Marine Functional Diversity

Ocean and land ecosystems may have different time scales for their responses to change

John H. Steele

The term *biological diversity* has the virtue of containing many different interpretations, scientifically and emotionally. A recent report (OTA 1987) suggested three technical meanings: genetic, species, and ecological diversity. I suggest a fourth category that needs to be considered, which I term *functional diversity*—the variety of different responses to environmental change, especially the diverse space and time scales with which organisms react to each other and to the environment.

The public is becoming increasingly aware of biological diversity losses imposed by human activity directly and through possible climatic change. Change as such is not new, and it is an integral element in systems. Concerns arise from the large scales of these changes and particularly from the rapid rates at which they may occur—rates that are much greater than any in the historical or even the geological past. Thus scientific and social interest focuses on the relative rates of change of so-called natural processes and of human interventions. In turn, this interest focuses on ecological aspects. How do ecological systems change through time? How diverse are these rates of change? How rapidly or slowly do communities respond to changes in their physical and chemical environments? In particular,

John H. Steele is a senior scientist at Woods Hole Oceanographic Institution, Woods Hole, MA 02543. © 1991 American Institute of Biological Sciences

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Changes can have major economic consequences without being ecological disasters

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I consider the response of marine communities to natural and human stresses, but in the context of current views of changes in terrestrial systems.

Marine and terrestrial ecosystems differ in their functional responses to environmental change. The current attention on climate focuses on time scales of several years to decades. I hypothesize that at these time scales marine systems are more closely coupled to their physical environment than are terrestrial systems (Steele 1985). I conclude that, in consequence, many open-sea systems respond to rapid changes in their overall environment, and they are adaptable in an ecological sense.

Comparison of land and marine systems

Trees, which are the longest-living component of terrestrial ecosystems, show changing geographic distributions with time scales usually measured in millenia (Delcourt et al. 1983). These changes are generally related to long-term large-scale climate trends such as the retreat of ice after the last Ice Age, 18,000 years

ago (Figure 1). But the probable rate of dispersion of forests is on the order of tens of kilometers per century (Davis 1989). Future geographical distributions can be predicted on the hypothetical rapid climate changes deduced from the large computer simulations. A 2–4° C increase in a century implies a northward movement of isotherms on the order of several hundred kilometers. Forests may not be able to keep up with this rapid climate change, and a disequilibrium in the overall ecological system is expected to result.

In the open sea, the longest-lived organisms are at the top of the food webs—just the opposite of the terrestrial system, where the oldest organisms are trees, which are primary producers (Steele 1985). For fish populations on the continental shelf, where we have the most data, we see changes in distribution where the spatial scales are comparable with forest patterns (Figure 1) but are much more rapid (Cushing 1982). A typical example is the sand lance (*Ammodytes* spp.), a benthic species of fish with pelagic larvae that lives on the continental shelf of the eastern United States (Figure 2). Sand lance distribution changed in three years as much as the boundaries of the hardwood forest moved in 5000 years.

Until recently, the major changes in fish populations were considered to result from fishing activities, which are certainly a factor. But other elements, particularly climate, contribute to these changes and may be dominant in the largest, longest-term fluctuations. These large variations in

abundance of fish stocks can have severe economic consequences. But are they ecologically deleterious? Do they upset the entire food web? Should we expect a breakdown in the overall marine ecological system similar to that predicted for the land?

Marine scales of response

Data from Georges Bank, describing the relative abundance of different species in the catches, shows that species changes can result in severe economic disturbance without any evidence of overall ecological deterioration. Figures 2 and 3 illustrate that the decline in the larger pelagic species such as herring and mackerel (Figure 4a) coincided with the increase in the sand lance. The North Sea shows a similar picture (Figure 4b), with the decline in the same large and commercially valuable pelagic species being balanced initially by an increase in smaller species, such as sand lance, that are used predominantly for animal feed. However, the most interesting feature of the changeover was the dramatic increase in the stocks of demersal fish species, such as haddock and whiting, that feed mainly on the sea bed. Are the simultaneous changes in the different species abundances shown in Figure 4 coincidental? Or are there causal links between the increase in one species and the decrease in another?

It is not clear whether succession—the slow and predictable sequence of dominant species—seen in terrestrial systems, occurs in the ocean. A focus of current research is to untangle the diverse functional interrelations that a population of one species has with its physical environment and with the other members of its biotic community. Some possible interactions can be seen in the population fluctuations of North Sea herring. The marked decline during the 1970s (Figure 4a) was associated with a decrease in recruitment of juveniles to the adult stock (Corten 1986). Over-fishing was blamed. But in the 1980s, there was a marked increase in numbers of larvae and juveniles before the sexually mature stock itself increased. This finding made it apparent that the increasing recruitment of larvae could not be ascribed solely to an increase in the adult stock (Rothschild 1986). Thus attention has focused on the

earlier life stages.

The striking feature of this development is the close correspondence between ocean currents and the life-cycle patterns of herring stocks (Figure 5; see Bailey and Steele in press and Corten 1986 for full discussion). The comparison illustrates not only the dependence on the average ocean-water circulation but the consequences of departures from this average. Data on interannual larval distributions (Corten 1986) suggest variable transport from the spawning grounds to the nursery areas. Numerical simulations of the wind-driven currents within the North Sea provide a possible mechanism (Backaus 1985). But inflow of water from the Atlantic is a dominant

feature (Figure 5) and can have effects lasting from several years to a decade (Dooley et al. 1984). Thus there may be several links between specific physical current patterns and different scales of climate variation. At the population level, such links are explained by a much closer interaction between the reproductive processes and the particular patterns of ocean currents and mixing.

This example may help to explain the importance of recruitment, the process by which populations of immature marine organisms settle into their adult habitats. Scientists are now examining the egg and larval stages of marine populations for factors affecting population density, es-
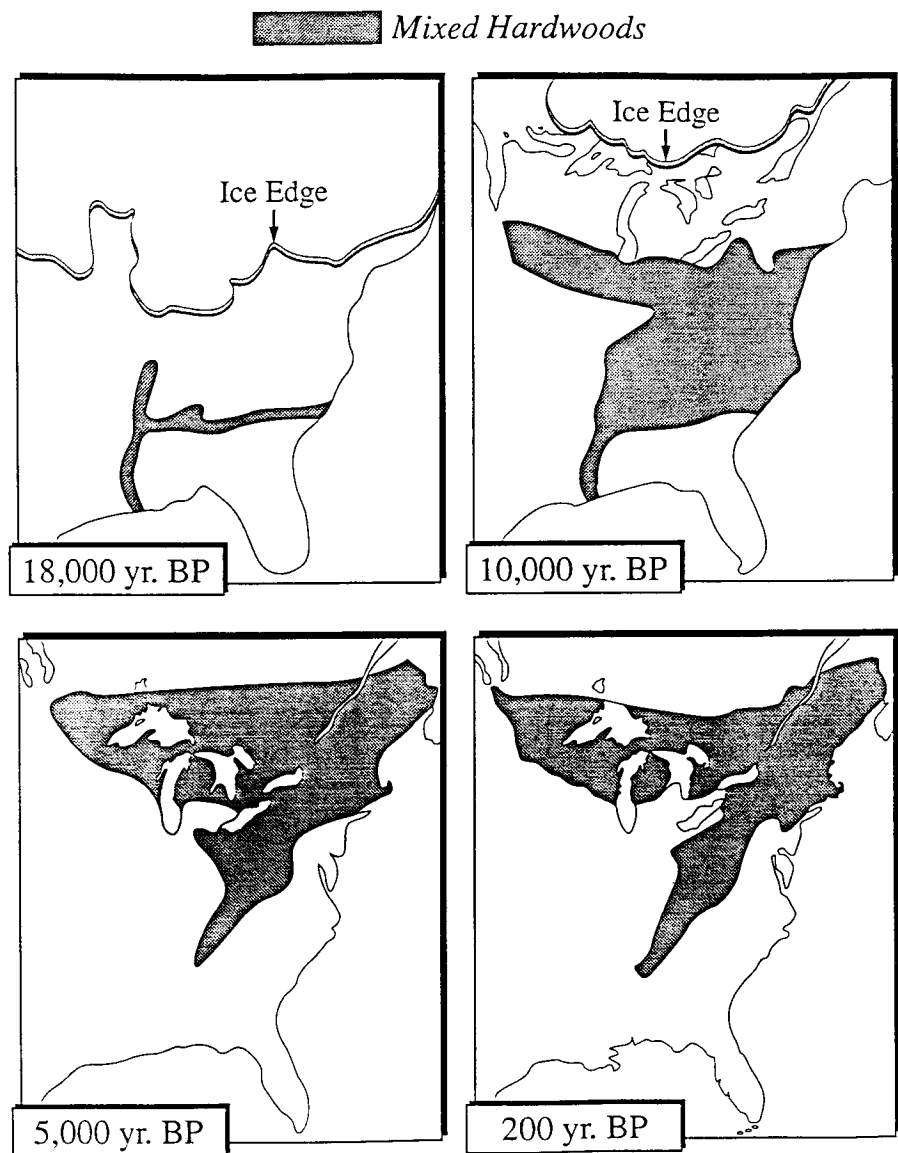

Figure 1. The changing distribution of hardwood trees since the last Ice Age. (After Delcourt et al. 1983.)
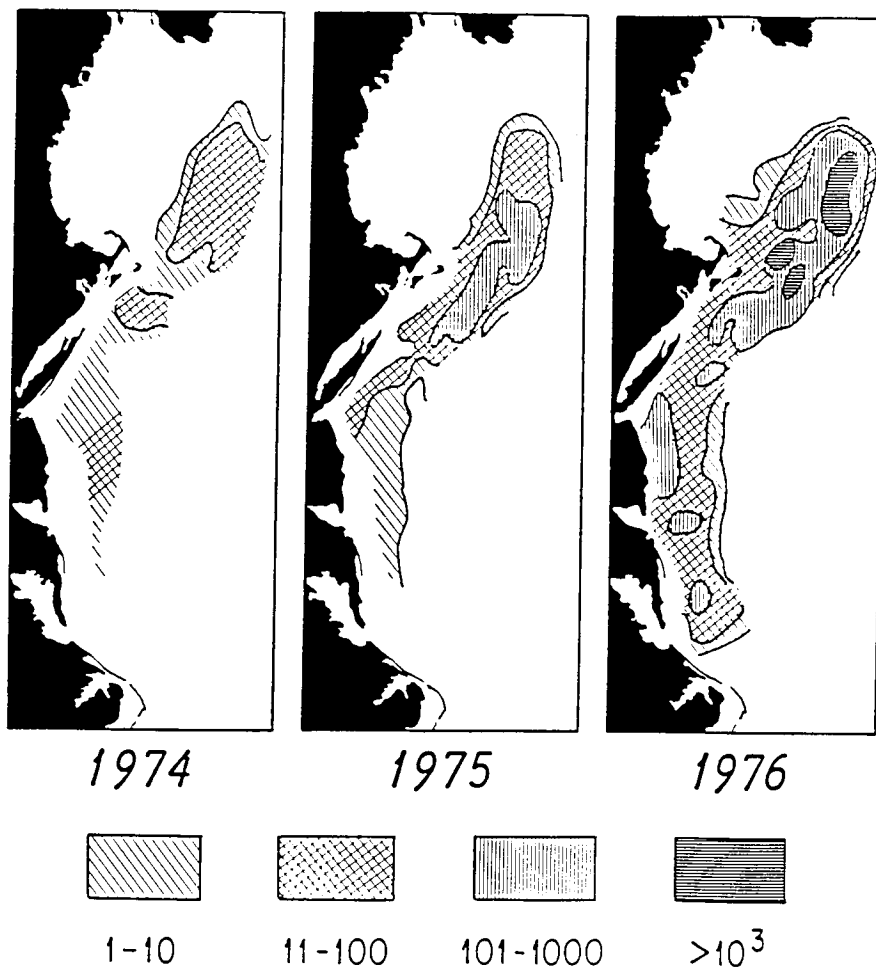
Figure 2. The changing distribution and density of the sand lance off the US East Coast from Cape Hatteras to Nova Scotia. (From Sherman et al. 1981.)

pecially variations in the physical dynamics at longer periods that are superimposed on the annual cycles. As in herring, in barnacle and reef fish populations (Roughgarden et al. 1988, Sale 1982), the effects of water movement on larval recruitment rather than adult competition for space may determine population densities.

Yet community interactions cannot be ignored. For example, the North Sea herring is part of a complex food web (Hardy 1924). In the last three decades, there have been changes in the relative abundances of herring and some of the planktonic organisms it consumes. These changes may be related to climate trends (Aebischer et al. 1990), but there have also been changes in demersal fish species (Figure 4). The food of demersal fish, such as haddock, is predominantly from the sea bed, so these fish occupy a different sector of the food web than herring

(Figure 6). But the collapse of the pelagic fish stocks in the North Sea during the 1970s corresponded to a marked increase in several demersal species (Figure 4). Even more striking, the subsequent return of the herring a decade later was accompanied by a severe decline in haddock. This reversal might be seen as a diversion of the energy flow from basic primary production between the pelagic and benthic components, but it has not proved possible to explain the switches in terms of particular causal processes in this web.

There are many other examples of striking switches in community structure; the Russell cycle in the English Channel (Southward 1980) consists of marked changes in the herring and pilchard populations during the last century. Primary explanations for each species are sought in terms of changes in the physical dynamics, but

those changes are insufficient to explain the community interactions where there are marked changes in balance and even in composition.

Three conclusions about changes in marine communities can be made:

- Large switches in open-sea marine communities can last several decades. These changes can have major economic consequences but cannot be considered as ecological disasters or even as being deleterious in any way within the marine systems.
- Such switches have occurred without human involvement, for example before heavy fishing was a factor, but they may be increased in frequency or amplitude by human actions.
- The effects of physical processes on particular populations during the early life stages can be explained, but observed changes at the community level have not been explained.

These conclusions differ greatly from the usual views of terrestrial changes. The focus in studies of terrestrial systems is generally on community interactions as the explanation for changing patterns in observations of species compositions.

Changes in the environment

The effects of fluctuations in the physical environment are usually treated as noise, depending on the time scales involved. Fluctuations are greater in terrestrial systems than in the ocean. For example, on top of the regular diurnal and seasonal cycles of temperature, there is a much larger unpredictable temperature variability on land than in the ocean. I have speculated that such variability has tended to result in the evolution of terrestrial adaptations that can eliminate or smooth out the consequences of this random component (Steele 1985).

On land, the coupling of ecosystems changes with large-scale trends in climate is observed at time-scales of centuries to millennia (Delcourt et al. 1983). But within the ocean it appears that responses to physical variability are found at decadal periods and may be closely coupled to variations in ocean dynamics.

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Comparing fish and trees

When we consider climate at the same time scales—from interannual to decadal—we see very different responses in marine and terrestrial systems, one illustration of functional diversity. These functional responses to changing physical environments depend on relative rates of growth and mortality, and these rates are known to be related to body size (Bonner 1965). Some elements of this diversity can be seen in the usual relations of size to trophic status when the pelagic marine and the terrestrial species are separated. Trees are the longest-lived organisms on land, whereas phytoplankton cells, the primary producers in the ocean, have lifetimes measured in days. There are several obvious biophysical reasons for these differences: among others, gravity and heat conduction. These differences in time scales must have an effect on the way the marine and terrestrial communities are structured.

The comparisons between trees and fish represent the extremes of pelagic marine communities and forests. What about the intermediate ecosystems? Should coral reefs and rocky shores be viewed as marine or terrestrial? It may be beneficial to use a combination of the classical terrestrial mechanism—competition for space—and the classical marine mechanism—larvae carried by currents.

The major difference between land and sea communities appears to be that marine systems have evolved to exploit regularities in the physical dynamics of the environment as part of their reproductive processes (Denman and Powell 1984) as well as using diffusive dispersal to counteract the longer-term consequences of variability in the physics. It has been pointed out by several ecologists, including Roughgarden (1988), that larval dispersal in marine communities provides for open systems, so that recruitment to areas where adults are not present can occur. This method of dispersion may allow populations in one area to live dangerously if there is always the possibility of recruiting larvae from elsewhere. Terrestrial systems can also recruit, but on much longer time scales, on the order of
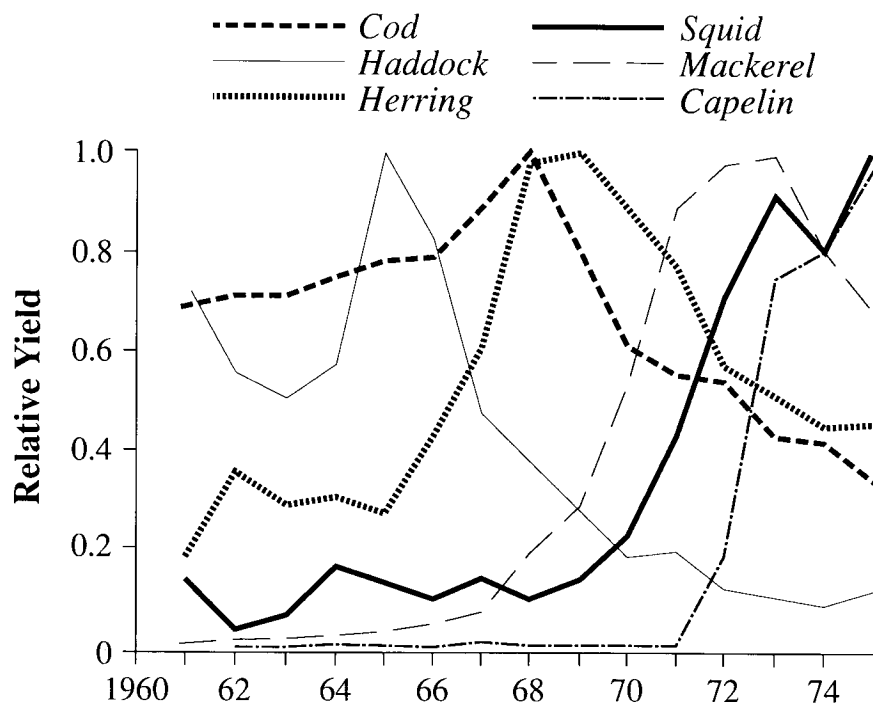
Figure 3. Relative yield of different fish and squid stocks off the East Coast of North America. (From Horwood 1981.)

centuries or millenia for forest spread.

The replacement of natural communities of trees or perennial grasses by annual crops can be viewed as a change in ecological time scales: from long to short, that is, annual or less. Agricultural systems often do not include any buffering mechanisms against environmental variability at time scales (years to decades) longer than those of agricultural practice (one or a few years) but shorter than those of the natural perennial communities. A few years of drought can be devastating to an agricultural system.

Conclusions

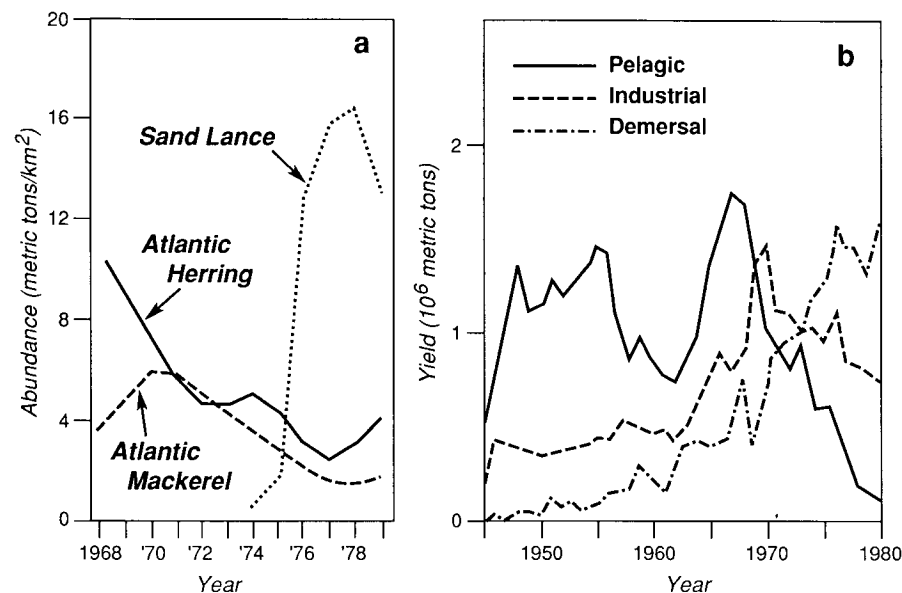Marine and terrestrial ecosystems differ significantly in their functional re-

Figure 4. Changes in fish stocks (a) for the US East Coast (from Sherman et al. 1981) and (b) for the North Sea (from Bailey and Steele in press).
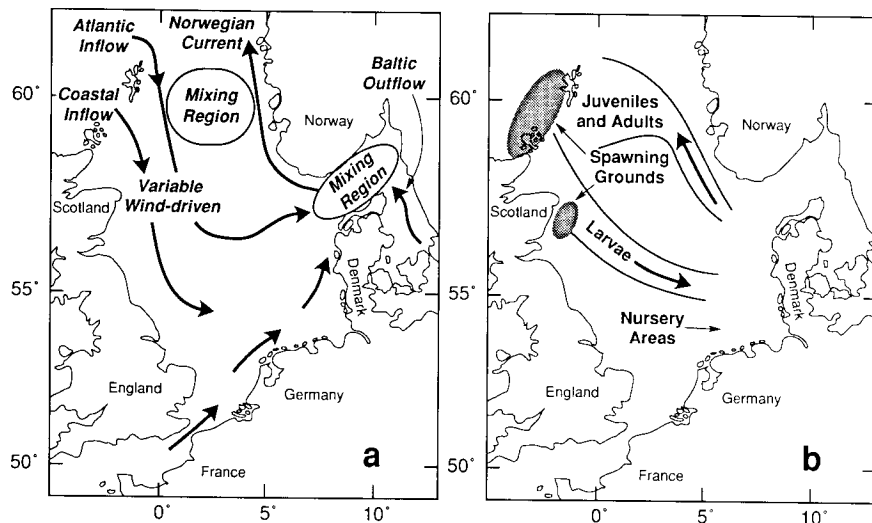
Figure 5. Schematic presentation for North Sea of (a) the main current systems (Dooley 1983) and (b) the life cycle and movements of herring stocks (Corten 1986, Cushing 1982). The larvae move by wind-driven currents, and the juveniles and adults move by the Norwegian current.

sponses to environmental change. Three principal functional relations exemplify this diversity.

- Size, life span, and trophic status. In the ocean and on land, the larger organisms are usually more long-lived, but they differ in trophic status—their places in the food web. Forest trees and open-ocean plankton represent the extremes.
- Relationship of organisms with physical processes. Marine reproductive cycles, particularly in the larval and juvenile phases, are closely linked to water movements. Terrestrial animals tend to evolve reproductive patterns that

Figure 6. A general food web for the North Sea, showing the pelagic and benthic pathways to the two main fish categories. (From Steele 1974.)

eliminate the effects of interannual or decadal variability in the physical environment.
- Differences in processes on the land and in the sea, observed on the same time scale. Some of this contrast can be eliminated by using different time scales; the same responses can occur in different systems at different time scales. The rates, rather than the magnitudes, of environmental change may have more effect on the disturbance of community structure.

The practical implication of land-sea functional diversity is that it would be inappropriate to apply terrestrial perspectives to marine communities, particularly in the context of management or conservation. Although marine systems may be much more sensitive to alterations in their environments, they may also be much more adaptable.

Acknowledgment

References cited

Aebischer, N. J., J. C. Coulson, and J. M. Colebrook. 1990. Parallel long term trends across four marine trophic levels and weather. *Nature* 347: 753–755.

Backhaus, J. O. 1985. A three-dimensional model of the simulation of shelf sea dynamics. *Deutsche Hydrographische Zeitschrift* 38: 165–187.

Bailey, R. S., and J. H. Steele. In press. North Sea herring fluctuations. In M. H. Glantz, ed. *Climate Variability, Climate Change and Fisheries.*

Bonner, J. T. 1965. *Size and Cycle: An Essay on the Structure of Biology.* Princeton University Press, Princeton, NJ.

Corten, A. 1986. On the cause of recruitment failure of herrings in the central and northern North Sea in the years 1972–78. *Journal du Conseil pour Exploration de la Mer* 42: 281–294.

Cushing, D. H. 1982. *Climate and Fisheries.* Academic Press, New York.

Davis, M. B. 1989. Lags in vegetation response to greenhouse warming. *Clim. Change* 15: 75–82.

Delcourt, H. R., P. A. Delcourt, and T. Webb. 1983. Dynamic plant ecology: the spectrum of vegetational change in space and time. *Quaternary Science Review* 1: 153–175.

Denman, K. L., and T. M. Powell. 1984. Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanogr. Mar. Biol. Annu. Rev.* 22: 125–168.

Dooley, H. D., J. H. A. Martin, and D. J. Ellettm. 1984. Abnormal hydrographic conditions in the Northeast Atlantic during the 1970s. Rapports et Process-Verbaux des Reunions. *Cons. Int. Explor. Mer* 185: 179–187.

Hardy, A. C. 1924. The herring in relation to its animate environment. *Fisheries Investigations London* 7: 1–53.

Horwood, J. W. 1981. Management and models of marine multispecies complexes. Pages 339–360 in C. W. Fowler and T. D. Smith, eds. *Dynamics of Large Mammal Populations.* John Wiley & Sons, New York.

Office of Technology Assessment (OTA). 1987. *Technologies to Maintain Biological Diversity.* OTA-F-330, US Govt. Printing Office, Washington, DC.

Rothschild, B. J. 1986. *Dynamics of Marine Fish Populations.* Harvard University Press, Cambridge, MA.

Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466.

Sale, P. F. 1982. Stock-recruit relations and regional coexistance in a lottery competitive system: a simulation study. *Am. Nat.* 120: 139–159.

Sherman, K., C. Jones, L. Sullivan, W. Smith, P. Berrien, and L. Ejsymont. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. *Nature* 291: 486–489.

Southward, A. J. 1980. The western English Channel—an inconstant ecosystem. *Nature* 285: 361–366.

Steele, J. H. 1974. *The Structure of Marine Ecosystems.* Harvard University Press, Cambridge, MA.

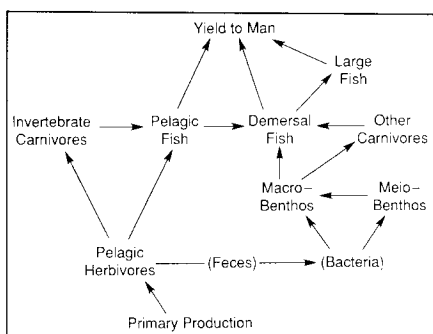_____. 1985. Comparison of marine and terrestrial ecological systems. *Nature* 313: 355–358.