produce half of the world's commercial fish harvest (Frye 1983; also see Sherman 1991:6–10). They are important areas for marine mammals as well.

The small geographic extent but large production of these upwelling areas (Table 4-1) leads to the first concept in the study of ecosystems:

Table 4-1. Productivity in Different Ocean Regimes

Ocean Regime	Standing Stock of Finfish Biomass (tons/km²)
Open continental shelf with upwelling circulation	
Tropics	24–45
Medium latitudes	40–60
Higher latitudes	30–40
Open continental shelf without upwelling circulation	
Tropics	15–30
Medium latitudes	25–45
Higher latitudes	20–35
Wide marginal seas	25–45
Semienclosed seas	12–288
Open ocean	
Low latitudes	3–6
High latitudes	5–12

Source: Bax and Laevastu (1990).

Concept 1: Patchiness and Variability in Space and Time Are Characteristics of Most Ecosystems

The study of marine ecosystems requires methods for investigating patchiness and variability. For example, the emerging technologies of earth-orbiting satellites, geographic information systems, and spatial statistics have the potential to be of great importance for the study of ecosystems.

Natural subdivisions of the ocean are delineated by the presence, size, and depth of the continental shelf, current systems and their boundaries, and regimes of temperatures (Bax and Laevastu 1990:190). Because of this complexity, understanding ecosystems holistically requires us to consider numerous cause-and-effect relationships, rather than focusing on a single cause or effect. In this sense, ecosystem science is similar to evolutionary biology because "explanations of all but the simplest biological phenomena usually consist of sets of causes" (Mayr 1976:370). For example, the walleye pollock (*Theragra chalcogramma*) supports a large fishery in the Bering Sea and the sources of mortality are varied. In addition to diseases and parasites, large predators cause substantial mortality (Table 4-2). Take by apex predators is estimated from abundance estimates, some food-habit data, and assumptions about consumption rates. Apex predators (marine mammals and birds) are believed to be responsible for about the same amount of predation as fishing, but neither is the main cause of mortality of walleye pollock. Thus, determining the cause of a change in walleye pollock population size must consider a variety of possibilities in addition to fishing mortality. Likewise, determining the cause of food-related declines in predator populations must consider more than fishing mortality.

Table 4-2. Sources of Mortality of
Walleye Pollock in the Bering Sea

Source	Contribution (%)
Other pollock (cannibalism)	61
Catch	9
Apex predators	9
Squid	3
Other fish	18

Source: Bax and Laevastu (1990).

We now turn to some specific LMEs chosen because they have implications for marine mammals and exemplify the concepts for thinking about ecosystems. Further details about particular LMEs can be found in publications by Sherman (1986, 1994) and Sherman et al. (1990, 1991).

The Weddell Sea (Hempel 1990) is a polar sea that has seasonal or permanent ice cover, year-round low temperatures, and intense seasonality in solar radiance. It contains a deep (approximately 100 m) surface mixed layer that is not a good environment for phytoplankton development. Annual primary production is poor and highly seasonal. The zooplankton are mainly a species of krill, *Euphausia superba*, and copepods. Many fish species depend upon the benthos for food. The top predators are mainly Weddell seals (*Leptonychotes weddellii*) and crabeater seals (*Lobodon carcinophagus*), emperor penguins (*Aptenodytes forsteri*), Adélie penguins (*Pygoscelis adeliae*), and southern minke whales (*Balaenoptera bonarensis*) and killer whales (*Orcinus orca*). Eight major land-based breeding sites are shared by emperor penguins and Weddell seals (150,000 adult penguins and 20,000 adult seals). Weddell seals feed on silverfish (*Pleuragramma antarcticum*) in summer and icefish in winter. Emperor penguins feed on krill, squid, and silverfish. Thus, the prey species are subject to a variety of sources of mortality.

Variability in sources of mortality is a common feature of ecosystems (Incze and Schumacher 1986; also see Fig. 4-1). Variability in top predators, combined with other biotic elements and variability in time and space, leads to:

*Concept 2: Ecosystems are Characterized by
Multiple Cause-Effect Relationships among
Biotic and Abiotic Ecosystem Components*

During at least one warming period, catches of Atlantic cod (*Gadus morhua*) in waters off western Greenland rose significantly (Hovgard and Buch 1990). This was followed (around 1970) by a cooling period in which cod catches decreased abruptly. During a second very strong cooling

(1982–1983), catches of cod declined to almost zero. This nearly total collapse can be traced to a combination of recruitment failure, surface transport of larvae, and changes in fishing technology and effort (Hovgard and Buch 1990:38).

The Caribbean Sea (Richards and Bohnsack 1990) is the second-largest semienclosed sea in the world. It contains many islands, most of which are small, nonindustrialized countries. Between 1976 and 1985, 38 Caribbean countries reported catches of fish, crustaceans, and mollusks. The fishery resources included spiny lobsters (*Panulirus argus*), coral reef fishes, turtles, conches, and sea urchins.

Several epizootics occurred recently in this ecosystem. A massive fish kill occurred in the reefs in 1980, the cause of which is still unknown (Richards and Bohnsack 1990). In 1983 there was a mass mortality of sea urchins (*Diadema* spp.); in many areas 98% of the population died (Lessios 1988). In areas where the urchins have recovered, the size distribution of the population has changed considerably even though the total biomass has not (Levitan 1988). Because urchins eat algae, and the urchins temporarily disappeared, the reefs are now carpeted by macroalgae that are smothering the corals. From these examples, we derive:

*Concept 3: The Consequences of Events at One Trophic Level
Often Will Be Manifested across Many Other Trophic Levels*

Fish and invertebrate resources of the Caribbean are transboundary resources (i.e., they are shared by two or more countries), but they are not treated as such, often with devastating consequences. Richards and Bohnsack (1990:51) noted that "many of the countries are poor and suffer overpopulation problems, but because of natural beauty and mild climate they are actively pursuing growth through tourism expansion. . . . the real crisis lies in the lack of coordinated support among the 38 nations to monitor the system." From this, we derive:

*Concept 4: Organisms Do Not Recognize Political Boundaries
and Management Should Be Structured Accordingly*

The sea urchin recovery in the Caribbean also reminds us that organisms adapt to new conditions through changes in behavior, development, and life history, as well as genetics. Early views of the ecosystem tended to focus on energy flows (Toft and Mangel 1991), but in a seminal paper Fowler and MacMahon (1982) argued that the structure and functioning of ecosystems can be explained effectively by the processes of selective extinction and speciation. Their ideas can be summarized as follows: new species are produced
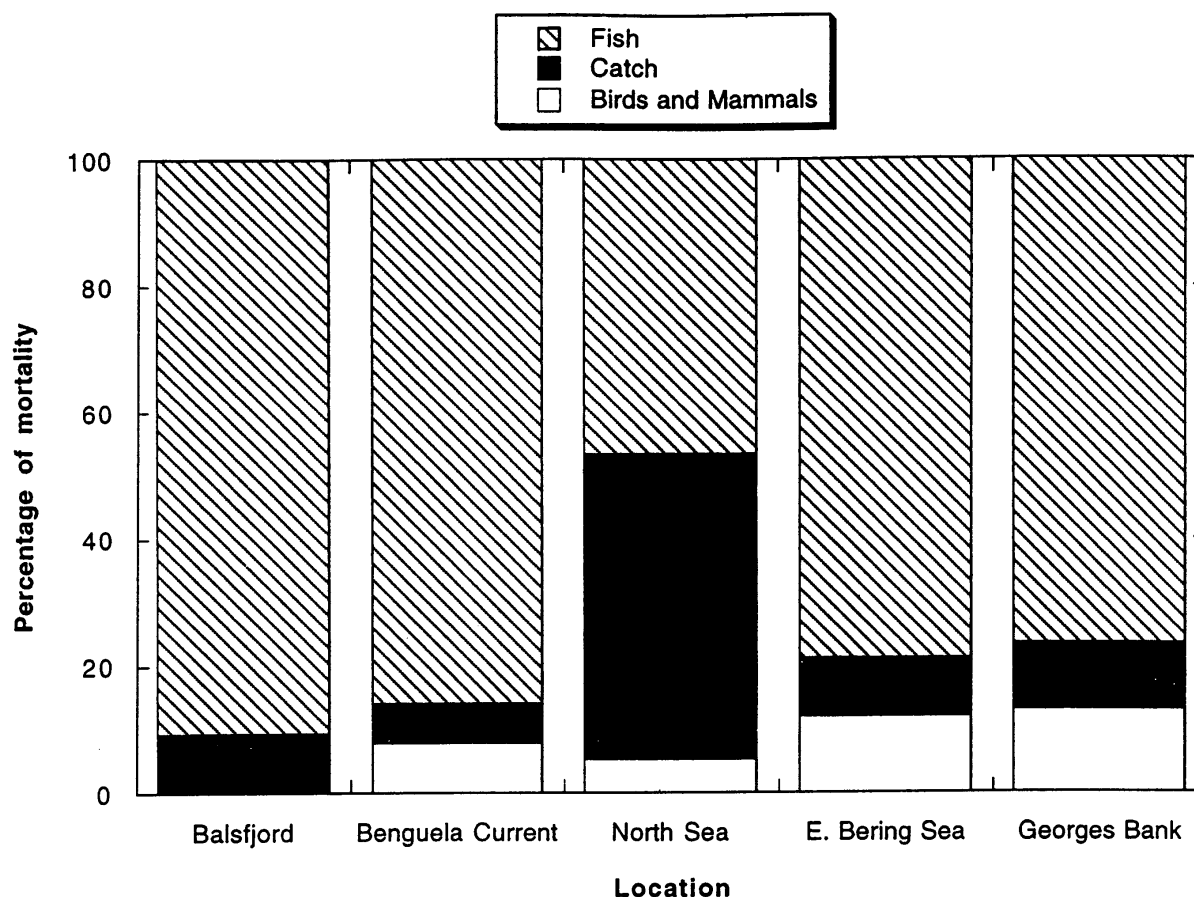
Figure 4-1. Sources of major mortality of fish in five different ecosystems, illustrating the variability of the sources. (From Bax and Laevastu 1990)

through natural selection and are subject to selective extinction and differential speciation. This means that the presence of species and their roles in ecosystems are not random but are the results of natural selection (especially at the species level). Thus, the current structure of living resource systems is shaped by evolutionary history (Fowler and MacMahon 1982, Crozier 1992), and resource managers must act within the constraints imposed by that history. This understanding can be summarized as:

Concept 5: Ecosystems Should Be Viewed as the Current State of an Ongoing Process of Selective Extinction and Differential Speciation

Furthermore, it is important to recognize that the ongoing processes of selective extinction and differential speciation involve considerable amounts of chance. Even if starting conditions are the same, we should not expect the same outcome. Instead, we should expect a distribution of poten-

tial ecosystem configurations from the same starting conditions. This concept, along with those covered earlier (over time and space) lead us to:

Concept 6: Change Is the Rule, Not the Exception, in Ecosystems

For example, the sources of variability and the strengths of various biotic interactions in marine mammal populations and other components of marine ecosystems may themselves vary over time and among ecosystems. Sherman (1990:215) offered the following hypotheses concerning changes in fish populations.

- In the Oyashio, Kuroshio, California, Humboldt, and Benguela Currents, and Iberian coastal ecosystems, increases in clupeid populations were due to natural environmental perturbations.
- In the Yellow Sea, the northeastern United States continental shelf, and Gulf of Thailand ecosystems, declines
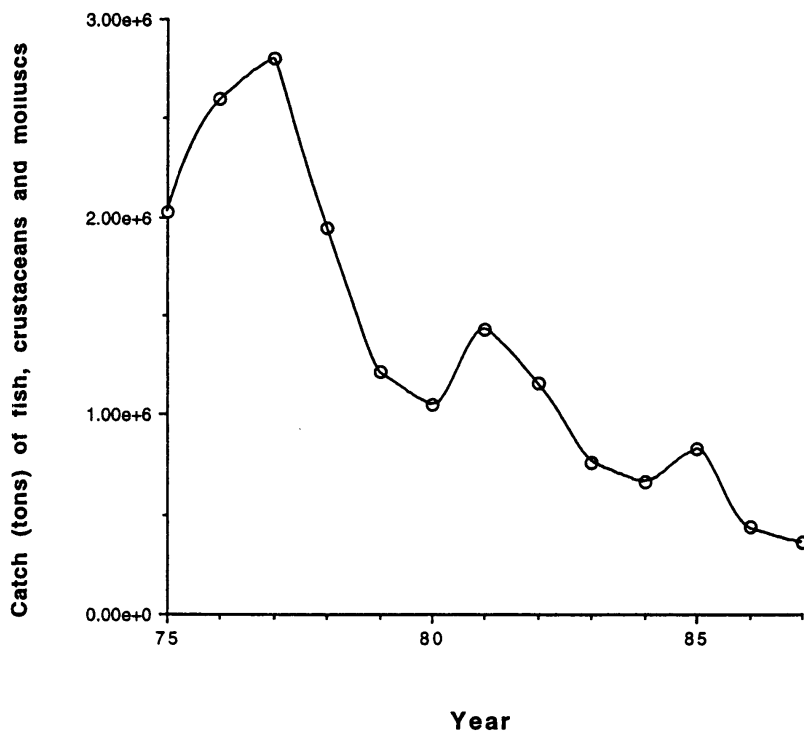
Figure 4-2. Collapse of the Barents Sea fishery. (Data from Borisov 1991)

of fish stocks were caused by a combination of excessive fishing mortality and predation.

• In the Great Barrier Reef ecosystem, predation on corals by the crown-of-thorns starfish (*Acanthaster planci*) interrupted the existing food chain between primary production and the fish components of the reef ecosystem.

• In the East Greenland shelf, Barents Sea, and Norwegian shelf ecosystems, natural environmental perturbations, such as large-scale changes in water movement and temperature, caused major shifts in the biomass of different fish stocks.

• In the Baltic Sea ecosystem, human-induced perturbations (mainly nitrate enrichment from agricultural runoff) increased primary production levels and ultimately increased the abundance of some fish stocks.

• In the Antarctic marine ecosystem, changes in krill abundance are caused by a combination of predation and environmental factors that may include changes in the ice edge, water movement and temperature, and ozone depletion.

The Barents Sea (Borisov 1991, Rosenberg et al. 1991) was traditionally one of the most productive areas of the ocean, with fish productivity (the main commercial species were capelin, herring, cod, haddock, redfish, and halibut) nearly three times that of the mean ocean fish production ($720 \, kg/km^2$ versus $225 \, kg/km^2$). This is no longer true (Fig. 4-2). A retrospective analysis points to two main reasons

for the recent collapse in the productivity of the Barents Sea: (1) a natural cyclic decrease in the inflow of warm Atlantic water in the 1980s and (2) the additional heavy stress of excessive fishing mortality, which impeded replacement. Overfishing occurred because fishery regulation was inadequate.

A further example of this kind of variability is seen in the California Current (MacCall 1990, Mullin 1991). This current sweeps southward along the west coast of North America. Coastal upwelling occurs along the more exposed sections of the coastline, creating a nutrient-rich environment that is highly productive. Natural variability is evidenced by changes in the deposition rates of sardine and anchovy scales found in bottom cores (Smith and Moser 1988).

During the 1800s, many marine mammal species in the ecosystem were seriously overexploited and driven to near extinction (both economic and biological). These include the northern fur seal (*Callorhinus ursinus*), the Guadalupe fur seal (*Arctocephalus townsendii*), the California sea otter (*Enhydra lutris*), the northern elephant seal (*Mirounga angustirostris*), the gray whale (*Eschrichtius robustus*), and the California sea lion (*Zalophus californianus*). We can only speculate how these reductions affected other ecosystem components. Under protection, some of these species are now recovering. We need methods to predict how the recovered stocks will influence ecosystem structure and productivity.

Table 4-3. Biological Interactions across Different Trophic Levels

Trophic Level	Main Biotic Interaction Limiting Abundance
A. The view proposed by Hairston et al. (1960) in which competition is the main factor limiting populations	
Piscivores	Competition
Planktivores	Predation
Producers	Competition
B. An alternative view proposed by Schoener (1989) in which predation and competition play more balanced roles	
Medium or large piscivores	Competition
Small piscivores or large planktivores	Predation
Small planktivores	Competition
Producers	Predation

MacCall (1990) showed that anchovy population size affects pelican production but not vice versa (because pelicans, when compared with all other predators, consume a relatively small number of anchovies). This is an example of a "one-way effect": components of the ecosystem affect a focal stock but not vice versa. On the other hand, California sea lions and northern elephant seals may consume 1.5 million mt of fish (Riedman 1990). Such consumption is likely to have a direct effect on fish population dynamics (that is, a two-way effect, discussed in more detail below). Likewise, sea otters consume large quantities of abalones, clams, and sea urchins and, as they reoccupy their former range in California, are having impacts on fisheries that developed in their absence. Consumption of sea urchins that eat macroalgae may be enhancing growth of kelp and kelp communities, including kelp-associated fish species valued by recreational and commercial fisheries (Estes and VanBlaricom 1985, Wendell et al. 1986). We thus conclude:

Concept 7: Interactions between Components of Ecosystems May Be Both One Way and Two Way

Interactions among biotic components of ecosystems are often portrayed by food webs (Schoener 1989, Collie 1991, Dagg et al. 1991, Yoder 1991). Brown et al. (1991) quantified the prey consumption requirements of several species in the Gulf of Mexico. They considered one cetacean (the bottlenose dolphin, *Tursiops truncatus*) and 33 species of fish, including 12 oceanic pelagics, 13 coastal pelagics, 5 reef fish, and 3 estuary-related species. Their work shows the complexity of linkages between predators and prey in food webs. Moreover, food webs are snapshots—the interactions between species often depend on the life history stage: fish that are prey as larvae or juveniles may be predators as adults. We summarize this by:

Concept 8: Marine Food Chains Are Complex, and in Many Species the Trophic Level Varies with Life Stage

What Structures Communities and Ecosystems?

When considering the factors that structure communities within ecosystems, Price (1984) stressed the importance of alternative paradigms and suggested a focus on resources, the response of individuals, and the response of populations to those resources. For more than 30 years, the dominant model was that of Hairston et al. (1960; also see Hairston and Hairston 1993). This model focused on three trophic levels, with competition as the major factor limiting populations (Table 4-3, A). That is, top predators are limited by competition among them for prey, the midtrophic-level planktivores are limited by predation from above, and the producers are once again limited by competition for resources, usually abiotic ones.

Schoener (1989) proposed an alternative model with four trophic levels, obtained by separating the larger predators from the smaller ones (Table 4-3, B). Schoener's model stressed the equal importance of competition and predation in the interactions. Thus:

Concept 9: Competition and Predation Both Contribute to the Structuring of Food Webs, But Their Relative Importance Varies

Predicting the effects of competition and predation is fraught with difficulty. For example, in approximately 20% of published studies, predator removal resulted in decline (rather than increase) in the prey population (Pimm 1991); these results should caution us about assuming that culling of marine mammal stocks will improve fisheries.

Next we consider how stocks interact with their physical environment. For example, how do physical processes, such

as oceanic transport, affect food chain dynamics? The most common view is based on the assumptions of stationarity and one-way linkage. To understand these, assume that in a particular environment, E, we observe a stock level, S, and recruitment level, R. Now assume that the environment is perturbed to E′, the stock to S′, and recruitment to R′. The assumption of stationarity is that when the environment returns to E after the perturbation is removed, the stock will return to S, and the recruitment to R (Walters 1987a,b; Walters and Collie 1988). This assumption allows one to draw a "stock-recruitment" curve without regard to how the stock got to where it is.

An alternative hypothesis is that the history of the stock matters in determining current recruitment. In other words, when the environment returns to E, the stock may not return to S or, even if it does, recruitment may not return to R (recall the sea urchins). The assumption of one-way linkage is that the environment affects the stock, but not vice versa. An alternative possibility is that the stock has itself changed the ecosystem, so that even when the perturbation is removed, the environment may equilibrate to a completely different state, E″, even if the stock returns to S. Herring stocks show the characteristics of two-way linkages (Walters 1987a). The assumption of two-way, nonstationary linkages is that the stock affects the ecosystem, which in turn affects the stock, which in turn affects the ecosystem. These linkages mean that the ecosystem may exist in more than one configuration and that, after relaxation of a perturbation, the system need not return to its preperturbation state. We should thus expect alternative population, community, and ecosystem states, none of which may persist for long periods of time.

The linkages just discussed are implicitly temporal phenomena. Ecosystems also contain many spatial scales. For example, in the California Current, the communities of zooplankton and their predators involve characteristic spatial scales of 50 m for fish schools, 300 m for plankton aggregations, 1,000 m for gaps between plankton aggregations, and 10,000 m for gaps between fish school groups (Smith et al. 1989). Assessment of the possible pros and cons of alternative approaches to fishery and marine mammal management must consider both the temporal and spatial variability in food webs and linkages between components of the web.

Marine Mammals as the "Canary in the Cage"

The notion of a "healthy ecosystem" has different meanings to different people. For example, from the perspective of some fishermen, the healthiest ecosystem might be one that is entirely devoid of marine mammals. Most scientists and conservationists do not share this perspective. However, one thing that can be agreed upon is that virtually all ecosystems have suffered some kind of human impact in recent times. For marine ecosystems, pollution and poor fishery practices, particularly those resulting in large bycatch, are major sources of stress, but they are not always acknowledged as affecting the ecosystem. For example, although there has been recent discussion of the relative costs and benefits of high-seas driftnet fisheries (Burke et al. 1994), there has been little study of the potential ecosystem effects of these fisheries (Dayton et al. 1995; Northridge 1995; Northridge and Hofman, this volume).

Can top-level predators, such as marine mammals, be used as "canaries in the cage" to assess the health of ecosystems in the same way canaries were used by miners to test quality of the air in a mine shaft? Levels of contaminants in certain marine mammals that die and wash ashore might provide a useful indicator of certain pollutants in coastal marine ecosystems, particularly pollutants that are lipophilic and are bio-magnified in marine food webs. However, robust or declining marine mammal stocks are not necessarily a reliable indicator of healthy or unhealthy ecosystems. The following example illustrates why the health of a component population may not be an indicator of the health of the ecosystem.

Suppose that a stock grows according to the logistic equation:

$$N(t + 1) = N(t) + rN(t)\left(1 - \frac{N(t)}{K(t)}\right) \tag{1}$$

where $N(t)$ is the number of individuals at the start of year t, r is the maximum per capita reproduction rate, and K is the carrying capacity. If r is not too large (to avoid deterministic chaos) and carrying capacity is fixed, then if the population starts below K, it will increase toward K; if it starts above K, it will decrease toward K.

Now assume that habitat degradation results in an annual decrease of carrying capacity. Thus, we append dynamics for the carrying capacity

$$K(t + 1) = fK(t) \tag{2}$$

where $f < 1$. In each year, carrying capacity decreases, and thus population size decreases. However, the decrease in population lags considerably behind the decrease in carrying capacity (Fig. 4-3), so that the marine mammal stock gives an overly optimistic view of what is happening in the environment. Things are worse than they appear, using the marine mammal populations as the "canary in the cage."

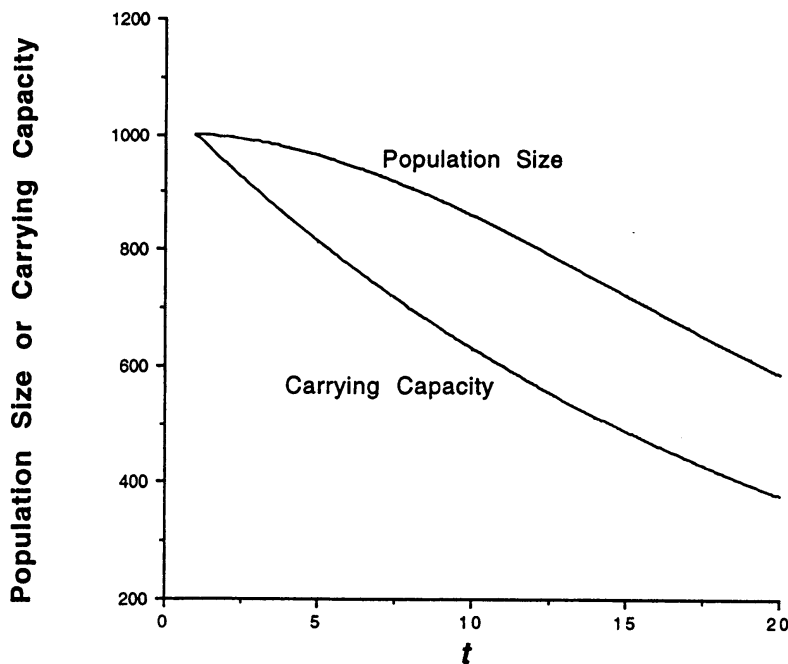The converse is also true when carrying capacity increases: the ecosystem, with "health" indexed by the

Figure 4-3. When a logistically growing population starts at carrying capacity, but the carrying capacity declines, the population declines but at a slower rate over time (t) than the carrying capacity. Parameters for this computation are r = 0.07 (a reasonable value for marine mammals), K = 1,000, and f = 0.95. Thus, the population does not provide an accurate picture of the decrease in habitat.

carrying capacity of the target species, is better off than indicated by the population trend. Thus we are led to:

Concept 10: Top Predators Such as Marine Mammals May Have Population Dynamics That Prohibit Using Their Abundance and Productivity as Effective Indicators of the Current Health of Ecosystems, Although They May Be Good Indicators of the Long-Term Effects of Certain Pollutants

In fact, it is unlikely that we can determine the health of ecosystems by monitoring any single species. A human metaphor may help: a healthy liver does not imply a healthy heart, or a healthy person for that matter. However, just as a diseased liver indicates an unhealthy person, a problem with one particular species could indicate an ecosystem-level problem. Unfortunately, finding a problem with a species often does not identify the cause or scale of the problem, particularly when the problem is not the product of direct human-caused mortality.

To assess ecosystem health, we must consider a variety of indicators. For example, Mullin (1991) described ways of measuring secondary production in the California Current ecosystem: indirect methods include extrapolation from primary production, metabolic mass balance, productivity/biomass ratio, biochemical measures, and egg production; direct measures involve counts at "sampling stations."

Another form of indirect observation involves using harvest data. There is a long history in fisheries science of using measures of catch and fishing effort to estimate and monitor relative abundance (Hilborn and Walters 1992, Smith 1994).

These methods are complicated by the generally nonlinear and unknown relationship between the abundance of the stock and catch. In the Southern Ocean, for example, the most accurate index of krill abundance in the areas commonly fished is derived from the catch per fishing effort per search time (Mangel 1989, 1990). The catch per fishing effort provides an index of the density of krill once the fishing vessel is in a patch of krill, and the reciprocal of search time provides an index of the density of such patches of krill. However, changes in characteristics of certain krill predators, such as egg production and hatching and fledging success of Adélie penguins, may provide a more accurate and sensitive index of regional krill abundance.

Management of Ecosystems and Conservation

Conservation is concerned with how we sustain renewable resources in ecosystems so that future options are maintained (Collie 1991, Sherman 1991). There are many causes for the loss of resources in ecosystems, ranging from blooms of noxious phytoplankton (Smayda 1991) to marine pollution caused by humans (Marine Mammal Commission 1993). Ludwig et al. (1993) stressed that human social factors must be given greater prominence than they have been in the assessment and management of resource systems. In his classic work, Clark (1976, 1990) demonstrated that we cannot think of biology or economics alone when considering the use of renewable natural resources. He derived what might be called the "golden rule of bioeconomics," which

relates the optimal size of the harvested stock to the growth rate of that stock and the interest rate that money can earn. This rule helps to explain some of the disastrous depletions of whale and fish stocks caused by commercial exploitation. Simply put, if the sole owner of a resource can earn more money in his or her lifetime (say, 8% per year) by killing and selling all of his or her slowly growing (say 3% per year) animals, then the economically "optimal" action for that individual is to drive the stock to extinction. Other factors common to the oceans, such as uncertainty concerning the future of the resource (Roughgarden and Smith 1996) and competition between harvesters, only exacerbate the situation. The implications of Clark's work are extremely important because they show that in many situations, the economically optimal action is to drive a stock or species to extinction. This means that we must perforce think of management and conservation with criteria broader than purely economic ones. A new kind of economics, based on ecological science, is required (Roughgarden and Smith 1996). It also means that biological-ecological considerations, not market demand, must set the limits on harvest levels.

Principles for Ecosystem Conservation

It is common now to speak of "ecosystem management." It would be better to speak of "ecosystem approaches" to management and to recognize from the outset that what is managed is almost always human intervention in ecosystems. Even those cases in which humans are removed completely from ecosystems involve managing human actions. Mangel et al. (1996) recently articulated a set of basic principles for the conservation of wild living resources.

An Example: Krill Fisheries in the Southern Ocean

In cases in which marine mammals are predators of the same fish or shellfish that humans harvest (Alverson 1992), how should we account for this competition? A particularly interesting example is the fishery for krill in the Southern Ocean, where nearly all fish, birds, and mammals are no more than one or two steps in the food chain away from krill (Everson 1992, Hunt et al. 1992, Nicol and de la Mare 1993 and references therein). Thus, a fishery for krill will potentially have effects on at least three trophic levels (concept 3). The fishery for krill has developed in the past 20-odd years and reached a peak catch of more than 500,000 mt of krill. There is inter-annual consistency and predictability in the fishing locations, suggesting that there is some constancy to the spatial and temporal patterns in the abundance of krill (concept 1).

It is clear that the standing biomass of krill is enormous.

Indeed, estimates of annual production range from 75 million to more than 1,500 million mt. The issue regarding krill harvest is how much of that can be taken from highly localized areas near the breeding colonies of marine mammals and birds (Butterworth et al. 1991, 1992; Nicol and de la Mare 1993) without affecting those colonies in unacceptable ways. In the early 1980s the Convention for the Conservation of Antarctic Marine Living Resources was concluded for dealing with this and other issues.

A motivation for the fishery for krill was the presumption that overharvesting and decline of the krill-eating whale stocks left a vast "surplus" of krill "unaccounted for" or "going to waste" each year that could be harvested (Mackintosh 1970). The argument presumed that the standing stock of krill could be partitioned, with a fraction going to the whales and other marine mammals, a fraction to the fish, a fraction to the birds, and so forth, and that when the whales were depleted, there was no response by the other predators to the increased availability of prey. Such a presumption violates the concepts about the complexity of food chains (concept 8), expecting multiple effects (concept 2), adaptability of organisms (concept 5), and change (concept 6). Furthermore, consistent with our concept of multiple causes, in at least one case it has been proposed that the observed increase in the abundance of at least some krill predators has nothing to do with the krill "surplus." Fraser et al. (1992) argued that the increase in penguin populations was due to a slow decrease in the frequency of cold years.

Article II of the Convention for the Conservation of Antarctic Marine Living Resources calls for harvesting and associated activities in the convention area to be carried out to (1) prevent any harvested population from being reduced below its maximum net productivity level, (2) maintain the ecological relationships between harvested, dependent, and related populations, (3) restore populations that have been depleted as a direct or indirect consequence of harvesting, and (4) prevent or minimize the risk of ecosystem changes that are not potentially reversible within two or three decades (see Hofman 1993 for a discussion of these and other features of the Convention).

In response to the developing fishery for krill, the commission established by the convention adopted "precautionary" krill catch limits in 1991 and refined them in 1992. In the first action, a cap of 1.5 million mt was placed on the annual catch in one of the most important fishing areas. It was further specified that if catch in that area exceeded the previously highest commercial take of 620,000 mt, then subarea quotas would be established. In the second action, a precautionary limit of 390,000 mt was established for the South Indian Ocean where there is currently exploratory fishing for krill. These catch limits were based on the work

of Butterworth et al. (1991, 1992) and are described in a less technical fashion in Nicol and de la Mare (1993). The models of Butterworth and colleagues are implicitly based on one-way linkages between krill and their predators, in which the predators have no effect on krill mortality. They also use a management goal of keeping the krill population size above an assumed critical level. The assumption of one-way linkages need not be true (concept 7), especially in cases in which interest is not in the entire Antarctic krill population but in those stocks that pass close to the land-based breeding colonies of predators. The Commission for the Conservation of Antarctic Marine Living Resources maintains a program of ecosystem monitoring to provide data that can be used to assess the status of the krill and their predators. As of now, however, available information is insufficient to ascertain the functional and numerical aspects of the linkages.

Conclusions

In this chapter we describe a set of general concepts to stimulate and guide further thinking about marine ecosystems and the marine mammals in them. These concepts reflect the view that ecosystems are dynamic and are the results of ongoing processes of speciation and extinction. Ecosystems are patchy in time and space and are characterized by multiple cause-effect relationships in which consequences at one trophic level are often experienced throughout the ecosystem. Interactions in ecosystems are sometimes one way and sometimes two ways. Marine food webs are expected to be complex, and both predation and competition play important roles in their structure and operations. Finally, ecosystems often cross international boundaries, which are human constructs not recognized by marine mammals or other biota.

Acknowledgments

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