

et al. 1990). Similarly, forestry practices can increase productivity and biomass where they favour rapidly growing hardwoods or where plantations of slow-growing conifers are fertilized (Mladenoff and Pastor 1993); however, the increased productivity in monoculture plantations comes at the expense of local species richness.

6.1.6.4 Soil structure and nutrients

Human impacts on biodiversity. The shifts in relative abundance of hardwoods and conifers through logging and climate warming noted above affect soil structure and nutrients through changes in the amounts and arrays of litter returned to the soil (Flanagan and van Cleve 1985; Pastor and Mladenoff 1993).

Ecosystem consequences of impacts. Where abundances of hardwoods increase, soil nutrient availability will also increase because the chemistry of litter from these species makes them easily decomposable (Flanagan and van Cleve 1983; Pastor and Post 1988; Pastor and Mladenoff 1993). In contrast, increased abundances of conifers on droughty soils in a warmer climate or in monoculture plantations will cause declines in soil nutrient availability because of the high lignin and low nutrient contents of their litter. These changes in nutrient availability will then feed back and affect productivity and biomass because of nutrient limitations to growth (Pastor and Post 1988; Pastor and Mladenoff 1993).

6.1.6.5 Water distribution, balance and quality

Human impacts on biodiversity. Climate warming will have the greatest effect on water distribution by changing the relative abundance of conifers and hardwoods and thus altering regional evapotranspiration rates, and by causing melting of permafrost in far northern regions.

Ecosystem consequences of impacts. The ecosystem consequences of the effects of altered biodiversity on the hydrologic cycle are less well studied than for other ecosystem processes. However, widespread melting of permafrost will certainly alter large-scale drainage patterns (Post 1990) with consequent region-wide impacts on water quality and river flows.

6.1.6.6 Feedbacks to atmospheric properties

Human impacts on biodiversity. By altering the relative abundance and distribution of functional groups, climate warming and logging will change the carbon balance of ecosystems. Furthermore, warming of the soils of peatlands and other northern wetlands will change the amount and types of trace gas loadings through changes in the microbial community (Gorham 1991).

Ecosystem consequences of impacts. Boreal regions contain large portions of the global carbon pool. Currently this biome is probably a net sink for carbon, but upon warming it can be converted to a net source (Post 1990;

Apps *et al.* 1993). Warming of the soils, particularly in wetlands, can increase trace gas loadings, especially that of methane (Gorham 1991). However, the net increase in trace gas loadings, and the balance of methane versus carbon dioxide, depends on the types of plant communities and the ease of decomposition of the soil or sediment organic matter (Roulet *et al.* 1992; Updegraff *et al.* 1994). Logging can increase productivity and thereby offset the net export of carbon, but only if rotations are long enough to allow the biomass to recover completely to achieve that in old-growth forests. If logging causes large losses of conifers over large areas, the albedo of the boreal region may increase and therefore its role in the heat and water budgets of the Earth may also be seriously changed (Bonan *et al.* 1992).

6.1.6.7 Landscape structure

Human impacts on biodiversity. By changing the relative distribution of stands composed largely of one functional group or another, both climate warming and logging alter the structural patterns of landscapes with consequent effects on the fauna that depend on them. Furthermore, climate warming can have secondary effects on landscape structure by increasing fire frequency and intensity (Clark 1989; Payette 1992).

Ecosystem consequences of impacts. Besides the impacts on productivity, nutrient cycling and atmospheric feedbacks noted above, changes in landscape structure have significant effects on habitat for important groups of fauna. By homogenizing stand and landscape structure and composition, logging has severe consequences for the diversity of those faunal groups — particularly avian and insect fauna — that depend on old-growth stands, microsite habitats, and a diversity of habitat elements (Jarvinen and Vaisanen 1977, 1978; Jarvinen *et al.* 1977; Helle 1984; Virkkula 1987, 1991; Telfer 1992). Fairly subtle changes in habitat structure can have large ecological consequences if they occur uniformly over large areas (von Haartman 1973; Jarvinen *et al.* 1977; Haila *et al.* 1980; Helle and Jarvinen 1986). Because many breeding birds are neotropical migrants, this loss of habitat has important consequences for tropical forests as well.

6.1.6.8 Biotic linkages and species interactions

Human impacts on biodiversity. Climate warming and logging will indirectly affect herbivore-ecosystem interactions by altering the relative abundance of plants used as food and, for mammalian herbivores, those used as cover. However, the herbivores themselves can alter the relative abundance of species, thus introducing strong feedbacks into the changes in biodiversity caused by human activities.

Ecosystem consequences of impacts. Browsing by moose (*Alces alces*) and other large ungulates changes the relative composition of the plant community from highly browsed

hardwoods with high litter quality and decay rate to unbrowsed conifers with low litter quality and decay rate (Bryant and Chapin 1986; Pastor *et al.* 1993a). Thus, heavily browsed areas have lower nutrient availability as conifers invade (Pastor *et al.* 1993a). Food quality is related to secondary chemistry and there is growing evidence that there are longitudinal gradients of palatability at the subspecies level across entire continents (Bryant *et al.* 1989, 1994). Changes in the relative abundance of aspen affect habitat for beaver, which in turn affects the abundance, diversity and distribution of wetlands created by this important keystone species (Johnston and Naiman 1990; Pastor *et al.* 1993b). Increased probability of insect outbreak can also be induced by increased drought upon climate warming (Mattson and Haack 1987; Holling 1992). There is therefore the very strong likelihood that climate and logging-induced changes in biodiversity and ecosystem functioning will be strongly conditioned by secondary feedbacks through herbivores and the entire food web.

6.1.6.9 Microbial activities

Human impacts on biodiversity. Human impacts on the microbial community and its activities are mediated primarily through changes in litter quality and quantity, with changes in the relative distribution of plant functional groups, and through changes in soil temperature and water balance.

Ecosystem consequences of impacts. The changes in nutrient cycling rates and trace gas loading to the atmosphere discussed above are all mediated through changes in the microbial community. The diversity of the microbial community appears to be more important in determining the relative proportion of trace gases and forms of inorganic nutrients than in determining the mass balance of carbon and nutrients through the soil (Roulet *et al.* 1992; Updegraff *et al.* 1994).

6.1.6.10 Summary and relevance to human activities

Properties of boreal ecosystems can change rapidly with changes in species composition, whether because of natural succession (Wien and El-Bayoumi 1983; Pastor and Mladenoff 1992; Payette 1992); herbivory (Bryant and Chapin 1986; Pastor *et al.* 1993); human-induced changes through climate warming (Pastor and Post 1988; Bonan *et al.* 1990), or logging (Mladenoff and Pastor 1993a; Haila 1994). The loss of a few species can therefore have significant consequences for ecosystem functioning, but the direction of change depends to a great extent on the functional group to which the species belongs.

References

- Apps, M.J., Kurz, W.A., Luxmoore, R.J., Nilsson, L.O., Sedjo, R.A., Schmidt, R., Simpson, L.G., and Vinson, T.S. 1993. Boreal forests and tundra. *Water, Air and Soil Pollution* 70: 39–53.

- Bonan, G.B., Pollard, D. and Thompson, S.L. 1992. Effects of boreal forest vegetation on global climate. *Nature* 359: 716–718.
- Bonan, G.B., Shugart, H.H. and Urban, D.L. 1990. The sensitivity of high-latitude forests to climatic parameters. *Climatic Change* 16: 9–29.
- Bryant, J.P. and Chapin, F.S., III. 1986. Browsing-woody plant interactions during boreal forest plant succession. In: Van Cleve, K., Chapin, F.S., III, Flanagan, P.W., Viereck, L.A. and Dryness, C.T. (eds), *Forest Ecosystems in the Alaskan Taiga*, 213–225. Springer-Verlag, New York.
- Bryant, J.P., Swihart, R.K., Reichardt, P.B. and Newton, L. 1994. Biogeography of woody plant chemical defense against snowshoe hare browsing: comparison of Alaska and eastern North America. *Oikos* (in press).
- Bryant, J.P., Tahvanainen, J., Sulkioja, M., Julkunen-Tiitto, R., Reichardt, P.B. and Green, T. 1989. Biogeographic evidence for the evolution of chemical defense by boreal birch and willow against mammalian browsing. *American Naturalist* 134: 20–34.
- Chapin, F.S., III. 1986. Controls over growth and nutrient use by taiga forest trees. In: Van Cleve, K., Chapin, F.S., III, Flanagan, P.W., Viereck, L.A., and Dryness, C.T. (eds), *Forest Ecosystems in the Alaskan Taiga*, 296–311. Springer-Verlag, New York.
- Clark, J.S. 1989. Effects of long-term water balances on fire regime, north-western Minnesota. *Journal of Ecology* 77: 989–1004.
- Davis, M.B. and Zabinski, C. 1992. Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. In: Peters, R.L. and Lovejoy, T. (eds), *Global Warming and Biodiversity*, 297–308. Yale University Press, New Haven, Conn.
- Flanagan, P.W. and Van Cleve, K. 1983. Nutrient cycling in relation to decomposition and organic matter quality in taiga ecosystems. *Canadian Journal of Forest Research* 13: 795–817.
- Gorham, E.A. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1: 182–195.
- Haartman, L. von 1973. Changes in the breeding bird fauna of North Europe. In: Farmer, D.S. (ed.), *Breeding Biology of Birds*, 448–481. National Academy of Sciences, Washington, DC.
- Haila, Y. 1994. Preserving ecological diversity in boreal forests: ecological background, research, and management. *Annales Zoologici Fennici* 31: 203–217.
- Haila, Y., Jarvinen, O. and Vaisanen, R.A. 1980. Effects of changing forest structure on long-term trends in bird populations in southwest Finland. *Ornis Scand.* 11: 12–22.
- Hansson, L. 1979. On the importance of landscape heterogeneity in northern regions for the breeding population densities of homeotherms: a general hypothesis. *Oikos* 33: 182–189.
- Haukioja, E., Kupiainen, K., Niemela, P. and Tuomi, J. 1983. Plant availability hypothesis and other explanations of herbivore cycles: complementary or exclusive alternatives? *Oikos* 40: 419–432.

- Helle, P. 1984. Effect of habitat area on breeding bird communities in northeastern Finland. *Annales Zoologici Fennici* 21: 421-425.
- Helle, P. and Jarvinen, O. 1986. Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. *Oikos* 46: 107-115.
- Holling, C.S. 1992. The role of forest insects in structuring the boreal landscape. In: Shugart, H.H., Leemans, R. and Bonan, G.B. (eds), *A Systems Analysis of the Global Boreal Forest*, 170-192. Cambridge University Press, Cambridge.
- Jarvinen, O. and Vaisanen, R. 1977. Long-term changes of the North European land bird fauna. *Oikos* 29: 225-228.
- Jarvinen, O. and Vaisanen, R. 1978. Long-term population changes of the most abundant south Finnish forest birds during the past 50 years. *Journal of Ornithology* 119: 441-449.
- Jarvinen, O., Vaisanen, R. and Kuusela, K. 1977. Effects of modern forestry on the numbers of breeding birds in Finland in 1945-1975. *Silvae Fennica* 11: 284-294.
- Johnston, C.A. and Naiman, R.J. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* 71: 1617-1621.
- MacDonald, G.M., Edwards, T.W.D., Moser, K.A., Pienetz, R. and Smol, J.P. 1993. Rapid response of tree-line vegetation and lakes to past climatic warming. *Nature* 361: 243-246.
- Mattson, W.J. and Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37: 110-118.
- Mladenoff, D.J. and Pastor, J. 1993. Sustainable forest ecosystems in the northern hardwood and conifer region: Concepts and management. In: Aplet, G.H., Johnson, N., Olson, J.T., and Sample, V.A. (eds), *Defining Sustainable Forestry*, 145-180. Island Press, New York.
- Olson, J.S., Watts, J.A., and Allison, L.J. 1983. Carbon in live vegetation of major world ecosystems. *Oak Ridge National Laboratory Technical Report ORNL-5862*. Oak Ridge, Tenn.
- Pastor, J., Bonde, J., Johnston, C.A. and Naiman, R.J. 1993b. Markovian analysis of the spatially dependent dynamics of beaver ponds. *Lectures on Mathematics in the Life Sciences* 23: 5-27.
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. and Cohen, Y. 1993a. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74: 467-480.
- Pastor, J. and Johnston, C.A. 1992. Using simulation models and geographic information systems to integrate ecosystem and landscape ecology. In: Naiman, R.J. (ed.), *Watershed Management: Balancing sustainability with environmental change*, 324-346. Springer-Verlag, New York.
- Pastor, J. and Mladenoff, D.J. 1993. The southern boreal-northern hardwood forest border. In: Shugart, H.H., Leemans, R. and Bonan, G.B. (eds), *A Systems Analysis of the Global Boreal Forest*, 216-240. Cambridge University Press, Cambridge.
- Pastor, J. and Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139: 690-705.
- Pastor, J. and Post, W.M. 1988. Response of northern forests to CO₂-induced climate change. *Nature* 334: 55-58.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R. and Bonan, G.B. (eds), *A Systems Analysis of the Global Boreal Forest*, 144-169. Cambridge University Press, Cambridge.
- Payette, S., Filion, L., Gauthier, L. and Boutin, Y. 1985. Secular climate change in old-growth tree-line vegetation of northern Quebec. *Nature* 315: 135-138.
- Post, W.M. (ed.) 1990. Report of a Workshop on Climate Feedbacks and the Role of Peatlands, Tundra, and Boreal Ecosystems in the Global Carbon Cycle. *Oak Ridge National Laboratory Technical Memorandum ORNL/TM-11457*, Oak Ridge, Tenn.
- Roulet, N.T., Ash, R. and Moore, T.R. 1992. Low boreal wetlands as a source of atmospheric methane. *Journal of Geophysical Research* 97: 3739-3749.
- Shugart, H.H., Leemans, R. and Bonan, G.B. (eds) 1992. *A Systems Analysis of the Global Boreal Forest*. Cambridge University Press, Cambridge.
- Telfer, E.S. 1992. Wildfire and the historical habitats of boreal forest avifauna. In: Kuhnke, D.H. (ed.), *Birds in the Boreal Forest*, 27-39. Northern Forestry Centre, Edmonton, Alberta.
- Updegraff, K., Pastor, J., Bridgman, S.D. and Johnston, C.A. 1995. Environmental and substrate quality controls over carbon and nitrogen mineralization in a beaver meadow and a bog. *Ecological Applications*, (in press).
- Virkkala, R. 1987. Effects of forest management on birds breeding in northern Finland. *Annales Zoologici Fennici* 24: 281-294.
- Virkkala, R. 1991. Population trends of forest birds in Finnish Lapland in a landscape of large habitat blocks: consequences of stochastic environmental variation or regional habitat alteration? *Biological Conservation* 56: 223-240.
- Wein, R.W. and El-Bayoumi, M.A. 1983. Limitations to predictability of plant succession in northern ecosystems. In: Wein, R.W., Riewe, R.R. and Methven, I.R. (eds), *Resources and Dynamics of the Boreal Zone*, 214-225. Association of Canadian Universities for Northern Studies, Ottawa.

6.1.7 Temperate grasslands

6.1.7.1 Introduction

Grasslands are the potential natural vegetation on approximately 25% ($33 \times 10^6 \text{ km}^2$) of the land surface of the Earth (Shantz 1954), although estimates of their current extent range from 16% (Whittaker and Likens 1975) to 30% (Ajtay *et al.* 1979).

Three aspects of grassland environments distinguish them from other ecosystem types (Anderson 1982; Milchunas *et al.* 1988): these are drought, fire and grazing by large ungulate herbivores. All three factors provide selection pressures favouring high turnover of above-ground plant organs, location of perennating organs near the soil surface, and location of a large fraction of plant biomass and activity below ground. Drought is a frequent influence on dry grasslands: fire is a much more significant force in shaping grasslands in humid regions than it is in dry regions. Grazing can be an important evolutionary force across the moisture gradient but its specific influence depends upon the moisture status of the site (Milchunas *et al.* 1988). Adaptations that enhance survival in arid and semi-arid environments may promote tolerance or

avoidance to grazing (Coughenour 1985). Therefore, grazing should have a larger effect on the species composition in humid than in arid and semi-arid grasslands (Milchunas *et al.* 1988).

6.1.7.2 Human impact on biodiversity

The most common use of grasslands is for grazing by domestic animals to produce mainly meat, milk and fibre. The first management action in most cases has been to replace native grazers and their predators with a few species of domestic animals. In an attempt to enhance animal production, humans have tried to increase primary production and/or animal consumption. Techniques aimed at increasing primary production, such as fertilization and irrigation, are all practices that raise resource availability for plants. Given that domestic animals have a selective intake, a large fraction of management techniques attempts to change species composition to match domestic animal preference. By their selective grazing behaviour, livestock tend to modify species composition in opposition to the efforts of managers. Even minimum husbandry has resulted in significant increases in animal biomass density in vast grassland regions (Oesterheld *et al.* 1992).

Grazing does not necessarily reduce plant biodiversity although overgrazing can result in losses of diversity at the population, species, ecosystem and landscape levels. The lack of grazing in some grassland types also results in biodiversity losses (Sala *et al.* 1986; Sala 1988). In general, ecosystem enrichment via fertilization or irrigation results in a decrease in diversity at the population and species levels (Tilman 1993). The replacement of animal or plant species by introduced species has a clear and direct negative effect on biological diversity. Changes in ecosystem and landscape diversity occur as a result of habitat selection by livestock (Smith *et al.* 1992) and replacement of native ecosystems by cultivated grasslands and croplands (Burke *et al.* 1991).

6.1.7.3 Productive capacity

Human impact on biodiversity. Primary production is most often manipulated by the addition of water or mineral nutrients. Both kinds of resource additions directly and indirectly modify biodiversity (Rosensweig 1971; Mellinger and McNaughton 1975; Lauenroth *et al.* 1978; Tilman 1993).

Ecosystem consequences of the impacts. A decrease in species richness, with initial deletion of the rarest species, results in no change in primary production until a threshold is reached beyond which there is a steady and substantial decrease in production (Figure 6.1-2). Removal of rare species in the Serengeti grasslands resulted in full compensation of production by the remaining species (McNaughton 1983). Deletion of species of intermediate

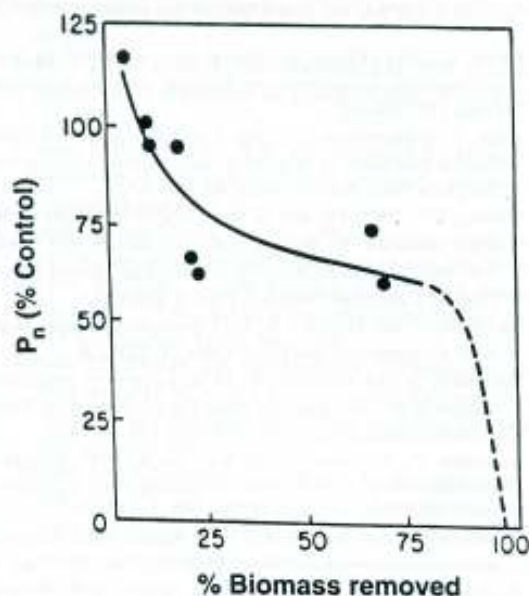


Figure 6.1-2: The effect upon primary productivity (P_n) of removing species that have different biomass in the intact ecosystems. In each case, all the individuals of a different species were removed. Remaining species were able to compensate for the removal of species with small biomass but were not able to compensate for the removal of the most abundant species (From: McNaughton 1983).

abundance resulted in production being only partially compensated. Finally, removal of dominant species resulted in a significant decrease in production.

Grasslands provide several examples in which the relationship between diversity and primary production has been assessed experimentally. The sites studied are geographically diverse and include California annual grasslands, old fields in New York, and grasslands in the Serengeti (McNaughton 1993). Results are contradictory: a negative relationship was observed between productivity and biodiversity in the annual grasslands of California and in the old fields of New York, whereas no relationship between productivity and diversity was found in the Serengeti. The effects of species diversity on production should be assessed with reference to which species have been deleted, and with respect to the driving forces behind the observed changes in diversity, rather than the diversity itself. In the case of the Serengeti, differences in diversity resulted from differences in grazing regime, while in the old fields in New York the diversity differences were a consequence of a successional process.

The diversity-stability hypothesis (McNaughton 1977) suggests that perturbations will result in a larger change in

ecosystem functioning in simple systems than in diverse systems. There is experimental evidence to test this hypothesis in grasslands. McNaughton (1993) analysed the response to a perturbation caused by fertilization along a diversity gradient which emerged as a result of a successional process. Similarly, Tilman and Downing (1994) analysed the response to a perturbation caused by a severe drought along a diversity gradient resulting from an experimental nitrogen fertilization where diversity was maximum in the native system and decreased as fertility increased (Figure 6.1-3). In both cases, the effect of perturbation on production was at a maximum in the simple systems and a minimum in the most diverse systems. The conclusions emerging from the experiment which used a diversity gradient created by differential fertilization has been criticized because greater soil fertility generally favours plants with lower root: shoot ratio, higher leaf conductance, and greater photosynthetic capacity (Givnish 1994). These characteristics also result in lower drought resistance. Therefore, the largest effect of drought observed in low diversity plots could have been the result of those plots being dominated by drought sensitive plants. The critical experiment to address this question has not been done yet: it would compare the response to similar perturbations of ecosystems with different levels of natural or experimentally created diversity, and should disentangle the effect of diversity from the effect of individual species.

6.1.7.4 Decomposition and soil structure

Human impact on biodiversity. Range managers use chemical, fire and mechanical means to modify plant species composition by deleting those species that are least preferred by domestic animals or by adding those that are highly preferred. Selective grazing by domestic herbivores also modifies plant species composition.

Ecosystem consequences of the impacts. The effects of biodiversity on decomposition in grasslands can be viewed from the plant perspective or the microbial perspective. Microbial diversity is not well documented in grasslands and its effect on decomposition is even less clearly understood. The effects of plant species diversity on decomposition result mainly from differences in litter quality among species. Several experiments have demonstrated the importance of species characteristics to total soil nutrients, nutrient availability and the rate of decomposition (e.g. Wedin and Tilman 1990; Matson 1990; Hobbie 1992; Vinton and Burke in press).

6.1.7.5 Water distribution and balance

Human impact on biodiversity. Management manipulations and foraging behaviour may change biodiversity. Large areas of grasslands in North America and Africa have slowly changed into shrublands and savannahs presumably as a result of grazing (Buffington

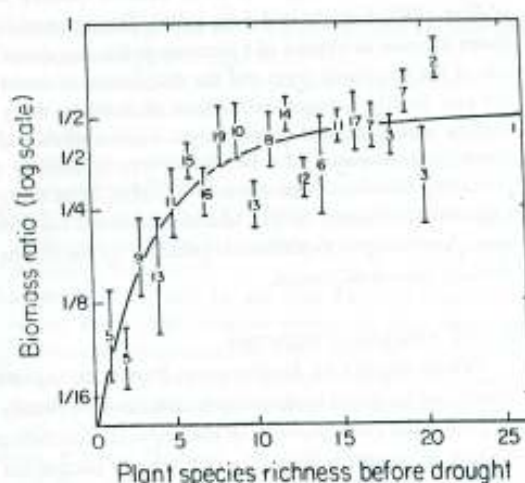


Figure 6.1-3: The effect of plant species richness before a severe drought on above-ground biomass during the drought year expressed as a fraction of previous year biomass. Standard error and number of plots with a given species richness are shown. The gradient of species richness was experimentally created by fertilization (from: Tilman and Downing 1994).

and Herbel 1965; Walker *et al.* 1981; van Vegten 1983; Neilson 1986; Archier 1989).

Ecosystem consequences of the impacts. Important input and output flows, which determine water balance and distribution of water, change with the scale of the unit under consideration. At the ecosystem level, the major flows are transpiration, bare soil evaporation, deep percolation, run-on, run-off and precipitation. At the plant level, transpiration is the only relevant flow but at higher levels of organization, watershed variables become dominant. All the output flows of water at one scale are intimately related, and although the biotic components directly affect mainly absorption and transpiration, they affect all other components of the water balance indirectly.

Reduction of transpiration as a result of species deletions is related to species-specific characteristics that affect water dynamics. Rooting depth, phenology, maximum transpiration rate, drought resistance or avoidance are all species characteristics that affect water balance. Species with deep roots are able to absorb water from a different part of the soil profile than species with shallow roots. Species with different phenological patterns (early vs late season) are able to use water available at different times of the year. In addition, many of these characteristics are self-associated. For example, late season phenology is associated in several systems to xerophytism or deep root systems (Gulmon *et al.* 1983; Golluscio and Sala 1993).

Experiments and associated models of grassland water dynamics have shown how removal of functional types such as perennial grasses or shrubs results in profound

alterations of the ecosystem water balance (Knoop and Walker 1985; Paruelo and Sala 1995). Deep percolation losses increase as a result of a decrease in the abundance of one of the functional types and the distribution of water in the soil profile changes as a result of deleting deep or shallow root functional types. Only a fraction of the water freed by the removal of a functional type is used by the remaining functional type (Sala *et al.* 1989). Most of these experiments focused on the deletions of entire functional types, providing no experimental evidence for the effects of deleting individual species.

6.1.7.6 Atmospheric properties

Human impact on biodiversity. Range management results in changes in biodiversity as described previously.

Ecosystem consequences of the impacts. Atmospheric CO_2 is an important trace gas and a major component of the carbon cycle. We have described how biological diversity at scales ranging from species to landscapes affects production and decomposition which are the major processes driving the carbon cycle. We are not aware of any studies relating species diversity to atmospheric properties. However, Burke *et al.* (1991) calculated the effects on the carbon balance of converting a large fraction of the North America Central Grassland Region into cropland. Cultivation resulted in a net release of carbon from soil organic matter larger than the expected loss as a result of climate change. The current increase in atmospheric methane is not related to an increase in the number of grazing mammals (Crutzen *et al.* 1986).

6.1.7.7 Landscape structure

Human impact on biodiversity. Croplands have expanded dramatically during this century, from 9.1×10^6 to $15 \times 10^6 \text{ km}^2$ (Richards 1990). This expansion has altered landscape heterogeneity in grasslands. Habitat selectivity by domestic livestock has differentially influenced riparian ecosystems and therefore altered landscape diversity. Domestic livestock, and especially cattle, tend to congregate in the topographically lowest portions of the landscape (Senft *et al.* 1985; Pinchak *et al.* 1991). Such habitat selectivity has negative effects on the plant and animal diversity of riparian ecosystems (Kauffman and Krueger 1984; Smith *et al.* 1992).

Ecosystem consequences of the impacts. The reduction in diversity of streamside vegetation and its productivity have negative effects on both physical and chemical indicators of water quality (Kauffman and Krueger 1984). Reduction in the diversity and productivity of the herbaceous vegetation layer can change the velocity and erosive energy of the stream flow, while losses of the woody overstorey have large effects on water temperature. Both the overstorey and understorey vegetation layers have important effects on the rates and kinds of aquatic

processes that occur in a stream (Kauffman and Krueger 1984), and the diversity and productivity of invertebrates and fishes are profoundly influenced by the diversity of the streamside vegetation.

6.1.7.8 Biotic linkages and species interactions

Human impact on biodiversity. Invasions in grasslands are common and in some cases have been associated with changes in grazing regime. Examples of grasslands that have been invaded by exotic species are the California grasslands and the intermontane west of North America, the pampas in South America, and the savannahs in tropical South America (Sala *et al.* 1986; D'Antonio and Vitousek 1992).

Ecosystem consequences of the impacts. Invasions in grasslands have usually occurred in association with an increase in grazing intensity and/or a change in dominant grazer. Vulnerability to invasions associated with grazing appears to be related to moisture availability and the grazing history in evolutionary time (Milchunas *et al.* 1988). Grasslands that evolved under light grazing conditions and under mesic conditions are more vulnerable to invasions than those that evolved under heavy grazing in xeric environments. Semi-arid grasslands of the northwest USA and southwest Canada have a short evolutionary grazing history, and before the introduction of cattle they were dominated by perennial tussock grasses (Tisdale 1947; Daubenmire 1970). The inability of these grasses to cope with heavy grazing resulted in the invasion and dominance of many areas by Eurasian weeds (Daubenmire 1940, 1970; Ellison 1960; Mack 1981; Mack and Thompson 1982). Invasions often disrupt competitive interactions (D'Antonio and Vitousek 1992) which result in changes in species composition with the ecosystem effects described above.

6.1.7.9 Microbial activities

Human impact on biodiversity. See discussion of decomposition and soil structure above.

Ecosystem consequences of the impacts. The effect of changes in plant species diversity on microbial activity as a result of changes in litter quality and quantity are described in the decomposition section above.

6.1.7.10 Summary and relevance to human activities

On a world-wide basis the response of grasslands to the major human use – domestic livestock grazing – has been variable (Milchunas and Lauenroth 1993). In some areas where the native vegetation is well adapted as a result of evolution, changes in biodiversity have been very small (Milchunas *et al.* 1988). In other areas changes have been very large. In some cases and especially in tropical and subtropical grasslands, the large changes have involved a shift from a grass-dominated vegetation to one dominated

by woody plants (Walker *et al.* 1981; vanVegten 1983; Archer 1989). In other cases the large changes have involved invasions of exotic plants which have profoundly altered the ecosystems. Conversion of grasslands to croplands or seeded pastures has also had a major influence on biodiversity and ecosystem functioning. In many cases these converted grasslands have become net sources of carbon and nutrients accelerating global change. These major transformations of grasslands and their effects on biodiversity modify the water, carbon and nutrient cycles to an extent that significantly contributes to altering the Earth's life support system.

References

- Ajtay, G.L., Ketner, P. and Duvigneaud, P. 1979. Terrestrial primary production and phytomass. In: Bolin, B., Degens, E., Kempe, S. and Ketner, P. (eds), *The Global Carbon Cycle*, SCOPE edition. Vol. 13, 129-182. John Wiley, Chichester.
- Anderson, R.C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands. In: Estes, J.R. and Tylor, R.J. (eds), *Grasses and Grasslands: Systematics and ecology*. 312. University of Oklahoma Press, Norman.
- Archer, S. 1989. Have southern Texas savannahs been converted to woodlands in recent history? *American Naturalist* 134: 545-561.
- Buffington, L.C. and Herbel, C.H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs* 35: 139-164.
- Burke, I.C., Kittel, T.G.F., Lauenroth, W.K., Snook, P., Yonker, C.M. and Parton, W.J. 1991. Regional analysis of the central great plains. *BioScience* 41 (10): 685-692.
- Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden* 72: 852-863.
- Crutzen, P.J., Aselmann, I. and Seiler, W. 1986. Methane production by domestic animals, wild ruminants, other herbivorous fauna and humans. *Tellus* 38B: 271-284.
- D'Antonio, C.M., and Vitousek, P.M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23: 63-87.
- Daubenmire, R. 1940. Plant succession due to overgrazing in the *Agropyron* bunchgrass prairie of south-eastern Washington. *Ecology* 21: 55-65.
- Daubenmire, R. 1970. *Steppe vegetation of Washington*. Washington Agriculture Experimental Station Technical Bulletin Edition. Vol. 62, Washington State University, Pullman.
- Ellison, L. 1960. Influence of grazing on plant succession of rangelands. *Botanical Review* 26: 1-78.
- Givnish, T.J. 1994. Does diversity beget stability? *Nature* 371: 113-114.
- Golluscio, R.A., and Sala, O.E. 1993. Plant functional types and ecological strategies in Patagonian forbs. *Journal of Vegetation Science* 4: 839-846.
- Gulmon, S.L., Chiarillo, N.R., Mooney, H.A. and Chu, C.C. 1983. Phenology and resource use in three co-occurring grassland annuals. *Oecologia* 58: 33-42.
- Hobbie, S.E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7: 336-339.
- Kauffman, J. B., and Krueger, W.C. 1984. Livestock impacts on riparian ecosystems and streamside management implications: a review. *Journal of Range Management* 37: 430-437.
- Knoop, W.T. and Walker, B.H. 1985. Interactions of woody and herbaceous vegetation in a Southern African Savannah. *Journal of Ecology* 73: 235-253.
- Lauenroth, W.K., Dodd, J.L. and Sims, P.L. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* 36: 211-222.
- Mack, R.N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro Ecosystems* 7: 145-165.
- Mack, R.N. and Thompson, J.N. 1982. Evolution in steppe with few large, hooved mammals. *American Naturalist* 119: 757-773.
- McNaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* 111: 515-525.
- McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53: 291-320.
- McNaughton, S.J. 1993. Biodiversity and function of grazing systems. In: Schulze, E.-D. and Mooney, H.A. (eds), *Biodiversity and Ecosystem Function*. 361-383. Springer-Verlag, Berlin.
- Matson, P. 1990. Plant-soil interactions in primary succession at Hawaii Volcanoes National Park. *Oecologia* 85: 241-246.
- Mellinger, M.V. and McNaughton, S.J. 1975. Structure and function of successional vascular plant communities in central New York. *Ecological Monographs* 45: 161-182.
- Milchunas, D.G. and Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327-366.
- Milchunas, D.G., Sala, O.E. and Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132: 87-106.
- Nelson, R.P. 1986. High resolution climatic analysis and Southwest biogeography. *Science* 232: 27-34.
- Oesterheld, M., Sala, O.E. and McNaughton, S.J. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature* 356: 234-236.
- Paruelo, J.M., and Sala, O.E. 1995. Water losses in the Patagonian steppe: a modelling approach. *Ecology* 76: 510-520.
- Pinchak, W.E., Smith, M.A., Hart, R. H. and Waggoner, J.W. 1991. Beef cattle grazing distribution patterns on foothill range. *Journal of Range Management* 44: 267-275.
- Richards, J.F. 1990. Land transformation. In: Turner, B.L., II, Clark, W.C., Kates, R.W., Richards, J., Mathews, J.T. and Meyer, W.B. (eds) *The Earth as Transformed by Human Action*. 161-178. Cambridge University Press, Melbourne.
- Rosenzweig, M.L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171: 385-387.

- Sala, O.E. 1988. The effect of herbivory on vegetation structure. In: Werger, M.G.A., van der Aart, P.J.M., During, H.J. and Verhoeven, J.T.A. (eds), *Plant Form and Vegetation Structure*. 317-330. SPB Academic Publishing, The Hague.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K. and Soriano, A. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81: 501-505.
- Sala, O.E., Oesterheld, M., León, R.J.C. and Soriano, A. 1986. Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio* 67: 27-32.
- Senft, R.L., Rittenhouse, L.R. and Woodmansee, R.G. 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. *Journal of Range Management* 38: 82-86.
- Shantz, H.L. 1954. The place of grasslands in the earth's cover of vegetation. *Ecology* 35: 142-145.
- Smith, M.A., Rogers, J.D., Dodd, J.L. and Skinner, Q.D. 1992. Habitat selection by cattle along an ephemeral channel. *Journal of Range Management* 45: 385-390.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179-2191.
- Tilman, D. and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature* 367: 363-365.
- Tisdale, E.W. 1947. The grasslands of the southern interior of British Columbia. *Ecology* 28: 346-382.
- van Vegten, J.A. 1983. Thornbush invasion in a savannah ecosystem in eastern Botswana. *Vegetatio* 56: 3-7.
- Walker, B.H., Ludwig, D., Holling, C.S. and Peterman, R.M. 1981. Stability of semi-arid savannah grazing systems. *Journal of Ecology* 69: 473-498.
- Wedin, D.A., and Tilman, D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84: 433-441.
- Whittaker, R.H. and Likens, G.E. 1975. The biosphere and man. In: Lieth, G.E. and Whittaker, R.H. (eds), *Primary productivity of the biosphere*. Ecological Studies Edition. Vol. 14, 305-328. Springer-Verlag, New York.
- and Sainz Ollero 1993). The five regions have markedly different biogeographic characteristics, histories and current patterns of human habitation and use, and markedly different patterns of biodiversity. These differences are most clearly obvious between the Mediterranean region, which has a long history of human habitation, and some of the areas more recently settled by Europeans, such as Australia. Mediterranean-type ecosystems consist of a variety of vegetation types, including forest, woodland, shrubland and grassland. A feature of many of the vegetation types is their sclerophyllous nature, and high levels of secondary compounds such as terpenes. Floristic diversity and degree of endemism are high in most Mediterranean areas, and shrublands in Australia and South Africa are particularly noted for their high floristic diversity.
- Human impacts on biodiversity vary between regions, and include both positive and negative components. In the Mediterranean Basin, where human activities have modified the landscape for thousands of years, current levels of biodiversity are in part maintained by continued human influence. Where traditional human activities cease, plant and animal diversity can be reduced (González Bernáldez 1991; Naveh 1994) and susceptibility to disturbances, especially fire, can be increased (Moreno 1989). This in turn can promote landscape homogenization, with resultant negative effects on biodiversity (Furaco *et al.* 1993; Pérez *et al.* in press). Landscape homogenization can also result from the abandonment of agricultural/pastoral land (Fernández-Alés *et al.* 1992). Human activities have also played an important role in determining the distribution of vegetation and ecosystems in Chile, and may be important in the retention of components of the biodiversity within these ecosystems (Fuentes and Muñoz 1994; Fuentes *et al.* 1995).

6.1.8 Mediterranean-type ecosystems

6.1.8.1 Introduction

Mediterranean-type ecosystems share a climate of cool wet winters and a distinct summer drought, and are found in the Mediterranean Basin, California, Chile, the Cape Province of South Africa and southwestern and southern Australia. Estimates of biome cover vary depending on the climatic classification used, but are approximately as follows, given as 10^6 km² (estimates of numbers of plant species in each region are given in parentheses where available): Mediterranean Basin 1.87 (c. 25 000), California 0.32 (5050), Chile 0.14 (c. 2100), Cape Province 0.09 (c. 8550), Southwestern Australia 0.31 (c. 8000) (Quézel 1981; Cowling *et al.* 1992; Fuentes *et al.* 1995; Hobbs *et al.* 1995; Keeley and Swift 1995). The last four regions are listed as 'hot spots' for species diversity by WCMC (1992), although parts of the Mediterranean Basin also possess high plant diversities, as estimated on a species per km² basis (Davis *et al.* 1986; Valdés *et al.* 1987; Moreno Saiz

In South Africa and Australia, and in California, human impacts are largely negative. These include reductions in population size and/or distribution of sensitive species which have occurred as a result of land-use changes and fragmentation (Saunders 1989, 1993; Hopper *et al.* 1990; Cowling and Bond 1992; Hopper 1992). Reduced age structure diversity of dominant species results from altered disturbance regimes (Yates *et al.* 1994); genetic diversity is reduced through habitat loss (Rebello 1992), and loss of species diversity is caused by introduced predators, herbivores, plants and diseases (Mooney *et al.* 1986; di Castri *et al.* 1990; Groves and di Castri 1991; Scougall *et al.* 1993; Wills 1993).

Reduced structural complexity can occur because of management practices such as post-fire re-seeding (Barro and Conrad 1987) or deforestation, but this is countered in some cases by local increases in complexity through reforestation (Blondel 1976). Human activities can maintain structural diversity where vegetation patterns are

largely a result of past activities, especially in the Mediterranean Basin and Chile. Ecosystem and landscape fragmentation and simplification result from agriculture, forestry and urbanization, and changed disturbance regimes. This includes the addition of new disturbances, modification of natural regimes, and the discontinuation of traditional human management (Le Houérou 1990; Van Wilgen *et al.* 1992; Aronson *et al.* 1993; Hobbs 1993; Hobbs *et al.* 1993; Keeley 1993). The introduction of exotic species and altered disturbance regimes affect biodiversity at all levels. The likely magnitude of impacts is uncertain and varies between regions.

6.1.8.2 Productive capacity, biomass and decomposition

Human impacts on biodiversity. Changes in productive capacity and biomass result from type conversions, the invasion of exotic species, grazing by introduced herbivores, spread of pathogens and changed disturbance/management regimes (references in Introduction).

Ecosystem consequences of impacts. Impacts on biodiversity can cause a net decline in biomass and productive capacity in areas subject to transformation by agriculture (with a switch toward human-orientated productivity), urbanization or grazing (Seougal *et al.* 1993; Keeley 1993). Reduced diversity may lead to reduced resilience to episodic disturbances such as fire, flood and drought (Atkins and Hobbs 1995). Effects on resilience will become apparent only over long time-frames. Localized increase in productive capacity can occur where invasion by N-fixers occurs (Macdonald and Richardson 1986; Stock and Allsop 1992). This also occurs after fire or abandonment in the Mediterranean Basin, where fast-growing native legumes invade (Faraco *et al.* 1993; Pérez *et al.*, 1995).

6.1.8.3 Soil structure and nutrients

Human impacts on biodiversity. Changes result from type conversions, agricultural development and loss of native plant cover, changes in grazing management, and changed fire regimes (references in Introduction).

Ecosystem consequences of impacts. Reduced uptake and increased efflux can occur where there is a loss of functional groups with specialized uptake mechanisms (Hobbs 1993b). Reduced soil aeration and loss of macropore structure result from the loss of soil macrofauna (Hobbs *et al.* 1995). These are certain, widespread impacts. Nitrogen fixation can increase or decrease following addition or deletion of N-fixers (Stock and Allsop 1992), with concomitant changes in ecosystem response to disturbance. The direction of change is dependent on which species are added or lost. Changed fire cycles and intensities lead to changes in soil chemical and structural properties, erodability and nutrient losses (Scott and van Wyk 1990; Marion *et al.* 1991; Giovannini 1994; Riggan *et al.* 1994). Fire intensity can profoundly alter post-fire

ecosystem functioning, both directly and indirectly (Moreno and Oechel 1994). These are likely to be localized effects.

6.1.8.4 Water distribution, balance and quality

Human impacts on biodiversity. Changes result from agricultural development and loss of native plant cover, loss of riparian and wetland vegetation, and reduced landscape heterogeneity through fragmentation, land abandonment and afforestation (references in Introduction).

Ecosystem consequences of impacts. Reduced structural and landscape diversity leads to reduced buffering and greater peak flows. Reduced diversity of groups with specialized water redistribution and uptake mechanisms leads to reduced internal redistribution, lower water use, greater vertical and horizontal water movement and increased salinization and erosion (Nulsen *et al.* 1986; Scott and van Wyk 1992; McFarlane *et al.* 1992, 1993). Reduced species and landscape diversity also lead to reduced resilience to episodic high rainfall events, for the same reasons. These are certain, widespread effects, which occur over time scales of years to decades. The use of natural water containing non-pathogenic levels of *Phytophthora cinammomi* for irrigation leads to pathogenic outbreaks in transformed systems (Von Broemsen 1984).

6.1.8.5 Atmospheric properties

Human impacts on biodiversity. Of potential importance is the large-scale removal of complex perennial vegetation and its replacement by agriculture (Hobbs *et al.* 1993).

Ecosystem consequences of impacts. Regional changes in albedo, evaporation, cloud formation and rainfall distribution may be caused by changes from complex perennial vegetation to annual crop and pasture land (Smith *et al.* 1992). Changes are uncertain, but could be widespread.

6.1.8.6 Landscape and waterscape structure

Human impacts on biodiversity. Fragmentation, urbanization, type conversion, deforestation and reforestation, and changes in disturbance regimes (references in Introduction) are particularly important.

Ecosystem consequences of impacts. Impacts result in reduced landscape diversity and connectivity and increased probability of landscape degradation (Fernández Alés *et al.* 1992; Hobbs *et al.* 1993; Keeley 1993). Reduced landscape and structural diversity around water bodies leads to changes in chemical, physical and biotic characteristics (e.g. a change from freshwater to saline: Froend *et al.* 1987; Bell and Froend 1990; Froend and McComb 1991). There is also a higher probability of irreversible system change following episodic storm events. Changes could be widespread.

6.1.8.7 Biotic linkages and species interactions

Human impacts on biodiversity. Species introductions have potentially large impacts on diversity at all levels

(Mooney *et al.* 1986; di Castri *et al.* 1990; Groves and di Castri 1991) and species deletions can result from changes in landscape structure caused by habitat modification, homogenization, fragmentation and changes in utilization patterns (references in Introduction).

Ecosystem consequences of impacts. Consequences include the disruption of obligatory mutualisms involving for example pollination or dispersal and the breakdown of complex systems of predator-prey and plant-herbivore interactions (Fuentes and Etcheberry 1983; Bond and Slingsby 1984; Bond and Stock 1989; Jaksic *et al.* 1992; Main 1992; Norton *et al.* 1994; Fuentes *et al.* 1995). Such changes may have potential follow-on effects on productive capacity, nutrient uptake and retention, and ecosystem response to disturbance, although the exact nature of these follow-on effects will be difficult to predict. Introduced plant species have been shown to have a positive effect on honey production in Chile, which is dependent on the presence of an array of species with different flowering times (Fuentes *et al.* 1995). Follow-on effects are most likely where the species lost are 'keystones' or have no functional equivalents.

6.1.8.8 Microbial activities

Human impacts on biodiversity: New suites of micro-organisms, including pathogens, soil micro-organisms and nitrogen-fixing and mycorrhizal symbionts have been introduced into areas where they were previously absent (Stock and Allsopp 1992). Human modification of ecosystems may also induce pathogenic outbreaks of organisms previously present at non-pathogenic levels (Von Broembsen 1984). Alterations to soil and litter characteristics resulting from agriculture and ecosystem modification will lead to changes in microbial activities, although it is not known exactly how microbial diversity is affected (e.g. Brandenburg and Sparling 1990).

Ecosystem consequences of impacts. Introduced pathogens dramatically alter ecosystem structure and functioning, and can differentially affect specific plant functional groups (Wills 1993; Hobbs 1993a). Loss of N-fixers through altered disturbance regimes, or their addition through introduction with invasive plants may alter nutrient cycling (Hobbs 1992; Stock and Allsopp 1992). Pathogens that cause the death of above-ground plant parts may also alter fuel properties and hence affect fire behaviour and intensity (Riggan *et al.* 1994). Changes in microbial populations also lead to changes in soil respiration (Brandenburg and Sparling 1994). The extent and importance of these changes is largely unknown.

6.1.8.9 Summary and relevance to human activities

Mediterranean-type ecosystems are generally made up of a mosaic of different vegetation types, and the five Mediterranean regions, while resembling each other in

some ways, differ greatly in their levels of diversity and degree of modification. This heterogeneity both between and within regions makes generalizations difficult. Mediterranean regions are generally heavily populated and modified, and the major impacts on biodiversity arise from this modification, particularly at the landscape scale. In the Mediterranean Basin, the continuation of traditional human activities maintains landscape heterogeneity and has a positive influence on biodiversity, while in Australia, recent human activities have had the opposite effect of reducing heterogeneity and negatively influencing biodiversity. The three other regions fall between these two extremes.

The likely consequences of changes in biodiversity are often unclear. In systems that are very species-rich, such as the South African *fynbos* or the Australian *kwongan* , the ecosystem effects of the loss of particular species may be minimal in the short term, although the longer term impacts on resilience to change and disturbance may be more important. On the other hand, reductions in ecosystem and landscape diversity have already had profound impacts in terms of altered hydrology and reduced agricultural production.

References

- Aronson, J., Floret, C., Le Floch, E., Ovalle, C. and Pontanier, R. 1993. Restoration and rehabilitation of degraded ecosystems. *Restoration Ecology* 1: 1-10.
- Atkins, L. and Hobbs, R.J. 1995. Measurement and effects of fire heterogeneity in southwest Australian wheatbelt vegetation. *CALMScience* 2: (in press).
- Barro, S.C. and Conrad, S.G. 1987. *Use of Ryegrass Seeding as an Emergency Revegetation Measure in Chaparral Ecosystems*. USDA Forest Service, General Technical Report PSW-102.
- Bell, D.T. and Friend, R.H. 1990. Mortality and growth of species under stress at Lake Toolibin in the Western Australian wheatbelt. *Journal of Royal Society of Western Australia* 72: 63-66.
- Blondel, J. 1976. L'influence des reboisements sur les communautés d'oiseaux, l'exemple du Mont-Ventoux. *Ann. Sci. Forest.* 33: 221-245.
- Bond, W.J. and Slingsby, P. 1984. Collapse of an ant plant mutualism - the Argentine ant, *Iridomyrmex humilis* and myrmecochorous Proteaceae. *Ecology* 65: 1031-1037.
- Bond, W.J. and Stock, W.D. 1989. The costs of leaving home: ants disperse myrmecochorous seeds to low nutrient sites. *Oecologia* 81: 412-417.
- Brandenburg, A. and Sparling, G.P. 1990. A comparison of total C, microbial C and respiration in revegetated, pasture and native woodland habitats in the Western Australian wheatbelt. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R. and Grace, P.R. (eds), *Soil Biota. Management in sustainable farming systems*. 173-176. CSIRO, Melbourne.
- Cowling, R.M. and Bond, W.J. 1992. How small can reserves be? An empirical approach in Cape fynbos. *Biological Conservation* 58: 243-256.

- Cowling, R.M., Holmes, P.M. and Rebelo, A.G. 1992. Plant diversity and endemism. In: Cowling, R.M. (ed.) *The Ecology of Fynbos: Nutrients, fire and diversity*. 62–112. Oxford University Press, Cape Town.
- Davis, D.D., Droop, S.J.M., Gregerson, P., Henson, L., Leon, C.J., Villa-Lobos, J., Synge, H. and Zantovska, J. 1986. *Plants in danger – What do we know?* IUCN, Gland, Switzerland.
- di Castri, F., Hansen, A.J. and Debussche, M. 1990. *Biological Invasions in Europe and the Mediterranean Basin*. Kluwer, Dordrecht.
- Faraco, A.M., Fernández, F. and Moreno, J.M. 1993. Post-fire dynamics of pine woodlands and shrublands in the Sierra de Gredos. In: Traubaud, L. and Prodron, R. (eds), *Fire in Mediterranean Ecosystems*. Ecosystems Research Report 5: 101–113.
- Fernández Alés, R., Martín, A., Ortega, F. and Alés, E.E. 1992. Recent changes in landscape structure and function in a Mediterranean region of SW Spain (1950–1984). *Landscape Ecology* 7: 3–18.
- Froend, R.H., Heddl, E.M., Bell, D.T. and McComb, A.J. 1987. Effects of salinity and waterlogging on the vegetation of Lake Toolibin, Western Australia. *Australian Journal of Ecology* 12: 281–298.
- Froend, R.H. and McComb, A.J. 1991. An account of the decline of Lake Towerrinning, a wheatbelt wetland. *Journal of the Royal Society Western Australia* 73: 123–128.
- Fuentes, E.R. and Etcheagaray, J. 1983. Defoliation patterns in natural ecosystems. In: Kruger, F.J., Mitchell, D.T. and Jarvis, J.V. (eds), *Mediterranean-type Ecosystems*. 525–542. Springer-Verlag, New York.
- Fuentes, E.R., Montenegro, G., Rundel, P.W., Arroyo, M.T.K., Ginocchio, R. and Jaksic, F.M. 1995. Functional approaches to biodiversity in the Mediterranean-type ecosystems of central Chile. In: Davis, G.W. and Richardson, D.M. (eds), *Biodiversity and Function in Mediterranean-type Ecosystems*. 185–232. Springer-Verlag, Heidelberg.
- Fuentes, E.R. and Muñoz, M. 1994. The role of humans in changing the landscapes of central Chile. In: Arroyo, M.T.K., Zedler, P.H. and Fox, M.D. (eds), *Ecology and biogeography of Mediterranean ecosystems in Chile, California and Australia*. Springer-Verlag, New York.
- Giovannini, G. 1994. The effect of fire on soil quality. In: Sala, M. and Rubio, J.L. (eds), *Soil Erosion and Degradation as a Consequence of Forest Fires*. 15–27. Geofoma Ediciones, Logroño, Spain.
- González Bernáldez, F. 1991. Ecological consequences of the abandonment of traditional land use systems in central Spain. In: Baudry, J. and Bunce, R.G.H. (eds), *Land Abandonment and Its Role in Conservation*. 23–29. Options Méditerranéennes Ser. A15.
- Groves, R.H. and di Castri, F. 1991. *Biogeography of Mediterranean Invasions*. Cambridge University Press, Cambridge.
- Hobbs, R.J. 1992. Is biodiversity important for ecosystem functioning? Implications for research and management. In: Hobbs, R.J. (ed.), *Biodiversity of Mediterranean Ecosystems in Australia*. 211–229. Surrey Beatty and Sons, Chipping Norton, NSW.
- Hobbs, R.J. 1993. Effects of landscape fragmentation on ecosystem processes in the Western Australian wheatbelt. *Biological Conservation* 64: 193–201.
- Hobbs, R.J. 1995. Can we use plant functional types to describe and predict responses to environmental change? In: Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds), *Plant Functional Types*. Cambridge University Press, Cambridge. (in press).
- Hobbs, R.J., Richardson, D.M. and Davis, G.W. 1995. Mediterranean-type ecosystems: opportunities and constraints for studying the function of biodiversity. In: Davis, G.W. and Richardson, D.M. (eds), *Biodiversity and Function in Mediterranean-type Ecosystems*. 233–284. Springer-Verlag, Heidelberg.
- Hobbs, R.J., Saunders, D.A., Lobry de Bruyn, L.A. and Main, A.R. 1993. Changes in biota. In: Hobbs, R.J. and Saunders, D.A. (eds), *Reintegrating Fragmented Landscapes. Towards sustainable production and nature conservation*. 65–106. Springer-Verlag, New York.
- Hopper, S.D. 1992. Patterns of plant diversity at the population and species level in south-west Australian mediterranean ecosystems. In: Hobbs, R.J. (ed.), *Biodiversity of Mediterranean Ecosystems in Australia*. 27–46. Surrey Beatty and Sons, Chipping Norton, NSW.
- Hopper, S.D., van Leeuwen, S., Brown, A.P. and Patrick, S.J. 1990. *Western Australia's Endangered Flora and Other Plants Under Consideration for Declaration*. Department of Conservation and Land Management, Wanneroo, Western Australia.
- Jaksic, F.M., Jiménez, J.E., Castro, S.A. and Feinsinger, P. 1992. Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid neotropical site. *Oecologia* 89: 90–101.
- Keeley, J.E. (ed.) 1993. *Interface Between Ecology and Land Development in California*. Southern California Academy of Sciences, Los Angeles.
- Keeley, J.E. and Swift, C.C. 1995. Biodiversity and ecosystem functioning in Mediterranean-climate California. In: Davis, G.W. and Richardson, D.M. (eds), *Biodiversity and Function in Mediterranean-type Ecosystems*. 122–183. Springer-Verlag, Heidelberg.
- Le Houérou, H.N. 1990. Global change: vegetation, ecosystems and land use in the southern Mediterranean Basin by the mid twenty-first century. *Israel Journal of Botany* 39: 481–508.
- Macdonald, I. A. W. and Richardson D. M. 1986. Alien species in terrestrial ecosystems of the fynbos biome. In: MacDonald, I.A., Kruger, F.J. and Ferrar, A.A. (eds), *The Ecology and Management of Biological Invasions in Southern Africa*. 77–91. Oxford, University Press.
- McFarlane, D.J., George, R.J. and Farrington, P. 1993. Changes in the hydrologic cycle. In: Hobbs, R.J. and Saunders, D.A. (eds), *Reintegrating Fragmented Landscapes. Towards sustainable production and nature conservation*. 146–86. Springer-Verlag, New York.
- McFarlane, D.J., Howell, M.R., Ryder, A.T. and Orr, G.J. 1992. The effect of agricultural development on the physical and hydraulic properties of four Western Australian soils. *Australian Journal of Soil Research* 30: 517–532.
- Main, A.R. 1992. The role of diversity in ecosystem function: an

- overview. In: Hobbs, R.J. (ed.) *Biodiversity of Mediterranean Ecosystems in Australia*. 77-93. Surrey Beatty and Sons, Chipping Norton, NSW.
- Marion, G.M., Moreno, J.M. and Oechel, W.C. 1991. Fire severity, ash deposition, and clipping effects on soil nutrients in chaparral. *Soil Science Society of America Journal* 55: 235-240.
- Mooney, H.A., Hamburg, S.P. and Drake, J.A. 1986. The invasion of plants and animals into California. In: Mooney, H.A. and Drake, J.A. (eds), *The Ecology of Biological Invasions of North America and Hawaii*. 250-272. Springer-Verlag, New York.
- Moreno, J.M. 1989. Los ecosistemas terrestres mediterráneos y el fuego. *Política Científica* 18: 46-50.
- Moreno, J.M. and Oechel, W.C. 1994. Fire intensity as a determinant factor of postfire plant recovery in southern California chaparral. In: Moreno, J.M., and Oechel, W.C. (eds), *The Role of Fire in Mediterranean-type Ecosystems*. 26-45. Springer-Verlag, New York.
- Moreno Salz, J. and J.C. Sainz Oller, H. 1993. El endemismo vegetal ibérico-baleár. *Vida silvestre* 75: 35-41.
- Naveh, Z. 1994. The role of fire and its management in the conservation of Mediterranean ecosystems and landscapes. In: Moreno, J.M. and Oechel, W.C. (eds), *The Role of Fire in Mediterranean-type Ecosystems*. 163-186. Springer-Verlag, New York.
- Norton, D.N., Hobbs, R.J. and Atkins, L. 1995. Fragmentation, disturbance and plant distribution: mistletoes in woodland remnants in the Western Australian wheatbelt. *Conservation Biology* (in press).
- Nulsen, R.A. 1992. Changes in soil properties. In: Hobbs, R.J. and Saunders, D.A. (eds), *Reintegrating Fragmented Landscapes: Towards sustainable production and nature conservation*. Springer-Verlag, New York.
- Pérez, B., Sánchez, D. and Moreno, J.M. 1995. Effects of past and current land-use on post-fire vegetation in Sierra de Gredos, Spain. In: Balabanis, P. (ed.), *Forest Fire Risk and Management*. Commission of the European Communities, EUR Report Series (in press).
- Quezel, P. 1981. The study of plant groupings in the countries surrounding the Mediterranean: Some methodological aspects. In: di Castri, F., Goodall, D.W. and Specht, R.L. (eds), *Mediterranean-type Shrublands*. Ecosystems of the World Vol. 11. 87-94. Elsevier, Amsterdam.
- Rebelo, A.G. 1992. Preservation of biotic diversity. In: Cowling, R.M. (ed.), *The Ecology of Fynbos: Nutrients, fire and diversity*. 309-344. Oxford University Press, Cape Town.
- Riggan, P.J., Franklin, S.E., Brass, J.A. and Brooks, F.E. 1994. Perspectives of fire management in Mediterranean ecosystems of southern California. In: Moreno, J.M. and Oechel, W.C. (eds), *The Role of Fire in Mediterranean-type Ecosystems*. 140-162. Springer-Verlag, New York.
- Saunders, D.A. 1989. Changes in the avifauna of a region, district and remnant as a result of fragmentation of native vegetation: the wheatbelt of Western Australia. A case study. *Biological Conservation* 50: 99-135.
- Saunders, D.A. 1993. Community based observer scheme to assess avian response to habitat reduction and fragmentation in south western Australia. *Biological Conservation* 64, 203-218.
- Scott, D.F. and van Wyk, D.B. 1990. Effects of wildfire on soil wettability and hydrological behaviour of a forested catchment. *Journal of Hydrology*. 121: 239-256.
- Scott, D.F. and van Wyk, D.B. 1992. The effects of fire on soil water repellency, catchment sediment yields and streamflow. In: van Wilgen, B.W., Richardson, D.M., Kruger, F.J. and van Hensbergen, H.J. (eds), *Fire in South African Mountain Fynbos. Ecosystem, community and species response at Swarboskloof*. 216-239. Springer-Verlag, Berlin.
- Scougall, S.A., Majer, J.D. and Hobbs, R.J. 1993. Edge effects in grazed and ungrazed Western Australian wheatbelt remnants in relation to ecosystem reconstruction. In: Saunders, D.A., Hobbs, R.J. and Ehrlich, P.R. (eds), *Reconstruction of Fragmented Ecosystems, Global and Regional Perspectives*. Nature Conservation 3. 163-178. Surrey Beatty and Sons, Chipping Norton, NSW.
- Smith, R.C., Huang X., Lyons, T.J., Hacker, J.H. and Hick, P.T. 1992. Change in land surface albedo and temperature in southwestern Australia following the replacement of native perennial vegetation: satellite observations. Paper No. 1A1-92-0117, 43rd Congress of the International Astronautical Federation, Washington, DC.
- Stock, W.D. and Allsopp, N. 1992. Functional perspective of ecosystems. In: Cowling, R.M. (ed.) *The Ecology of Fynbos. Nutrients, Fire and Diversity*. 241-259. Oxford University Press, Cape Town.
- Valdés, B., Talavera, S. and Fernández-Galiano, E. (eds). 1987. *Flora Vascular de Andalucía Occidental*. KETRES Editora, Barcelona, Spain.
- Van Wilgen, B.W., Bond W.J. and Richardson D.M. 1992. Ecosystem management. In: Cowling, R.M. (ed.) *The Ecology of Fynbos: Nutrients, fire and diversity*. 345-371. Oxford University Press, Cape Town.
- Von Broembsen, S. 1984. Distribution of *Phytophthora cinammomi* in rivers of the south-western Cape Province. *Phytophylactica* 16: 227-229.
- World Conservation Monitoring Centre. 1992. *Global Biodiversity. Status of the Earth's Living Resources*. Chapman and Hall, London.
- Wills, R.T. 1993. The ecological impact of *Phytophthora cinammomi* in the Stirling Range National Park, Western Australia. *Australian Journal of Ecology* 18: 145-160.
- Yates, C.J., Hobbs, R.J. and Bell, R.W. 1994. Landscape-scale disturbances and regeneration of semi-arid woodlands of south-western Australia. *Pacific Conservation Biology* 1, (in press).

6.1.9 Coastal systems

6.1.9.1 Introduction

We use the term 'coastal systems' to mean the general marine region extending from the upper tidal limits out across the continental shelf, slope and rise (Brink 1993). This definition includes rocky shores, sandy beaches, kelp forests, subtidal benthos and the water column over the shelf, slope and rise. 'Coastal systems' are generally considered to encompass the Exclusive Economic Zones of nations (Hight 1992), a strip approximately 200 nautical miles wide along the 440 000 km long outlines of the

continents (Ryther 1969; Highet 1992; Goldberg 1993). This simple geographic definition is used for convenience. In reality, 'coastal systems' often represent the margins of larger ecosystems (Sherman *et al.* 1990), and they vary considerably depending on atmospheric, oceanographic, historical and geological factors. For example, island coastal systems often have much higher endemism than continental coastal systems (Castilla 1988). This review focuses on the nearshore benthic communities whose biological dynamics are better known than those of pelagic or deep sea communities. Estuaries, mangroves and coral reefs are covered elsewhere in this Section.

The importance of coastal systems to humanity is high: most of the world's people live within 80 km of the coast (Sobel 1993). Both land- and ocean-based activities are concentrated at the coastal margins: tourism, recreation, fishing, mariculture, domestic and industrial waste disposal, military activities, transportation, mining and energy industries (Goldberg 1993). Many kelp forests and rocky intertidal shores are among the most productive of any ecosystem in the world (Valiela 1984; Leigh *et al.* 1987; Highsmith and Coyle 1990). Coastal fisheries are the richest in the world, with more than 75% of the world's fish catch coming from coastal waters (FAO 1991; Brink 1993). In addition to the commercial importance of coastal fisheries, many people in developing countries obtain a significant amount of their nutrition from the consumption of local seaweeds, shellfish and fish (Tseng 1984; Bustamante and Castilla 1987; Durán *et al.* 1987; Santelices 1989; FAO 1991; Norse 1993). The aesthetic beauty of coastal shores, though difficult to evaluate in economic terms, is nonetheless real and invaluable to many.

Coastal and other marine systems differ from terrestrial systems in several important ways, both with respect to patterns of diversity and with respect to the functional implications of those patterns. High diversity is found not only at the species level as in terrestrial systems (where insects constitute the vast majority of animal species), but also at higher taxonomic levels. In general, marine systems have a much greater diversity of types of organisms and types of body plans than do terrestrial systems. For example, of the 33 extant phyla of animals (Margulis and Schwartz 1988), 32 occur in the sea, 15 are exclusively marine, and five are nearly so (see Section 3.2; Norse 1993). Most of these phyla are abundant in coastal systems (Ray 1991; Ray and Grassle 1991).

One consequence of the high level of diversity is that functional groups (see Section 5.2.2) often include species that are physiologically and genetically more distinct from one another than is the case within a comparable assemblage on land. One possible consequence of the greater differences among members of a functional group is a greater probability that the members will respond

differently to environmental changes. In other words, the greater the taxonomic diversity within a functional group, the greater the genetic and physiological base for adaptation to change. It is possible that this higher level of diversity confers on the marine world a greater potential for ecosystem resilience to change (see Section 5.2.2).

Primary producers in coastal systems are particularly diverse in many important ways. They range in size from microscopic plankton to giant kelps up to 60 m long. Most seaweeds are anchored to the bottom, but others, like the phytoplankton suspended in the water column, are transported in and out of the anchored communities. One result of this fluid transport is that carbon that is fixed in one place may be consumed or decomposed many kilometres away. The generally smaller size and faster growth rates of primary producers in the oceans is one reason why changes occurring over very large spatial scales (thousands of kilometres) can take place over much shorter temporal scales (weeks) compared to equivalent changes on land (Steele 1985). Primary producers in coastal systems are taxonomically diverse, and photosynthetic bacteria and protists play a much more prominent role than these groups do on land.

Biogeographic diversity patterns are well known for many marine taxa. Although some taxa (e.g. molluscs, fishes) exhibit the highest species diversity at lower latitudes, others (seaweeds) are most diverse at mid latitudes (Gaines and Lubchenco 1982; Bolton 1994), still others (marine mammals and bryozoa) are most diverse at higher latitudes, and many other taxa show no latitudinal cline at all (Clarke 1992). In temperate regions, the eastern margins of ocean basins tend to be more diverse than the western margins. Large inter-oceanic differences in diversity occur, and reflect, in part, geological and historical phenomena (see Section 3.2). The coastal biota of the temperate North Atlantic, for example, is less diverse than that of the North Pacific; and the macrophyte flora of temperate South America is depauperate compared with the temperate North Pacific or temperate Australasia.

6.1.9.2 Major human-induced impacts on and threats to biodiversity

Diversity of coastal systems is affected directly and indirectly by numerous human activities (Aronson 1990; Folke *et al.* 1991; Hammer *et al.* 1993; Norse 1993; Barbier *et al.* 1994; Perrings *et al.* 1994; National Research Council 1995). Threats include over-exploitation of fishes, invertebrates and seaweeds (for fishery and non-fishery uses); coastal aquaculture; physical alteration of the habitat (by trampling, trawling, dredging, drilling, dynamiting, building and dumping); noise pollution; thermal pollution; and chemical pollution from both toxins and nutrients. Long-term effects of oil spills are generally not well known, but some impacts have been found to be substantial

(Keller and Jackson 1993a, b). Biological invasions are a serious threat to biodiversity, especially in bays, estuaries and inland seas (Ben-Tuvia 1973; Ben-Yami and Glaser 1974; Dromgoole and Foster 1983; Spanier and Galil 1991; Carlton and Hodder 1995), and the transportation of potential invaders in the ballast water of ships has only recently been recognized as a serious concern (Carlton and Geller 1993; McCarthy and Khambaty 1994). Numerous activities occurring on land also have strong impacts on coastal systems: for example, logging, livestock grazing, agricultural practices, industrial activities, residential and resort development and damming vary the load of sediment, pesticides, sewage, industrial pollutants and other wastes delivered to coastal waters. Although global-scale threats such as climate change and increases in ultra violet-B radiation have strong potential to affect coastal regions (Smith *et al.* 1992; Castilla *et al.* 1993; Lubchenco *et al.* 1993; Peterson *et al.* 1993; Barry *et al.* 1995; Roemmich and McGowan 1995a, b), the threats to diversity from land-use practices and overfishing are real, serious and more immediate (Paine 1993; Perrings *et al.* 1994; National Research Council 1995). Many areas are already severely degraded. Moreover, the rates, spatial extent and types of perturbations are increasing alarmingly.

Documentation of the effects of these threats is severely hampered by several factors which, though applicable to many terrestrial systems, are often more chronic in marine systems (Grassle *et al.* 1991): they include (1) lack of long-term, basic baseline information about the distribution and abundance of biota and how the patterns change through time (Wood *et al.* 1993; but see Barry *et al.* 1995 and Roemmich and McGowan 1995a, b for exceptions); (2) inadequate basic systematic information and a paucity of trained taxonomists (Andersen 1992; Wood and Leatham 1992; Knowlton 1993; Knowlton and Jackson 1994; National Research Council 1995); (3) lack of documentation of extinctions (Carlton 1993); (4) difficulty in adequately surveying and sampling benthic and pelagic systems; (5) slow expression of the consequences, which often take years or decades to occur, and thus appear 'invisible' to humans (Magnuson 1990); (6) long-distance transport of chemicals (Bacon *et al.* 1992; Tatsukawa *et al.* 1994); organisms and phenomena. Coastal systems are strongly affected by processes occurring both in the immediate vicinity and far away, not only via air-water interactions but also through long-distance transportation within the aquatic medium. Spatial scale, transport and dispersal events are of particular importance to the dynamics of coastal systems (Gaines *et al.* 1985; Roughgarden *et al.* 1985; Grassle *et al.* 1991; Steele 1991; Levin 1992) and to the evolution of species within these systems (Palumbi 1992; Steinberg *et al.* 1995).

Despite these limitations to adequate documentation of impacts, many effects are all too obvious. The extinction of

numerous wild salmon runs and the ongoing decline of many of the remaining runs in the Pacific Northwest of the United States; eutrophication in Chesapeake Bay and Buzzards Bay in the eastern USA; effects of sewage sludge dumping off New Jersey, and the massive decline of most major fisheries, provide ample evidence of adverse impacts. Human exclusion experiments along the coast of Chile document previously unknown but dramatic direct impacts of people on the shore (Moreno *et al.* 1984; Castilla and Durán 1985; Durán *et al.* 1987; Durán and Castilla 1989; Castilla *et al.* 1993, 1994). Comparable changes may be occurring elsewhere (Dethier *et al.* 1989; Hawkes 1992; Addressi 1994).

6.1.9.3 Productive capacity, biomass, decomposition and nutrient cycling

Human impacts on biodiversity. Over-exploitation of coastal fisheries world-wide represents one of the most serious but least well documented threats to nearshore biodiversity. Despite the fact that overfishing of many commercially important fish and shellfish stocks has resulted in the demise of numerous fisheries throughout the world, there is often little specific information about the overall consequences to genetic, species or ecosystem diversity in most of the affected systems. The largest impacts may well be caused by indirect effects, as initial declines in target species in turn affect other species.

The effects of over-exploitation of a few species are known or can be inferred, especially where ecological relationships with the species' predators, symbionts, competitors or prey are known (Barkai and MacQuaid 1988; Paine 1993). The over-exploitation of sea otters along the northeastern rim of the Pacific Ocean, for example, has been well documented. Comparison of Aleutian Islands with and without otters suggests that the removal of this keystone predator in Alaska results in profound changes in the biodiversity of the rest of the kelp forest community (Box 6.1-1; Estes and Palmisano 1974; Estes *et al.* 1978; Duggins *et al.* 1989). Other changes in diversity resulting from overfishing have been described for Northwest Atlantic continental shelf systems (Sherman 1990), Haiti, the US Virgin Islands (Hay 1984), Hainan Island, China (Hutchings and Wu 1987) and the Baltic Sea (Hammer *et al.* 1993).

Ecosystem consequences of impacts. Little information is available with which to evaluate comprehensively the consequences of changes in diversity on production biomass, decomposition or nutrient cycling. We know of no studies evaluating the consequences of changes in number of species *per se*. However, there is evidence that changes in abundance of certain species can have profound impacts on these processes. For example, in the sea otter—sea urchin—kelp interaction (Box 6.1-1), the deletion of a single species (the otter) resulted in dramatic changes in biomass and probably also primary and secondary

Box 6.1-1: Sea otters: keystone predators in Alaskan kelp forests.

Sea otters in Alaska demonstrate the strong influence that a single species can have on an entire community. Otters play a pivotal role in maintaining kelp forests by eating and controlling sea urchins which consume kelps. In the absence of otters, urchins increase in size and numbers and overgraze the kelps. A lush kelp forest is thus converted to an 'urchin barren', a community composed primarily of a pavement of encrusting coralline algae and urchins (Estes and Palmisano 1974; Simenstad *et al.* 1978; Duggins *et al.* 1989). Urchin barrens are devoid of kelps and other large seaweeds, and lack the diverse assemblage of macroscopic benthic and pelagic invertebrates and fishes, and marine mammals associated with kelp forests. The otter is thus a 'keystone' species because it exerts a disproportionately large influence on the entire community (see Box 5.2-1).

Conversion of a kelp forest to an urchin barren results in the loss of important ecosystem services. In addition to providing a habitat for resident species, kelp forests may also function as important nursery areas for many fish (Carr 1994) and may modify larval transport to adjacent shores (Guines *et al.* 1985). They also provide dissolved and particulate organic matter that is consumed locally and by organisms such as deposit- and filter-feeding mussels, clams and barnacles in adjacent intertidal and subtidal communities (Duggins *et al.* 1989). Moreover, kelp forests often protect coastal shorelines from the full force of waves, especially during winter storms. In this case, the absence of a keystone species results in the conversion of a community from a lush forest to a depauperate plain with attendant loss of habitat, primary and secondary production, export to nearby systems and buffering capacity to nearshore areas.

production, nutrient cycling, decomposition, and export of organic matter to nearby systems (Estes and Palmisano 1974; Simenstad *et al.* 1978; Duggins *et al.* 1989). Alterations in the relative abundance of phytoplankton or macrophytes resulting from climate change could have important cascading consequences for the structure and functioning of the rest of the coastal systems (Peterson *et al.* 1993), but the specific consequences to primary production, biomass, decomposition and nutrient cycling cannot be predicted with confidence.

Climate change has been predicted to result in warmer water, sea level rise (Houghton *et al.* 1990, 1992) and alterations in coastal upwelling patterns (Bakun 1990). Each of these would be likely to have effects on biodiversity, though the direct and indirect changes are difficult to predict (Castilla *et al.* 1993; Lubchenco *et al.* 1993; Paine 1993; Peterson *et al.* 1993). Barry *et al.* (1995) report shifts in temperatures and in intertidal plants and animals over a 50-year time span in Monterey Bay, California, USA, which may be due to global warming. Different taxa of macrophytes as well as phytoplankton vary considerably in their responses to changes in temperature and their ability to take up and store nutrients (Wheeler 1983; Fujita 1985). Changes in the frequency, duration or intensity of coastal upwelling would be expected to alter the relative abundances of the major taxa of macrophytes and phytoplankton as well as affect the overall levels of productivity (Menge *et al.* 1995; Roemmich and McGowan 1995a, b).

6.1.9.4 Sediment structure

Human impacts on biodiversity. Dredging, trawling, anchoring, trampling, raking and digging have wide-

ranging but sporadically documented consequences for marine biota. These activities disrupt sediment structure, destroy burrows, bury or clog organisms and suspend particles, and modify wave and tidal energy, all of which may affect patterns of diversity in soft-sediment environments (McLachlan *et al.* 1993). One short-term effect of sediment resuspension should be increased respiration and mineralization of sediment organic matter and a consequent increase in inorganic nutrients into the water column. Increase in nuisance phytoplankton blooms would be expected to follow. Other expected consequences include mobilization of toxic metals and inorganics into the water column and a disruption of anaerobic microzones and thus biogeochemical cycles.

The use of new, economically more efficient techniques for harvesting shellfish can sometimes have negative consequences on the target commercial species and the rest of the community compared with traditional hand-gathering techniques (Defeo 1989, 1993). Contamination of freshwater effluents by human activities (e.g. through the use of chemicals and increased nutrients from agriculture) can affect the composition of these communities and potentially reduce species diversity above and beyond the effect produced by the reduction in salinity (Defeo *et al.* 1990; Defeo 1993). Taxa vary widely in the extent to which they themselves modify the structure of the sediments and thus alteration of sediment structure may result in further modifications through trophic and non-trophic interactions among species. Intra- and interspecific biological interactions are poorly understood in these systems.

Ecosystem consequences of impacts. The ecosystem consequences of these disruptive activities are largely

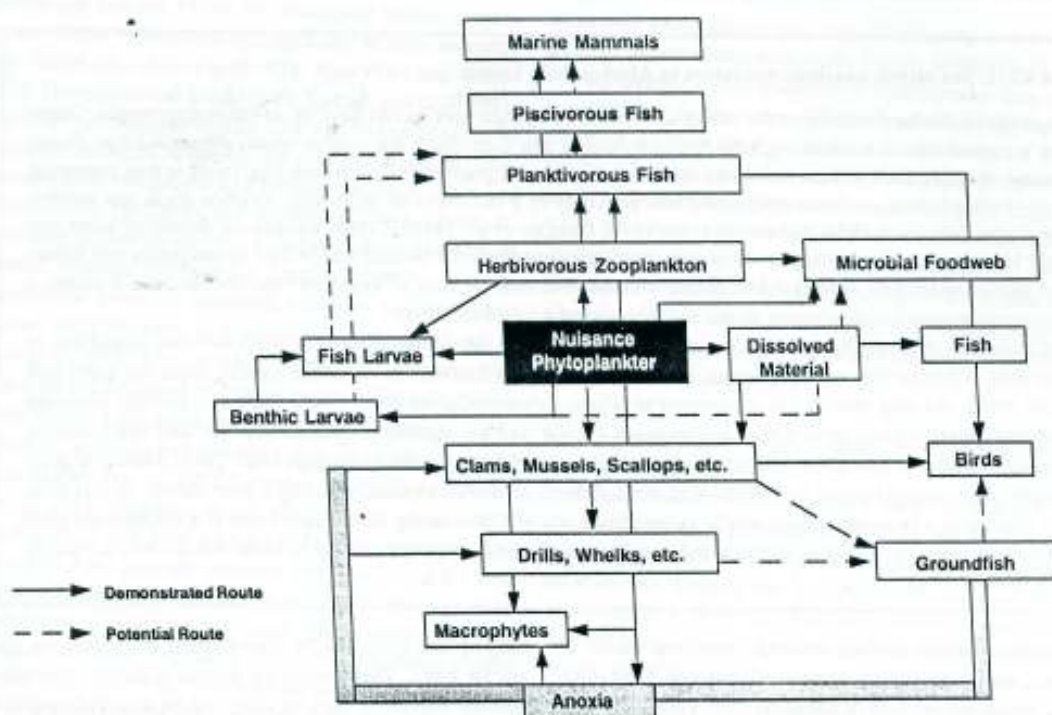


Figure 6.1-4: Trophic linkages between nuisance phytoplankton blooms and species illustrating some direct and vectored routes through which toxins, inimical species and anoxia affect the depicted compartments and may cause recruitment failure and/or mortality (after: Smayda 1992).

unknown. The experimental exclusion of humans to create a *de facto* closing of the fishery of the yellow clam *Mesodesma mactroides* from a sandy beach on the coast of Uruguay illustrates, however, that these activities can have far-reaching consequences. The yellow clam is an important artisanal fishery in Uruguay, and many fishing communities are devoted to its extraction (Defeo 1989). The experimental manipulation of the fishery led to important changes in overall abundance and in the kinds of processes regulating the dynamics of the populations of not only *M. mactroides* but also the coexisting wedge clam, *Donax hanleyanus*, which is not exploited by humans (Defeo 1993; Defeo and DeAlava 1995). Changes in the abundance of other non-exploited species were also observed following the 'exclusion' of humans.

6.1.9.5 Water movement and quality

Human impacts on biodiversity. Nutrients in shallow coastal systems are taken up directly from the aquatic medium, and nutrient availability is heavily affected by sewage discharge, freshwater runoff, dumping of industrial wastes, and atmospheric deposition of toxics and nutrients. In 1982, anthropogenic inputs of nutrients to coastal waters were estimated to equal or exceed natural inputs (Meybeck

1982). The UN's Group of Experts on the Scientific Aspects of Marine Pollution (GESAMP 1991) has 'identified nutrients as the most damaging class of pollutants in the marine realm' (Norse 1993). Nutrient enrichment of coastal waters is generally characterized by increases in primary production, shifts in the relative abundance of phytoplankton species, dense plankton blooms and nuisance macro-algal blooms (GESAMP 1991; Norse 1993). One specific mechanism of these shifts appears to be alteration in the Si:N and Si:P ratios, which favour non-diatom blooms (Smayda 1992). Explosive increases in certain taxa such as various dinoflagellates produce 'red tides'. The diversity of organisms producing toxic phytoplankton blooms has increased during the last few decades (Wood *et al.* 1993), and the frequency, extent and intensity of toxic phytoplankton blooms is increasing (Dundas *et al.* 1989; Smayda 1990; Hallegraeff 1993). Moreover, certain blooming species are apparently spreading globally, perhaps aided by transport in the ballast water of ships (Hallegraeff and Bolch 1991). Smayda (1990) terms this 'a global epidemic' with far-reaching consequences.

Ecosystem consequences of impacts. Coastal eutrophication has dramatic effects on water quality,

aquaculture, fisheries, human health and ecosystem structure and functioning. The well-known effects of coastal eutrophication include toxic algal blooms, anoxia, fish kills, shifts to a decomposition food web, and loss of water quality (Fenchel *et al.* 1990; Turner and Rabalais 1991). Red-tide or other algal blooms can result in human health hazards such as paralytic shellfish poisoning or aquacultural die-offs (Richardson 1989). Toxins produced by red-tide blooms have recently been shown to result in a wide variety of other ecosystem effects, ranging from reduced fecundity and recruitment and increased mortality of fishes (Smayda 1992) to marine mammal die-offs (Geraci *et al.* 1989) (Figure 6.1-4). Hence, differential responses of phytoplankton taxa to nutrient shifts can result in substantial alteration of the relative abundance of phytoplankton with far-reaching consequences involving not only water quality but also other ecosystem properties as well. Changes in the relative abundance of phytoplankton taxa are also influenced by shifts in the relative abundance of zooplankton and higher trophic level taxa.

6.1.9.6 Feedbacks to atmospheric properties

Human impacts on biodiversity. A wide variety of bacteria, phytoplankton and macrophytes produce gases that have been suggested to be of potential importance to the radiative balance of the Earth's atmosphere. Chemically important marine biogases include species of carbon (CO_2 , CO , CH_4), sulphur (DMS), nitrogen (N_2O , NH_3), and halogens (CH_3I , CH_3Cl , and CH_3Br) (Wolfe *et al.* 1991). Some of these gases are also produced by terrestrial biota. However, the marine environment is thought to be the main source of dimethylsulphide (DMS) and carbonylsulphide (COS), two trace constituents of the atmosphere which have important effects on the global atmospheric and climatic balance (Charlson *et al.* 1987; see also 6.2.4). The production of atmospherically active gases is not uniformly distributed among species within a given habitat. A few species produce a disproportionate fraction of the most active atmospheric constituents (e.g. bacterial catabolism of certain phytoplankton species produces a large fraction of all the atmospheric DMS). Factors affecting the relative abundance of these species have the potential to exert large effects on the atmosphere and consequently the global climate. Pollutants, eutrophication of coastal waters, sedimentation, and depletion of atmospheric ozone with the consequence of increasing UV-B radiation (Karentz 1991; Helbling *et al.* 1992; Smith *et al.* 1992) can all alter the diversity and abundance of these producers and thus have the potential to alter global climate.

Ecosystem consequences of impacts. Emission of DMS from the open ocean and its effect in the formation of cloud condensation nuclei (CCN) has been hypothesized to be a

major regulatory factor of the global climate. Production of DMS varies dramatically depending on species composition (Keller *et al.* 1989). It is also known that blooms of calcifying coccolithophorids found in coastal waters have global significance in the CO_2 and DMS cycles (Holligan *et al.* 1983; Matrai and Keller 1993; Brown and Yoder 1994). Although factors regulating both species composition and the outbreak of blooms are not clearly understood in these systems, alteration of these regulatory factors (e.g. the relative availability of nutrients) by human activities can have potential global consequences.

The coastal marine environment is the main biogenic source of COS, which is thought to be the major source of sulphur in the stratosphere. After oxidation, these constituents play a major role in the global radiation budget and thus climate, by scattering sunlight back to space and interfering with stratospheric ozone (Lazrus and Gandrun 1977; Hofman 1990). The general degradation of coastal environments can affect the global levels of CS_2 , changing the atmospheric composition and in turn affecting the rest of the biota.

6.1.9.7 Landscape and waterscape structure

Human impacts on biodiversity. Coastal systems are characterized by steep physical gradients in desiccation, wave action, water movement, depth, light attenuation, mixing, temperature, particle size, particle movement, salinity and substrate type. One consequence of these steep gradients is a high landscape diversity, with rocky shores closely juxtaposed with sandy beaches, kelp forests, estuaries or other habitats. The linkage of these different communities by water flowing and organisms moving within and among them provides for substantial interchange. Human activities such as over-exploitation of resources, physical alteration of the habitat, pollution, introduction of alien species and climate change are already affecting genetic, species and ecosystem diversity and hence modifying landscape structure.

Ecosystem consequences of impacts. Most landscape-level alterations resulting from changes in biodiversity have not been well documented. The potential for these changes is illustrated in the greater Everglades ecosystem in Florida, USA. Massive alteration of natural hydrologic patterns for flood control and development throughout the entire Everglades region appears to be one of the primary triggers of the ecological collapse of Florida Bay (Butler *et al.* 1994). The enormous anthropogenic flows of flood waters into coastal waters to the east and west of Lake Okeechobee have decimated hard-bottom communities.

Two smaller-scale examples provide more information about possible roles of biodiversity in mediating landscape-level changes. The absence of sea otters from certain Aleutian islands (Box 6.1-1), and the creation of marine

protected areas in intertidal sites in Chile, illustrate how changes in diversity mediated through deletions of a top predator have resulted in drastic alteration of the ecosystem and landscape structure. Conversion of a kelp forest to an urchin barren modifies water movement patterns, delivery of dissolved and particulate organic matter to adjacent intertidal beaches and intertidal and subtidal rocky shores, protection of juvenile fishes and hence recruitment into pelagic communities. In Chile, humans remove gastropods (Oliva and Castilla 1986; Durán *et al.* 1987), seaweeds (Castilla and Bustamante 1989) and fishes, and because of the effects of each of these groups on other species in the community, the result is a transformation of the community.

6.1.9.8 Biotic linkages and species interactions

Human impacts on biodiversity. Overfishing, overcollecting, trampling, modification of the physical structure, pollution and species introductions are all substantial threats to coastal biodiversity. Influences range from 'bottom-up' effects wherein species at the base of the food web are affected first (e.g. eutrophication or harvesting of macrophytes) to 'middle-out' effects involving alterations in herbivores (e.g. harvesting of sea urchins or herbivorous fishes), to 'top-down' effects where top predators are directly affected (e.g. removals of otters, molluscs, sea stars, lobsters, sharks and other fishes). The relative importance of these regulatory effects may vary among communities and along environmental gradients (Sousa 1979; Menge 1992). None of these impacts is limited to the taxon, functional group or trophic level first affected; all of these effects reverberate throughout the rest of the ecosystem via biological interactions.

Ecosystem consequences of impacts. Biotic interactions and species linkages are particularly well known from nearshore coastal benthic communities where experimental manipulation of species has resulted in a mechanistic understanding of the links among species, including the importance of interaction strength, keystone species, and compensation among species within a functional group (reviewed in Paine 1980, 1992; Menge *et al.* 1994; Power *et al.* 1995; Power and Mills 1995). If keystone species are removed, for example, the entire ecosystem can be affected. Sea otters and sea-stars provide well-documented examples (Box 6.1-1). In contrast, some systems are characterized by the lack of a keystone species (Menge and Lubchenco 1981; Robles and Robb 1993). These systems provide an interesting comparison which is immediately relevant to the relationship between biodiversity and ecosystem functioning. Rocky intertidal shores on the Pacific coast of Panama have rich diversity within all trophic and functional groups (Lubchenco *et al.* 1984). Experiments demonstrate that the entire assemblage of

predators and herbivores has dramatic effects in maintaining the barren appearance of the shores. However, no single species or group of species has a demonstrable effect. Removal of species or functional group such as molluscan predators or molluscan herbivores or large fishes or small fishes and crabs has little effect on the community because other groups with overlapping functions compensate for the absence of the target group (Menge *et al.* 1986). High diversity within the functional groups of this community provides for continuation of the function in the absence of any individual constituents (Menge *et al.* 1986; Menge and Lubchenco 1981). This is a fundamentally different result from that obtained in Alaskan kelp communities or rocky intertidal shores off Washington and Oregon (Paine 1966, 1994; Menge *et al.* 1994) or tide pools in New England (Lubchenco 1978) where removal of a single keystone species totally changes the community. The Panama system is characterized by high functional overlap and thus the potential for compensation.

Even in communities such as rocky intertidal systems where the relationships between species diversity and community patterns and processes are among the best understood of any assemblage, relatively little is known about effects at the ecosystem level. The consequence of removal of keystone species to nutrient flows, rates of production or decomposition have not been measured.

6.1.9.9 Microbial activities

Human impacts on biodiversity. Several anthropogenic changes have had broad impacts on micro-organisms. Excess nutrient input from sewage, fertilizers and soil erosion can drastically change nutrient availability in many coastal systems (GESAMP 1991; Norse 1993). Increased UV irradiation from a thinning ozone layer probably has a detrimental effect on phytoplankton over vast areas (Hebling *et al.* 1992; Smith *et al.* 1992). Warming from climate change reduces available oxygen and probably favours some species over others (Epstein *et al.* 1993) or causes evolutionary change in organisms that experience these environmental impacts as a form of directional selection (Lynch *et al.* 1991; Lynch and Lande 1993). Both processes are likely to change the structure of microbial communities, with unpredictable impacts on ecosystem functioning.

The biodiversity of marine microorganisms has been greatly underestimated in the past. Only recently, through molecular methods, has the tremendous taxonomic diversity of these groups begun to be documented (Giovannoni *et al.* 1990; Fuhrman *et al.* 1993). Specific impacts on this diversity are thus poorly understood.

Ecosystem consequences of impacts. These broad impacts may have several consequences. Nutrient influx has created a variety of eutrophication problems in many

coastal regions (Richardson 1989; Turner and Rabalais 1994). For example, a cascade of disturbances, apparently caused by an increase in cyanobacterial blooms in Florida Bay, Florida, USA, has caused the widespread loss of sponge populations and a decline in lobster abundance (Butler *et al.* 1994). Outbreaks of human disease, such as cholera, have been linked to plankton reservoirs that have been enhanced by nutrient addition (Epstein *et al.* 1993). Further, anoxic conditions created by algal blooms have been implicated in significant mortality of fish stocks and benthic fauna in several regions (Tulki 1965; Jorgensen 1980; Richardson 1989). Numerous unexplained mass mortalities or disease outbreaks remain enigmatic, though pathogens are often suspected of playing key roles, for example in urchins (Lessios *et al.* 1984; Lessios 1988), asteroids (Dungan *et al.* 1982), abalone (Steinbeck *et al.* 1992; Richards and Davis 1993), sea grasses (Rasmussen 1977) and marine mammals (Dietz *et al.* 1989). In most cases, neither the causes of the outbreaks nor the specific vectors are known.

Viruses, previously disregarded by marine microbiologists, are clearly important in regulating phytoplankton (Suttle *et al.* 1990) and bacterioplankton populations (Bergh *et al.* 1989; Bratbak *et al.* 1990; Proctor and Fuhrman 1990). As with symbiotic relations, virus-host interactions are highly species-specific and changes in diversity will change the dynamics of these interactions (Steward *et al.* 1992).

Loss of certain functional groups (see Section 5.2.2) such as methane oxidizers would have a dramatic effect on global biogeochemistry because these functional groups are taxonomically limited in scope.

Close coupling of temperature for maximum growth rate and average temperatures *in situ* have profound impacts on bacterial growth and the fate of carbon from phytoplankton in high latitude seas (Pomeroy and Deibel 1986; Pomeroy *et al.* 1991; Wiebe *et al.* 1992). Similar close correlation between *in situ* temperatures and optimum growth rate has been observed in other members of the microbial community from the Arctic (Choi and Peters 1992) and bacterial communities from temperate ecosystems (Shiah and Ducklow 1994), suggesting that the entire microbial food web of a given environment will be very sensitive to changes in average temperature, even if this involves a change of only a few degrees.

6.1.9.10 Summary and relevance to human activities

Coastal systems are among those most heavily affected by humans. They are also among the systems most vital to humans, and provide food, recreation, inspiration, transportation, waste disposal, and the buffering of coastlines from erosion. Threats to biodiversity in these systems are multiple and serious; they may also be synergistic. The full impact of the resulting changes to

diversity are not sufficiently known, but early indications suggest they may be profound. The effects of over-exploitation and pollution are increasingly obvious and serious but the full consequences of species introductions, physical habitat destruction, changes in UV-B radiation and climate change are yet to be documented.

References

- Addressi, L. 1994. Human disturbance and long-term changes on a rocky intertidal community. *Ecological Applications* 4: 786-797.
- Andersen, R.A. 1992. Diversity of eukaryotic algae. *Biodiversity and Conservation* 1: 267-292.
- Aronson, R.B. 1990. Onshore-offshore patterns of human fishing activity. *Palaios* 5: 88-93.
- Bacon, C.E., Jarman, W.M. and Costa, D.P. 1992. Organochlorine and polychlorinated biphenyl levels in pinniped milk from the Arctic, Antarctic, California, and Australia. *Chemosphere* 24: 779-791.
- Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science* 247: 198-201.
- Barbier, E.B., Burgess, J.C. and Folke, C. 1994. *Paradise Lost? The ecological economics of biodiversity*. Earthscan, London.
- Barkai, A. and MacQuaid, J. 1988. Predator-prey role reversal in a marine benthic ecosystem. *Science* 242: 62-64.
- Barry, J.P., Baxter, C.H., Sagarin, R.D. and Gilman, S.E. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267: 672-675.
- Ben-Tuvia, A. 1973. Man-made changes in the eastern Mediterranean Sea and their effect on the fishery resources. *Marine Biology* 19: 197-203.
- Ben-Yami, M. and Glaser, T. 1974. The invasion of *Saurida undosquamis* (Richardson) into the Levant Basin - an example of biological effect of interoceanic canals. *Fishery Bulletin* 72: 359-373.
- Bergh, Ø., Børsheim, K.Y., Bratbak, G. and Haldal, M. 1989. High abundance of viruses found in aquatic environments. *Nature* 340: 467-468.
- Bolton, J.J. 1994. Global seaweed diversity: patterns and anomalies. *Botanica Marina* 37: 241-247.
- Bratbak, G., Haldal, M., Norland, S. and Thingstad, T.F. 1990. Viruses as partners in spring bloom microbial trophodynamics. *Applied and Environmental Microbiology* 56: 1400-1405.
- Brink, K.H. 1993. The coastal ocean processes (CoOP) effort. *Oceanus* 36: 47-49.
- Brown, C.W. and Yoder, A. 1994. Distribution patterns of coccolithophorids in the western North Atlantic Ocean. *Continental Shelf Research* 14: 175-197.
- Bustamante, R.H. and Castilla, J.C. 1987. The shellfishery in Chile: An analysis of 26 years of landings (1960-1985). *Biología Pesquera (Chile)* 16: 79-97.
- Butler, M.J., Hermkind, W.F. and Hunt, J.H. 1994. Cascading disturbances in an ailing marine ecosystem impact the spiny lobster nursery of south Florida. *Bulletin of the Ecological Society of America* (Supplement). 75 (2): 29.
- Carlton, J.T. 1993. Neoeinctions of marine invertebrates. *American Zoologist* 33: 499-509.

- Carlton, J.T. and Geller, J.B. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. *Science* 261: 78-82.
- Carlton, J.T. and Hodder, J. 1995. Biogeography and dispersal of coastal organisms: experimental studies on a replica of a 16th century sailing vessel. *Marine Biology* 121: 721-730.
- Carr, M.H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75: 1320-1333.
- Castilla, J.C. (ed.) 1988. *Islas Oceanicas Chilenas: Conocimiento Científico y Necesidades de Investigaciones*. Ediciones Universidad Católica de Chile, Santiago, Chile.
- Castilla, J.C. and Bustamante, R.H. 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on *Durvillaea antarctica* (Phaeophyta, Curvillales). *Marine Ecological Progress Series* 50: 203-214.
- Castilla, J.C. and Durán, L.R. 1985. Human exclusion from the rocky intertidal of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* 45: 391-399.
- Castilla, J.C., Branch, G.M. and Barkai, A. 1994. Exploitation of two critical predators: the gastropod *Concholepas concholepas* and the rock lobster *Jasus lalandi*. In: Siegfried, W.R. (ed.), *Rocky Shores: Exploitation in Chile and South Africa*. Ecological Studies Vol. 103. 101-130. Springer-Verlag, Berlin.
- Castilla, J.C., Navarrete, S.A. and Lubchenco, J. 1993. Southeastern Pacific coastal environments: main features, large-scale perturbations and global climate change. In: Mooney, H.A., Fuentes, E.R. and Kronberg, B.I. (eds), *Earth System Response to Global Change: Contrasts between North and South America*. 167-188. Academic Press, San Diego.
- Charlson, R.J., Lovelock, J.E., Andreae, M.O. and Warren, S.G. 1987. Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. *Nature* 326: 655-661.
- Choi, J.W. and Peters, F. 1992. Effects of temperature on two psychrophilic ecotypes of a heterotrophic nanoflagellate, *Paraphysomonas imperforata*. *Applied and Environmental Microbiology* 58: 593-599.
- Clarke, A. 1992. Is there a latitudinal diversity cline in the sea? *Trends in Ecology and Evolution* 7: 286-287.
- Defeo, O. 1989. Development and management of artisanal fishery for yellow clam *Mesodesma mactroides* in Uruguay. *Fishbyte* 7: 21-25.
- Defeo, O., Mendez, S., Riestra, G. and Brazeiro, A. 1990. Agriculture drainage affecting the community structure of organisms of an Uruguayan sandy beach. *International Conference on Marine Coastal Eutrophication* (Abstract).
- Defeo, O. 1993. The effect of spatial scales in population dynamics and modelling of sedentary fisheries: the yellow clam *Mesodesma mactroides* of an Uruguayan exposed sandy beach. Doctoral dissertation, CINVESTAV-IPN Unidad Mérida, México.
- Defeo, O. and DeAlava, A. 1995. Effects of human activities on long-term trends in sandy beach populations: the wedge clam *Donax hanleyanus* in Uruguay. *Marine Ecology Progress Series* (in press).
- Dethier, M.N., Duggins, D.O. and Mumford, T.F. Jr. 1989. Harvesting of non-traditional marine resources in Washington State: trends and concerns. *Northwest Environmental Journal* 5: 71-87.
- Dietz, R., Jorgensen, M.P.H. and Harkonen, T. 1989. Mass deaths of harbor seals (*Phoca vitulina*) in Europe. *Ambio* 18: 258-264.
- Dromgoole, F.I. and Foster, B.A. 1983. Changes to the marine biota of the Auckland Harbour. *Tane* 29: 79-96.
- Duggins, D.O., Simenstad, C.A. and Estes, J.A. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245: 170-173.
- Dundas, I., Johannessen, O.M., Berge, G. and Heimdal, B. 1989. Toxic algal bloom in Scandinavian waters, May-June 1988. *Oceanography* (April) 9-14.
- Dungan, M.L., Miller, T.E. and Thomson, D.A. 1982. Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone. *Science* 216: 989-991.
- Durán, R., Castilla, J.C. and Oliva, D. 1987. Intensity of human predation on rocky shores at Las Cruces, central Chile. *Environmental Conservation* 14: 143-149.
- Durán, R.L. and Castilla, J.C. 1989. Variation and persistence of middle rocky intertidal community of central Chile with and without human harvesting. *Marine Biology* 103: 555-562.
- Epstein, P.R., Ford, T.E. and Colwell, R.R. 1993. Marine ecosystems. *The Lancet* 343: 1216-1219.
- Estes, J.A. and Palmisano, J.F. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185: 1058-1060.
- Estes, J.A., Smith, N.S. and Palmisano, J.F. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59: 822-833.
- Food and Agriculture Organization of the United Nations. 1991. *Catches and Landings*. Statistics Series No. 68. FAO, Rome.
- Fenchel, T., Kristensen, L.D. and Rasmussen, L. 1990. Water column anoxia: vertical zonation of planktonic protozoa. *Marine Ecology Progress Series* 62: 1-10.
- Folke, C., Hammer, M. and Jansson, A.M. 1991. Life-support value of ecosystems: a case study of the Baltic Sea region. *Ecological Economics* 3: 123-137.
- Fuhrman, J.A., McCallum, K. and Davis, A.A. 1993. Phylogenetic diversity of subsurface marine microbial communities from the Atlantic and Pacific Oceans. *Applied and Environmental Microbiology* 59: 1294-1302.
- Fujita, R.M. 1985. The role of nitrogen status in regulating transient ammonium uptake and nitrogen storage by macroalgae. *Journal of Experimental Marine Biology and Ecology* 92: 283-301.
- Guines, S.D., Brown, S. and Roughgarden, J. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* 67: 267-272.
- Guines, S.D. and Lubchenco, J. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. *Annual Review of Ecology and Systematics* 13: 111-138.
- Geraci, J.R., Anderson, D.M., Timperi, R.J., St. Aubin, D.J., Early, G.A., Prescott, J.H. and Mayo, C.A. 1989. Humpback whales (*Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxin. *Canadian Journal of Fisheries and Aquatic Science* 46: 1895-1898.
- GESAMP (Joint Group of Experts on the Scientific Aspects of Marine Pollution) 1991. *The State of the Marine Environment*. Blackwell Scientific Publications, Oxford.

- Giovannoni, S.J., Britschgi, T.B., Moyer, C.L. and Field, K.G. 1990. Genetic diversity in Sargasso Sea bacterioplankton. *Nature* 345: 60-63.
- Goldberg, E.D. 1993. Competitors for coastal ocean space. *Oceanus* 36 (1): 12-18.
- Grassle, J.F., Lasserre, P., McIntyre, A.D. and Ray, G.C. 1991. *Biology International: Marine Biodiversity and Ecosystem Function*. Vol. 23. International Union of Biological Sciences, Paris.
- Hallegraeff, G.M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32: 79-99.
- Hallegraeff, G. and Bösch, C. 1991. Transport of toxic dinoflagellate cysts via ships' ballast water. *Marine Pollution Bulletin* 22 (1): 27-30.
- Hammer, M., Jansson, A.M. and Jansson, B.-O. 1993. Diversity, change and sustainability: implications for fisheries. *Ambio* 22 (2-3): 97-105.
- Hawkes, M.W. 1992. Seaweed biodiversity and marine conservation in the Pacific Northwest. *Northwest Environmental Journal* 8: 146-148.
- Hay, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65: 446-54.
- Heibling, E.W., Villafañe, V., Ferrario, M. and Holm-Hansen, O. 1992. Impact of natural ultraviolet radiation on rates of photosynthesis and on specific marine phytoplankton species. *Marine Ecology Progress Series* 80: 89-100.
- Hight, K. 1992. The legal odyssey of the continental shelf: Is it a shelf? Is it a slope? Is it only a legal concept? *Oceanus* 35 (4): 6-8.
- Highsmith, R.C. and Coyle, K.O. 1990. High productivity of northern Bering Sea benthic amphipods. *Nature* 344: 862-864.
- Hofman, D.J. 1990. Increase in stratospheric background sulfuric acid aerosol mass in the past 10 years. *Science* 248: 996-1000.
- Holligan, P.M., Viollier, M., Harbour, D.S., Camus, P. and Champagne-Philippe, M. 1983. Satellite and ship studies of coccolithophore production along a continental shelf edge. *Nature* 304: 339-342.
- Houghton, J.T., Jenkins, G.J. and Ephraïm, J.J. (eds) 1990. *Climate Change: The IPCC Scientific Assessment*. Cambridge University Press, Cambridge.
- Houghton, J.T., Callander, B.A. and Varney, S.K. (eds) 1992. *Climate Change 1992: The Supplementary Report to the IPCC Assessment*. Cambridge University Press, Cambridge.
- Hutchings, P.A. and Wu, B.L. 1987. Coral reefs of Hainan Island, South China Sea. *Marine Pollution Bulletin* 18: 25-26.
- Jørgensen, B.B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos* 34: 68-76.
- Karentz, D. 1991. Ecological considerations of Antarctic ozone depletion. *Antarctic Science* 3 (1): 3-11.
- Keller, B.D. and Jackson, J.B.C. (eds) 1993a. *Long-term Assessment of the Oil Spill at Bahía Las Minas, Panama. Synthesis Report*. Vol. I. Executive Summary. US Department of the Interior, Minerals Management Service, New Orleans.
- Keller, B.D. and Jackson, J.B.C. (eds) 1993b. *Long-term Assessment of the Oil Spill at Bahía Las Minas, Panama. Synthesis Report*. Vol. II. Technical Report. US Department of the Interior, Minerals Management Service, New Orleans.
- Keller, M.D., Bellows, W.K. and Guillard, R.R.L. 1989. Dimethylsulfide production in marine phytoplankton. In: Saltzman, E.S. and Cooper, W.J. (eds), *Biogenic Sulfur in the environment*, 167-182. ACS Symposium Series No. 393.
- Knowlton, N. 1993. Sibling species in the sea. *Annual Reviews of Ecology and Systematics* 24: 189-216.
- Knowlton, N. and Jackson, J.B.C. 1994. New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some? *Trends in Ecology and Evolution* 9: 7-9.
- Lazrus, A.L. and Gandrud, B.W. 1977. Stratospheric sulfate at high altitudes. *Geophysical Research Letter* 4: 521-522.
- Leigh, E.G., Paine, R.T., Quinn, J.F. and Suchanek, T.H. 1987. Wave energy and intertidal productivity. *Proceedings of the National Academy of Sciences, USA* 84: 1314-1318.
- Lessios, H.A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned. *Annual Review of Ecology and Systematics* 19: 371-394.
- Lessios, H.A., Robertson, D.R. and Cubitt, J.D. 1984. The spread of *Diadema* mass mortality through the Caribbean. *Science* 226: 335-337.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1983.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112: 23-39.
- Lubchenco, J., Menge, B.A., Garrity, S.D., Lubchenco, P.J., Ashkenas, L.R., Gaines, S.D., Emler, R., Lucas, J. and Strauss, S. 1984. Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). *Journal of Experimental Marine Biology and Ecology* 78: 23-73.
- Lubchenco, J., Navarrete, S.A., Tissot, B.N. and Castilla, J.C. 1993. Possible ecological responses to global climate change: nearshore benthic biota of Northeastern Pacific Coastal Ecosystems. In: Mooney, H.A., Fuentes, E.R. and Kronberg, B.J. (eds), *Earth System Response to Global Change: Contrasts between North and South America*, 147-166. Academic Press, San Diego.
- Lynch, M., Gabriel, W. and Wood, A.M. 1991. Adaptive and demographic responses of plankton populations to environmental change. *Limnology and Oceanography* 36 (7): 1301-1312.
- Lynch, M. and Lande, R. 1993. Evolution and extinction in response to environmental change. In: Kareiva, P.M., Kingsolver, J.G. and Huey, R.B. (eds), *Biotic Interactions and Global Change*, 234-250. Sinauer Associates, Sunderland, Mass.
- McCarthy, S. and Khamhaty, F. 1994. International dissemination of epidemic *Vibrio cholerae* by cargo ship ballast and other nonpotable waters. *Applied and Environmental Microbiology* 60 (7): 2597-2601.
- McLachlan, A., Jaramillo, E., Donn, T.E. and Wessels, F. 1993. Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison. *Journal of Coastal Research* 11: 27-38.
- Magnuson, J.J. 1990. Long-term ecological research and the invisible present. *BioScience* 40: 495-501.
- Margulis, L. and Schwartz, K.V. 1988. *Five Kingdoms: An*

- Illustrated Guide to the Phyla of Life on Earth*, 2nd edn. W.H. Freeman, New York.
- Matrai, P.A. and Keller, M.D. 1993. Dimethylsulfide in a large-scale coccolithophore bloom in the Gulf of Maine. *Continental Shelf Research* 13: 831-843.
- Menge, B.A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73: 755-765.
- Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A. and Yamada, S.B. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* 64: 249-286.
- Menge, B.A. and Lubchenco, J. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs* 51: 429-450.
- Menge, B.A., Lubchenco, J., Ashkenas, L.R. and Ramsey, F. 1986. Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. *Journal of Experimental Marine Biology and Ecology* 100: 225-269.
- Menge, B.A., Daley, B. and Wheeler, P.A. 1995. Control of interaction strength in marine benthic communities. In: Polis, G.A. and Winemiller, R. (eds), *Food Webs: Integration of pattern and dynamics*. Chapman and Hall, New York (in press).
- Meybeck, M. 1982. Carbon, nitrogen and phosphorus transport by world rivers. *American Journal of Science* 282: 401-450.
- Moreno, C.A., Sutherland, J.P. and Jara, F.H. 1984. Man as a predator in the intertidal zone of southern Chile. *Oikos* 46: 359-364.
- National Research Council 1995. Understanding Marine Biodiversity. National Academy of Sciences, Washington, DC.
- Norse, E.A. (ed.) 1993. *Global Marine Biological Diversity. A strategy for building conservation into decision making*. Island Press, Washington, DC.
- Oliva, D. and Castilla, J.C. 1986. The effect of human exclusion on the population structure of key-hole limpets *Fissurella crassa* and *F. limbatia* on the coast of central Chile. *Publ. Staz. Zool. Napoli (I. Mar. Ecol.)* 7: 201-217.
- Paine, R.T. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65-75.
- Paine, R.T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49: 667-685.
- Paine, R.T. 1992. Food-web analysis through field measurements of per capita interaction strength. *Nature* 355: 73-75.
- Paine, R.T. 1993. A salty and salutary perspective on global change. In: Kareiva, P.M., Kingsolver, J.G. and Huey, R.B. (eds), *Biotic Interactions and Global Change*. 347-355. Sinauer Associates, Sunderland, Mass.
- Paine, R.T. 1994. *Marine Rocky Shores and Community Ecology: An experimentalist's perspective*. Ecology Institute, Oldendorf/Luhe, Germany.
- Palumbi, S.R. 1992. Marine speciation on a small planet. *Trends in Ecology and Evolution* 7: 114-118.
- Perrings, C., Müller, K.-G., Folke, C., Holling, C.S. and Jansson, B.-O. (eds), 1994. *Biodiversity Loss: Ecological and Economic Issues*. Cambridge University Press, Cambridge.
- Peterson, C.H., Barber, R.T. and Skilleter, G.A. 1993. Global warming and coastal ecosystem response: how northern and southern hemispheres may differ in the Eastern Pacific Ocean. In: Mooney, H.A., Fuentes, E.R. and Kronberg, B.I. (eds), *Earth System Response to Global Change: Contrasts between North and South America*. 17-34. Academic Press, San Diego.
- Pomeroy, L.R. and Deibel, D. 1986. Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. *Science* 233: 359-361.
- Pomeroy, L.R., Wiebe, W.J., Deibel, D., Thompson, R.J., Rowe, G.T. and Pakulski, J.D. 1991. Bacterial responses to temperature and substrate concentration during the Newfoundland spring bloom. *Marine Ecology Progress Series* 75: 143-159.
- Power, M.E., Tilman, D., Estes, J., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Mooney, H.A. and Paine, R.T. 1995. Challenges in the quest for keystones. *BioScience* (in press).
- Power, M.E. and Mills, L.S., 1995. The keystone cops meet Hilo. *Trends in Ecology and Evolution* 10 (5): 182-184.
- Proctor, L.R. and Fuhrman, J.A. 1990. Viral mortality of marine bacteria and cyanobacteria. *Nature* 343: 60-62.
- Rasmussen, E. 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. In: McRoy, C.P. and Helferich, C. (eds), *Seagrass Ecosystems*. 1-51. Marcel Dekker, New York.
- Ray, G.C. 1991. Coastal-zone biodiversity patterns. *BioScience* 41: 490-498.
- Ray, G.C. and Grassle, J.F. 1991. Marine biological diversity. *BioScience* 41: 453-457.
- Richards, D.V. and Davis, G.E. 1993. Early warnings of modern population collapse in black abalone *Haliotis cracherodii*, Leach, 1814, at the California Channel Islands. *Journal of Shellfish Research* 12 (2): 189-194.
- Richardson, K. 1989. Algal blooms in the North Sea: the good, the bad and the ugly. *Dana* 8: 83-93.
- Robles, C. and Robb, J. 1993. Varied carnivore effects and the prevalence of intertidal algal turfs. *Journal of Experimental Marine Biology and Ecology* 166: 65-91.
- Roemmich, D. and McGowan, J. 1995a. Climatic warming and the decline of zooplankton in the California Current. *Science* 267: 1324-1326.
- Roemmich, D. and McGowan, J. 1995b. Climatic warming and the decline of zooplankton in the California Current. *Science* 268: 352-353.
- Roughgarden, J., Iwasa, Y. and Baxter, C. 1985. Theory of population processes for marine organisms. I. Demography of an open population with space-limited recruitment. *Ecology* 66: 54-67.
- Ryther, J.H. 1969. Photosynthesis and fish production in the sea. *Science* 166: 72-76.
- Santelices, B. 1989. *Algas Marinas De Chile*. Ediciones Universidad Católica de Chile, Santiago, Chile.
- Sherman, K. 1990. Productivity, perturbations and options for biomass yields in Large Marine Ecosystems. In: Sherman, K., Alexander, L.M. and Gold, B.D. (eds), *Large Marine Ecosystems: Patterns, processes and yields*. 206. American Association for the Advancement of Science, Washington, DC.

- Sherman, K., Alexander, L.M. and Gold, B.D. (eds) 1990. *Large Marine Ecosystems: patterns, processes and yields*. American Association for the Advancement of Science, Washington, DC.
- Shiah, F.-K. and Ducklow, H.W. 1994. Temperature and substrate regulation of bacterial abundance, production and specific growth rate in Chesapeake Bay, USA. *Marine Ecology Progress Series* 103: 297-308.
- Simenstad, C.A., Estes, J.A. and Kenyon, K.W. 1978. Aleuts, sea otters and alternate stable-state communities. *Science* 200: 403-411.
- Smayda, T. 1990. Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. In: Graneli, E., Sundström, B., Elder, L. and Anderson, D.M. (eds), *Toxic Marine Phytoplankton*, 29-40. Elsevier, New York.
- Smayda, T. 1992. Global epidemic of noxious phytoplankton blooms and food chain consequences in large ecosystems. In: Sherman, K., Alexander, L.M. and Gold, B.D. (eds), *Food Chains, Yields, Models and Management of Large Marine Ecosystems*, 275-307. Westview Press, Boulder, Colorado.
- Smith, R.C., Prezelin, B.B., Baker, K.S., Bidigare, R.R., Boucher, N.P., Coley, T., Karentz, D., MacIntyre, S., Matlick, H.A., Menzies, D., Ondrusek, M., Wan, Z. and Waters, K.J. 1992. Ozone depletion: ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science* 255: 952-959.
- Sobel, J. 1993. Conserving biological diversity through marine protected areas. *Oceanus* 36: 19-26.
- Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. *Ecology* 60: 1225-1239.
- Spanier, E. and Galil, B. 1991. Lessepsian migration: a continuous biogeographical process. *Endeavour*, New Series, 15 (3): 102-106.
- Steele, J.H. 1985. A comparison of terrestrial and marine ecological systems. *Nature* 313: 355-358.
- Steele, J.H. 1991. Marine functional diversity. *BioScience* 41: 470-474.
- Steinbeck, J.R., Groff, J.M., Friedman, C.S., McDowell, T. and Hedrick, R.P. 1992. Investigations into a mortality among populations of the California black abalone *Haliotis cracherodii* on the central coast of California, USA. In: Shepherd, S. and Tegner, M. (eds), *Proceedings of the First International Abalone Symposium: Biology, fisheries, and culture*, Chapter 16. Blackwell Scientific Publications Ltd., Sydney.
- Steinberg, P.D., Estes, J.A. and Winter, F.C. 1995. Evolutionary consequences of food chain length in kelp forest communities. *Proceedings of the National Academy of Sciences, USA* (in Press).
- Steward, G.F., Wikner, J., Cochlan, W.P., Smith, D.C. and Azam, F. 1992. Estimation of virus production in the sea: II. Field results. *Marine Microbial Food Webs* 6: 79-90.
- Suttle, C.A., Chan, A.M. and Cottrell, M.T. 1990. Infection of phytoplankton by viruses and reduction of primary productivity. *Nature* 347: 467-469.
- Tatsukawa, R., Tanabe, S., Miyazaki, N. and Tobayama, T. (eds.) 1994. Marine pollution - mammals and toxic contaminants. *The Science of the Total Environment*, Vol. 154/2,3. Elsevier, New York.
- Tseng, C. K. 1984. *Common Seaweeds of China*. Science Press, Beijing.
- Tulkki, P. 1965. Disappearance of the benthic fauna from basins of Bornholm (southern Baltic) due to oxygen deficiency. *Cahiers de Biologie Marine* 6: 445-463.
- Turner, R.E. and Rabalais, N.N. 1991. Changes in Mississippi River water quality this century: implications for coastal food webs. *BioScience* 41 (3): 140-147.
- Turner, R.E. and Rabalais, N.N. 1994. Coastal eutrophication near the Mississippi River delta. *Nature* 368: 619-621.
- Valiela, I. 1984. *Marine Ecological Processes*. Springer-Verlag, New York.
- Wheeler, P.A. 1983. Phytoplankton nitrogen metabolism. In: Carpenter, E.J. and Capone, D.G. (eds), *Nitrogen in the Marine Environment*, 309-346. Academic Press, New York.
- Wiebe, W.J., Sheldon W.M. Jr. and Pomeroy, L.R. 1992. Bacterial growth in the cold: evidence for an enhanced substrate requirement. *Applied and Environmental Microbiology* 58: 359-364.
- Wolfe, G.V., Bates, T.S. and Charlson, R.J. 1991. Climatic and environmental implication of biogas exchange at the sea surface: modeling DMS and the marine biological sulfur cycle. In: Mantoura, R.F.C., Martin, J.-M. and Wollast, R. (eds), *Ocean Margin Processes in Global Change*, 383-400. John Wiley, Chichester.
- Wood, A.M., Apelian, N. and Shapiro, L. 1993. Novel toxic phytoplankton: a component of global change? In: Guerrero, R. and Pedro-Alio, C. (eds), *Trends in Microbial Ecology, Proceedings, VI International Symposium on Microbial Ecology*, 479-483. Spanish Society for Microbiology, Barcelona.
- Wood, A.M. and Leatham, T. 1992. The species concept in phytoplankton ecology. *Journal of Phycology* 28: 723-729.

6.1.10 Coral reefs

6.1.10.1 Introduction

The complex and diverse assemblage of organisms that constitutes the coral reef ecosystem covers over 600 000 km² (<30 m deep) of the tropical ocean. Over half this area is in the Indo-Western Pacific and about 15% is in the tropical Atlantic, the two centres of reef diversity (Smith 1978; Veron 1986; World Conservation Monitoring Centre 1992) (Figure 6.1-5). Modern coral reefs, representing approximately 6000 years of growth during the most recent period of sea-level rise, have an average gross carbonate production of 10 kg/m²/yr and average vertical growth rates of 3 mm/yr (Chave *et al.* 1972; Smith 1983). They are the oldest and largest biogenic structures in nature, holding detailed palaeoecological and climate records (Smith and Buddemeier 1992; Dunbar and Cole 1993). Coral reefs have more species per unit area than any other marine ecosystem but, with the exception of a few groups such as fishes and corals, most are poorly studied (Böhlke and Chaplin 1968; Springer 1982; Achituv and Dubinsky 1990; National Research Council 1995). Reefs have fewer species than tropical forests, with which they are often compared, but a much higher phyletic diversity (Ray and Grassle 1991; Briggs 1994). Disturbance appears to play a major role in the maintenance of species diversity in coral reefs,

(Connell 1978; Harmelin-Vivien and Bourlière 1989; Sale 1991a, b). However, the uncertain species-level taxonomy of even the best-known organisms makes it difficult to evaluate with confidence either the total number of species or the role of niche diversification among them (Knowlton and Jackson 1994). Many coral reef species rely for population replenishment on larvae released from 'upstream' reefs. This reliance may increase opportunities for genetic diversification compared to populations replenished from local stocks and/or by vegetative reproduction, which are also common among reef species (Benzie 1994). Day-to-day metabolic requirements are provided by a low steady supply of inorganic nutrients (D'Elia and Wiebe 1990). While reefs are characterized by the complexity of their biological relationships, it is their ability to construct massive calcium carbonate frameworks which sets them apart from all other ecosystems. The construction comes about through interactions of organisms, heuristically lumped into functional groups, including framework builders (corals), facilitators (symbiotic algae), and grazers (Figure 6.1-6). Studies of reef communities through geological time or across gradients of diversity indicate that different combinations of species may constitute a functional group (Jackson 1992, 1994a). However, changes in keystone species (single-species functional groups) can cause dramatic alterations in reef structure and functioning.

6.1.10.2 Threats to reefs

The principal direct human impacts that threaten reefs are nutrient loading, sedimentation and destruction from poor land-use practices, dredging and coral mining. Reefs hold a significant proportion of the world's fishery resources, and they are very sensitive to overfishing, particularly the removal of large predators and herbivorous fishes (Salvat 1987; Wells 1988; Hatcher *et al.* 1989; Russ 1991). A key feature of human impact on reefs is the disturbance of biotic and abiotic factors which shift reef composition from framework builders (corals) to non-framework builders

(algae; Figure 6.1-6). While global climate change, including sea-level rise, increased seawater temperatures, and increased ultraviolet (UV-B) radiation, are a potential long-term threat to reefs, there is an immediate need to manage the impact of relentless coastal human population growth (D'Elia *et al.* 1991; Norse 1993).

6.1.10.3 Productive capacity, biomass and decomposition

Human impacts on biodiversity. Reef corals thrive in the low but steady input of nutrients from the oligotrophic ocean waters of the tropics. Extreme nutrient loading may disrupt the dynamic balance of corals and algae in favour of the benthic algae which can overgrow, shade and smother corals (Littler and Littler 1985). Suspended sediments and planktonic algal blooms may shade corals and result in over-dominance of benthic algae.

Ecosystem consequences of impacts. Coral reef productivity, respiration and calcification have been well studied, and 'standards of functional performance' have been suggested as indicators of ecosystem health (Odum and Odum 1955; Johannes *et al.* 1972; Kinsey 1991). In a healthy reef, the ratio of gross Productivity/Respiration = 1, indicating internal cycling. This P/R ratio can shift to >1 if there are excessive nutrients, additional production and export, or to <1 if there is increased respiration over production implying import of material (D'Elia and Wiebe 1990; Kinsey 1991). Excess nutrients stimulate algal growth and can inhibit calcification and reef bioconstruction, shifting the balance to bioerosion (Kinsey and Davies 1979; Hallock and Schlager 1986).

6.1.10.4 Sediment structure and nutrients

Human impacts on biodiversity. Increased sedimentation from poor land-use practices may change sediments from aerobic to anaerobic as organic material accumulates. Nutrients may then 'bleed' out of the sediments over time, stimulating benthic productivity and prolonging the impact long after corrective measures have been taken (Maragos *et al.* 1985; Smith *et al.* 1981).

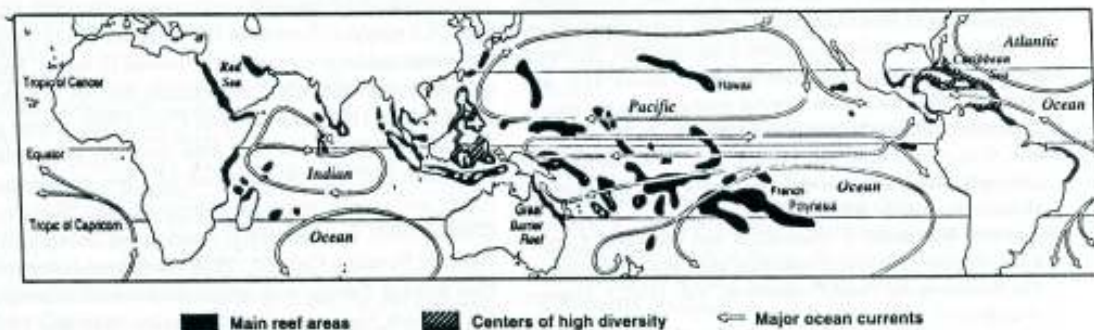


Figure 6.1-5: Global distribution of the coral reef biome. (From: Wells and Hanna, 1992.)

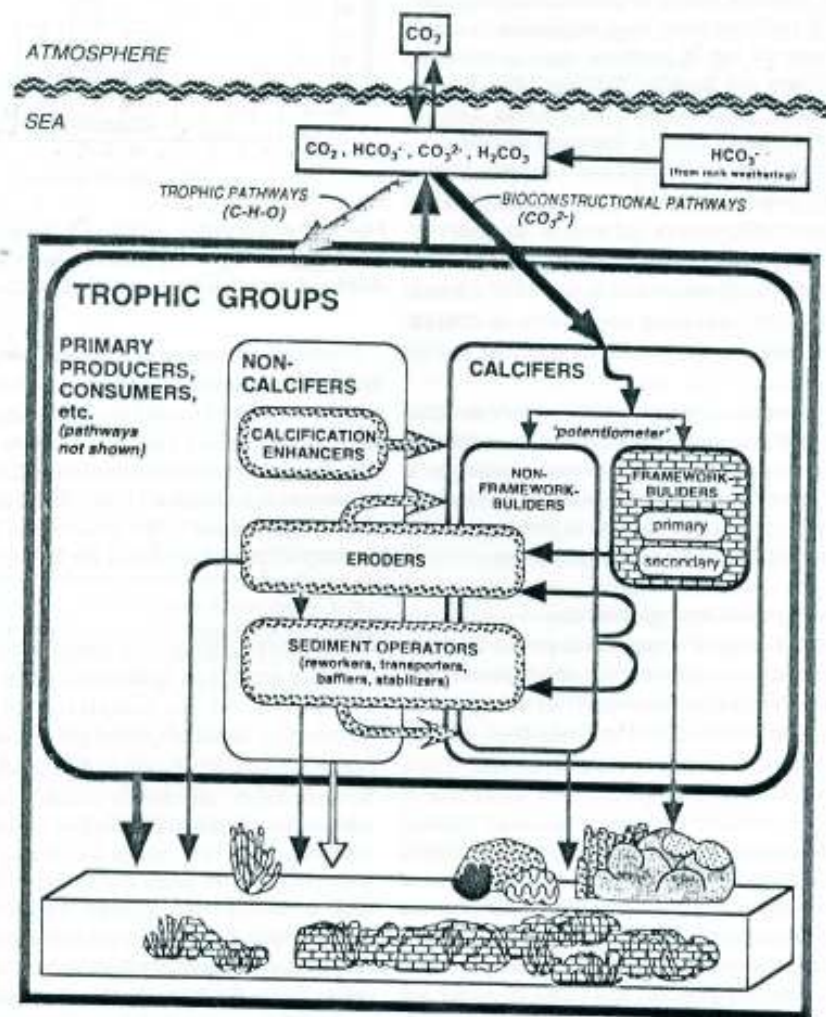


Figure 6.1-6: The principal bioconstructional functional groups of the coral reef ecosystem. Reef construction is a result of the activities of stony coral-framework builders which are influenced by 'modifier groups' such as calcification enhancers, eroders and sediment operators. A key feature of the figure is the 'potentiometer' which shifts between framework-builders and non-framework-builders depending on changes in nutrients, grazing and physical conditions.

Ecosystem consequences of impacts. Coral reef ecosystems are characterized by slow removal and loss of nutrients and relatively low sediment accumulation (Johannes *et al.* 1983; Pomeroy *et al.* 1974). Human impact can switch the reef ecosystem to external cycling of nutrients and shift benthic dominance from corals to algae (D'Elia and Wiebe 1990).

6.1.10.5 Water circulation and quality

Human impacts on biodiversity. Coral reefs thrive in well circulated waters, both clear and naturally turbid (Done 1982). However, enhanced turbidity and freshwater

runoff from land is generally inimical to reef growth and development (Kühlmann 1988). Coral and sand mining and dredging can alter the configuration of reefs and hence water circulation patterns.

Ecosystem consequences of impacts. Coral atolls (necklaces of oceanic reefs and coral islands surrounding a central lagoon) provide good examples of functional differences driven by water circulation. Atolls may be characterized by their connection to surrounding water masses. The lagoons of 'closed' atolls are profoundly different from 'open' ones with increased nutrient retention time and productivity (Birkeland 1987).

6.1.10.6 Atmospheric properties

Human impacts on biodiversity. Increased seawater temperatures, possibly linked to global warming, and elevated UV-B radiation have been implicated in coral bleaching through the loss of symbiotic algae and/or their pigments (Williams and Bunkley-Williams 1991; Brown and Ogden 1992; Gleason and Wellington 1993). Bleaching stresses corals causing decreased calcification and reproductive capacity (Szmant and Gassman 1990), death and extirpation over wide areas (Glynn 1988). Increased seawater temperatures and rates of sea-level rise may 'drown' some reefs and cause a geographic shift in reef distribution (Buddemeier and Smith 1988). Some scenarios of global warming suggest an increased frequency of tropical storms, which may affect the rate of reef growth.

Ecosystem consequences of impacts. While reefs are sinks for CO_2 over geologic time, reef calcification causes pH reduction and release of CO_2 from seawater resulting in a net positive flux to the atmosphere (Smith and Buddemeier 1992). It is not expected that changes in reef biodiversity will have major impacts on the global atmosphere.

6.1.10.7 Landscape and seascape structure

Human impacts on biodiversity. Reefs protect the coast from the open ocean, fostering the development of a complex interdependent 'seascape' of ecosystems, including mangrove forests and seagrass beds. Human occupation and exploitation of the coastal zone cause profound changes in the configuration and interaction of the major ecosystems of the coastal seascape. Coastal clearing and deforestation for development, construction materials, charcoal and mariculture and destruction of seagrass beds, cause increased runoff of sediments and nutrients inimical to coral reefs. Reef biodiversity is dependent on the accessibility of adjacent ecosystems for feeding areas, nursery grounds, and flows of energy and materials (Ogden 1987, 1988; Figure 6.1-7).

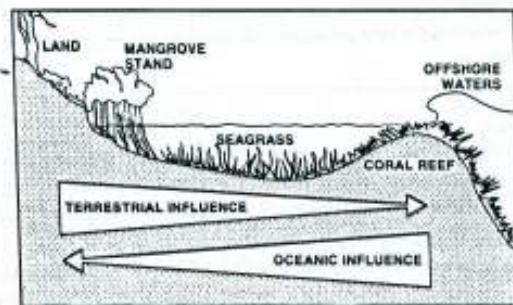


Figure 6.1-7: The tropical coastal seascape showing buffering of the land from the ocean by reefs and the buffering of reefs from the land by coastal forests and seagrass beds (see text for detail). (After: Ogden 1987.)

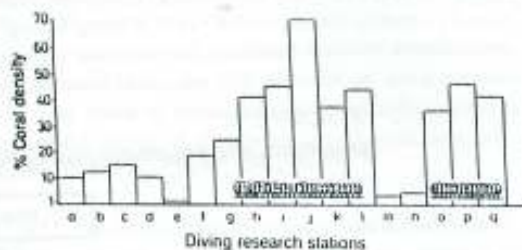


Figure 6.1-8: The average coral density (cover) around Ishigaki Island, Ryukyu, Japan. The pollutant-absorbing effects of the shoreline forest belt is illustrated. (From: Kühlmann 1988.)

Ecosystem consequences of impacts. Coastal reefs attain their greatest development when isolated or otherwise protected from land run-off by coastal forests and adjoining seagrass beds which slow and baffle water movements allowing sediments to fall from suspension and nutrients to be absorbed. Kühlmann (1988) found that coral density was directly related to the preservation of this buffering capacity of forest margins in the Ryukyu Islands (Figure 6.1-8).

6.1.10.8 Biotic linkages and species interactions

Human impacts on biodiversity. Coral reefs are perhaps best known for the complexity of the biological relationships between species and functional groups. For example, Figure 6.1-9,a shows the hypothetical relationship between fishes, the ratio of corals/algae, and the major herbivorous sea urchin *Diadema* on undisturbed reefs in the Caribbean. The first critical disturbance was overfishing, which removed the larger size classes of predatory fishes as well as herbivorous groups. This impact 'released' *Diadema* populations from predation and competition and they attained artificially high population densities (Hay 1984; Figure 6.1-9,b). The mass mortality of *Diadema* in 1983-84 removed this remaining herbivore and the coral/algal ratio of Caribbean reefs shifted to an alternate state of algal dominance (Lessios *et al.* 1984; Carpenter 1986; Knowlton 1992; Hughes 1994; Figure 6.1-9,c).

This Caribbean basin-wide phenomenon has been exacerbated by circumstances that lower thresholds for macroalgal dominance over corals (Knowlton 1992): they include increased availability of nutrients (Hallock and Schlager 1986); increased sedimentation associated with deforestation (Cortes and Risk 1985); storm damage (Woodley *et al.* 1981), oil spills (Jackson *et al.* 1989), and mass bleaching of corals (Williams and Bunkley-Williams 1991). Similarly, 'outbreaks' of crown-of-thorns starfish populations in the Indo-Pacific can dominate the dynamics of many coral reefs (Done 1987, 1992).

Ecosystem consequences of impacts. The complex biotic linkages characteristic of reefs depend upon the ecosystem-

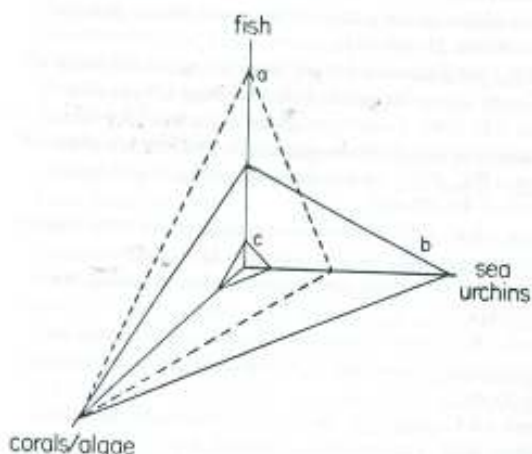


Figure 6.1-9: Model of the negative synergistic response of Caribbean coral reef communities to overfishing and sea urchin disease. Prior to overfishing, reefs existed in state (a), with high fish abundance, moderate urchin abundance, and large amounts of coral relative to algae. Overfishing (state b) led to a switch in the relative abundances of fishes and sea urchins, but no change in the relative abundances of coral and algae. Collapse of the sea urchins due to disease (state c) resulted in the replacement of corals by algae and further declines in fishes (From: Jackson, 1994b.)

wide effects of a few functional groups and organisms and influences such as nutrients which can shift the balance of reefs from framework-building corals to non-framework-builders such as benthic algae (Figure 6.1-6).

6.1.10.9 Microbial activities

Human impacts on biodiversity. Little is known about the human impact on reef microbial populations with the exception of inorganic nutrient processing. Under undisturbed conditions, virtually all microbial activity takes place within the benthos. Nitrogen gas is fixed by prokaryotes on reef fronts and microbially transformed to nitrate, some of which is exported out of the reef system (Wiebe 1985). Phosphate is slowly exchanged by the benthos (Atkinson and Smith 1983).

Ecosystem consequences of impacts. Nutrient pollution (sewage, runoff) reduces N fixation and causes: (1) accumulation of PO_4 and fixed N within the sediments; (2) benthic macro-algal blooms; (3) micro-algal blooms in the water column. These blooms reduce light penetration which adversely affects the normal benthic plants and symbiotic algae. Prolonged exposure to high nutrients can lead to the smothering of corals and the transformation of the benthos into a low-diversity, benthic algal dominated system (D'Elia and Wiebe 1990).

6.1.10.10 Summary and relevance to human activities

Coral reefs, which are exploited by millions of people, are

acknowledged to be the most diverse marine ecosystem. Periodic disturbance plays a major role in the maintenance of their biodiversity, the persistence of which relies on the interconnections among often widely dispersed metapopulations, and on a low, steady supply of inorganic nutrients. The massive calcium carbonate structures of reefs are formed through the collaboration of unique functional groups including framework-builders (corals), facilitators (symbiotic algae) and grazers. Studies of reef communities through geological time or across gradients of diversity show that the composition of functional groups can vary greatly. However, changes in keystone species (single-species functional groups) can cause dramatic alterations in reef structure and functioning. The most common manifestation of disturbance is a shift from coral dominance to benthic algal dominance. Reefs protect the coast from the open ocean, fostering the development of a complex interdependent 'seascape' of ecosystems, including mangrove forests and seagrass beds. Reef biodiversity is dependent on adjacent ecosystems for feeding areas and nursery grounds and for protection against land runoff, allowing sediments to be trapped and nutrients to be sequestered. It is generally conceded that global reef diversity is declining from the impact of chronic human disturbances and is threatened by global climate change. Some effects of chronic human disturbance may be temporarily 'invisible': for example, few reef scientists worried about the effects of prolonged overfishing on corals until the demise of the sea urchin *Diadema* led to the wholesale replacement of corals by algae on these reefs (Figure 6.1-9). Similarly, some currently abundant species may already be doomed because of 'extinction debts' associated with habitat reduction. There appears to be little hope for the survival of reefs that are near relentlessly expanding coastal populations. Protection of more remote reefs will require inter-governmental co-operation in surveying, monitoring, comparative research and integrated coastal management within global sub-regions, such as the tropical western Atlantic, encompassing the geographic range of reef metapopulations and of key ocean processes.

6.1.10.11 Management implications

Reefs have responded to efforts to protect them from exploitation in parks and reserves (McClanahan 1994) and to pollution control (Maragos *et al.* 1985), and these efforts at the grassroots and local government level should be encouraged and expanded. However, the meta-population characteristics of most reef organisms argue strongly that the ultimate conservation of reefs, as much of the ocean environment, will be through inter-governmental management of human impact within ecologically defined sectors of the world's tropical oceans.

References

- Achituv, Y. and Dubinsky, Z. 1990. Evolution and zoogeography of coral reefs. In: Dubinsky, Z. (ed.), *Ecosystems of the World* 25: Coral Reefs. 1-9. Elsevier, Amsterdam.
- Atkinson, M.J. and Smith, S.V. 1983. C:N:P ratios of benthic marine plants. *Limnology Oceanography* 28: 568-574.
- Benzie, J.A.H. 1994. Patterns of genetic variation in the Great Barrier Reef. In: Beaumont, A. (ed.), *Genetics and Evolution of Aquatic Organisms*, 69-79. Chapman and Hall, London.
- Birkeland, C. (ed.) 1987. Comparison between Atlantic and Pacific tropical marine coastal ecosystems: community structure, ecological processes, and productivity. *UNESCO Reports in Marine Science* 46. UNESCO, Paris.
- Böhlke, J.E. and Chaplin, C.C.G. 1968. *Fishes of the Bahamas and adjacent waters*. Livingston Publ. Co., Wynnewood, Pa.
- Briggs, J.C. 1994. Species diversity: land and sea. *Systematic Biology* 43: 130-135.
- Brown, B.E. and Ogden, J.C. 1992. Coral bleaching. *Scientific American* 268 (1): 64-70.
- Buddemeier, R.W. and Smith, S.V. 1988. Coral reef growth in an era of rapidly rising sea levels: predictions and suggestions for long-term research. *Coral Reefs* 7: 51-56.
- Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecology Monographs* 56: 345-365.
- Chave, K.E., Smith, S.V. and Roy, K.J. 1972. Carbonate production by coral reefs. *Marine Geology* 12: 123-140.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. *Science* 199: 1302-1310.
- Cortes, J. and Risk, M.J. 1985. A reef under siltation stress: Cahuita, Costa Rica. *Bulletin of Marine Science* 36: 339-356.
- D'Elia, C.F., Buddemeier, R.W. and Smith, S.V. 1991. Workshop on coral bleaching, coral reef ecosystems and global change: report of proceedings. *Maryland Sea Grant*, 49.
- D'Elia, C.F. and Wiebe, W.J. 1990. Biochemical nutrient cycles in coral reef ecosystems. In: Dubinsky, Z. (ed.), *Ecosystems of the World* 25: Coral Reefs. 49-74. Elsevier, Amsterdam.
- Done, T.J. 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. *Coral Reefs* 1: 95-107.
- Done, T.J. 1987. Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus *Porites*: evidence of population resilience? *Coral Reefs* 6: 75-90.
- Done, T.J. 1992. Constancy and change in some Great Barrier Reef coral communities: 1980-1990. *American Zoologist* 32: 655-662.
- Dunbar, R.B. and Cole, J.E. (eds) 1993. Coral records of ocean atmosphere variability. *Publ. Univ. Corp. for Atmospheric Research (UCAR)*, Boulder, Col.
- Gleason, D.F. and Wellington, G.M. 1993. Ultraviolet radiation and coral bleaching. *Nature* 365: 836-838.
- Glynn, P.W. 1988. El Niño-Southern Oscillation 1982-83: nearshore population, community, and ecosystem responses. *Annual Review of Ecology and Systematics* 19: 309-345.
- Hallock, P. and Schlager, W. 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. *Palaos* 1: 389-398.
- Harmelin-Vivien, M.L. and Bourlière, F. (eds). 1989. *Vertebrates in Complex Tropical Systems. Ecological Studies* 69: Springer-Verlag, Berlin.
- Hatcher, B.G., Johannes, R.E. and Robertson, A.I. 1989. Review of research relevant to the conservation of shallow water tropical marine systems. *Oceanography and Marine Biology Annual Review* 27: 337-414.
- Hay, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65: 446-454.
- Hughes, T.P. 1994. Catastrophe, phase shifts and large scale degradation of a Caribbean coral reef. *Science* 226: 1547-1549.
- Jackson, J.B.C. 1991. Adaptation and diversity of reef corals. *Bioscience* 41: 475-482.
- Jackson, J.B.C. 1992. Pleistocene perspectives on coral reef community structure. *American Zoologist* 32: 719-731.
- Jackson, J.B.C. 1994a. Community unity? *Science* 264: 1412-1413.
- Jackson, J.B.C. 1994b. Constancy and change of life in the sea. *Philosophical Transactions of the Royal Society of London, B* 344: 55-60.
- Jackson, J.B.C., Cubitt, J.D., Keller, B.D., Batista, V., Burns, K., Caffey, H.M., Caldwell, R.L., Garrity, S.D., Getter, C.D., Gonzales, C., Guzman, H.M., Kaufman, K.W., Knap, A.H., Levings, S.C., Marshall, M.J., Steger, R., Thompson, R.C. and Weil, E. 1989. Ecological effects of a major oil spill on Panamanian coastal marine communities. *Science* 243: 37-44.
- Johannes, R.E., Alberts, J., D'Elia, C., Kinzie, R.A., Pomeroy, L.R., Sottile, L., Wiebe, W., Marsh, J.A. Jr., Helfrich, P., Maragos, J., Meyer, J., Smith, S., Crabtree, D., Roth, A., McClosky, L.R., Betzer, S., Marshall, N., Pilson, M.E.Q., Telek, G., Clutter, R.I., DuPaul, W.D., Webb, K.L. and Wells, J.M. Jr. 1972. The metabolism of some coral reef communities: a team study of nutrient and energy flux at Eniwetok. *Bioscience* 22: 541-543.
- Johannes, R.E., Wiebe, W.J. and Crossland, C.J. 1983. Three patterns of nutrient flux in a coral reef community. *Marine Ecology Progress Series* 12: 131-136.
- Kinsey, D.W. 1991. The coral reef: an owner-built, high-density, fully-serviced, self-sufficient, housing estate in the desert: or is it? *Symbiosis* 10: 1-22.
- Kinsey, D.W. and Davies, P.J. 1979. Effects of elevated nitrogen and phosphorous on coral reef growth. *Limnology Oceanography* 24: 935-940.
- Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32: 674-682.
- Knowlton, N. and Jackson, J.B.C. 1994. New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some? *Trends in Ecology and Evolution* 9: 7-9.
- Kühlmann, D.H.H. 1988. The sensitivity of coral reefs to environmental pollution. *Ambio* 17: 13-21.
- Lessios, H.A., Robertson, D.R. and Cubitt, J.D. 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science* 226: 335-337.
- Little, M.M. and Littler, D.S. 1985. Factors controlling relative dominance of primary producers on biotic reefs. *Proceedings Fifth International Coral Reef Congress, Tahiti*, Vol. 4: 35-39.
- McClanahan, T.R. 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity and sea urchins. *Coral Reefs* 13: 231-241.
- Maragos, J.E., Evans, C. and Holthuis, P. 1985. Reef corals in Kaneohe Bay six years before and after termination of sewage

- discharges (Oahu, Hawaiian Archipelago) *Proceedings, Fifth International Coral Reef Congress, Tahiti*, Vol. 4: 189-194.
- National Research Council 1995. *Understanding Marine Biodiversity: A research agenda for the nation*. National Academy Press, Washington, DC.
- Norse, E.A. (ed.) 1993. *Global Marine Biological Diversity: A strategy for building conservation into decision making*. Island Press, Washington, DC.
- Odum, H.T. and Odum, E.P. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs* 25: 295-320.
- Ogden, J.C. 1987. Cooperative coastal ecology at Caribbean marine laboratories. *Oreanus* 30: 9-15.
- Ogden, J.C. 1988. The influence of adjacent systems on the structure and function of coral reefs. *Proceedings, Sixth International Coral Reef Symposium*, Australia, Vol. 1: 123-129.
- Pomeroy, L.R., Pilson, M.E.Q. and Wiebe, W.J. 1974. Tracer studies of the exchange of phosphorus between reef water and organisms on the windward reef of Eniwetok Atoll. *Proceedings, Second Internat. Coral Reef Symposium* 1: 87-96.
- Ray, G.C. and Grassle, J.F. 1991. Marine biological diversity. *Bioscience* 41: 453-457.
- Russ, G.R. 1991. Coral reef fisheries: effects and yields. In: Sale, P.F. (ed.), *The Ecology of Fishes on Coral Reefs*. 601-635. Academic Press, New York.
- Sale, P.F. (ed.) 1991a. *The Ecology of Fishes on Coral Reefs*. Academic Press, New York.
- Sale, P.F. 1991b. Reef fish communities: open non-equilibrium systems. In: P.F. Sale (ed.), *The Ecology of Fishes on Coral Reefs*. 564-598. Academic Press, New York.
- Sulvat, B. (ed.) 1987. *Human Impacts on Coral Reefs: Facts and recommendations*. Antenne Museum Ecole Pratique des Hautes Etudes, French Polynesia.
- Smith, S.V. 1978. Coral-reef area and the contributions of reefs to processes and resources of the world's oceans. *Nature* 273: 225-226.
- Smith, S.V. 1983. Coral reef calcification. In: Barnes, D.J. (ed.), *Perspectives on Coral Reefs*. 240-247. Australian Institute of Marine Science, Townsville, Qld.
- Smith, S.V. and Buddemeier, R.W. 1992. Global change and coral reef ecosystems. *Annual Review of Ecology and Systematics* 23: 89-118.
- Smith, S.V., Kimmerer, W.J., Laws, E.A., Brock, R.E. and Walsh, T.W. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pacific Science* 35: 279-402.
- Springer, V.G. 1982. Pacific Plate biogeography, with special reference to shorefishes. *Smithsonian Contributions in Zoology* 367: 1-182.
- Szmant, A.M. and Gassman, N.J. 1990. The effects of prolonged bleaching on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* 8: 217-224.
- Veron, J.E.N. 1986. *Coral Reefs of Australia and the Indo-Pacific*. Angus and Robertson, Australia.
- Wells, S.M. 1988. *Coral Reefs of the World*, 3 Vols. UNEP/IUCN.
- Wells, S. and Hanna, N. 1992. *The Greenpeace Book of Coral Reefs*. Sterling Publ. Co., New York.
- Wiebe, W.J. 1985. Nitrogen dynamics on coral reefs. *Proceedings, Fifth International Coral Reef Symposium*, Vol. 3: 401-406.
- Williams, E.H. and Bunkley-Williams, L. 1991. The world-wide coral reef bleaching cycle and related sources of coral mortality. *Atoll Research Bulletin* 331: 1-17.
- Woodley, J., Chornesky, E., Clifford, P., Jackson, J., Kaufman, L., Knowlton, N., Lang, J., Pearson, M., Porter, J., Rooney, M., Rylaarsdam, K., Tunnicliffe, V., Wahle, C., Wulff, J., Curtis, A., Dallmeyer, M., Jupp, B., Koehl, M., Niel, J. and Sides, E. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214: 749-755.
- World Conservation Monitoring Centre. 1992. *Global Biodiversity: Status of the Earth's living resources*. Chapman and Hall, London.

6.1.11 Mangrove systems

6.1.11.1 Introduction

The major form of vegetation supporting biodiversity in tropical estuarine ecosystems is the intertidal forested wetland known as mangrove. About $240 \times 10^3 \text{ km}^2$ of mangroves (Lugo *et al.* 1990; Twilley *et al.* 1992) dominate tropical river deltas, lagoons and estuarine complexes developed from terrigenous sediments (Thom 1982). In addition, mangroves colonize shorelines and islands in sheltered shallow coastal waters formed principally from carbonate sediments. These are geomorphologically distinct regional landscapes with local variations in topography and hydrology that result in the evolution of distinct ecological types of mangroves (with respect to both structure and function) such as riverine, fringe, basin and dwarf forests (Lugo and Snedaker 1974). Although there are relatively few species of mangrove trees (54 species; Tomlinson 1986), mangrove ecosystems are nevertheless unique because they include structural niches and refugia for numerous non-mangrove species. Mangroves are salt-tolerant forested wetlands at the land-sea interface which form interdependent links between inland terrestrial landscapes and the nearshore marine environment (Macnae 1968; Chapman 1976; Odum *et al.* 1982; Tomlinson 1986; Gilmore and Snedaker 1993; Twilley *et al.* 1993). The dominant ecological 'services' of mangroves are the maintenance of nearshore marine habitats and the concomitant provision of food and refugia to a variety of organisms at different trophic levels (Odum and Heald 1972; Thayer *et al.* 1987; Sasekumar *et al.* 1992; Yañez-Arancibia *et al.* 1988, 1993; Rojas *et al.* 1992). Mangroves also play a major role in maintaining water quality and shoreline stability by controlling nutrient and sediment distributions in estuarine waters (Walsh 1967; Twilley 1988).

6.1.11.2 Human impacts on relevant biodiversity components

The coupling of mangroves to coastal waters is considered to be the most important link in the sustainability of

subsistence, commercial and recreational fisheries in estuaries and related nearshore marine habitats. Historically, the establishment of mangrove plantations promoted sustainable use of this valuable resource for forest products such as timber, fuelwood, tannins, pulpwood and charcoal in the Old World tropics (see Watson 1928; Saenger *et al.* 1983; Snedaker 1986). Recent forms of direct impact include the destruction of biodiversity by land uses such as aquaculture (shrimp ponds), agriculture (rice and salt ponds), urban development, and forest clear-felling for economic gain and other purposes (see Pannier 1979). Indirect loss of mangrove biodiversity components has resulted from human alterations of upland watersheds, causing diversion of freshwater flows (dams and canals), and deterioration of water quality from the input of toxic materials (heavy metals, oil spills, pesticides) and nutrients to rivers and coastal waters.

6.1.11.3 Productive capacity, biomass and decomposition

Ecosystem consequences of impacts: On a global scale, the highest species diversity and primary productivity occur in low-latitude regions where precipitation exceeds evaporation. Standing crop may reach 300–400 Mg/ha (Twilley *et al.* 1992; Saenger and Snedaker 1993). Human impacts change productivity, distribution and biomass accumulation by altering soil conditions such as salinity, sulphide concentrations, waterlogging, redox potentials, nutrient concentrations, soil structure and pH (Cintrón *et al.* 1978). Regional rates of litter production in mangroves are a function of water turnover and have been ranked according to ecological type as riverine > fringe > basin > dwarf (Pool *et al.* 1975; Twilley *et al.* 1986). The surficial hydrology is a critical factor in maintaining these diverse functions. Artificially reduced exposure to tides, and lower freshwater input, cause higher soil salinity (Cintrón *et al.* 1978), anoxia, and the accumulation of growth-inhibiting toxic substances such as hydrogen sulphide (Carlson *et al.* 1983; Nickerson and Thibodeau 1985; McKee *et al.* 1988) which result in increased stress (Hicks and Burns 1975). Regional-scale changes in freshwater surface inflow into mangrove areas have also caused reduction in the secondary productivity of tropical estuarine ecosystems due to the degradation of habitat and water quality of estuarine ecosystems. Changes in the species composition of mangrove communities alter the quality of leaf litter and result in different rates of decomposition and an altered quality of organic matter export (POC vs DOC) to the adjacent estuary (Boto and Bunt 1981; Twilley 1985, 1988; Snedaker 1989). Eliminating a given species of mangrove along zones of edaphic conditions may also alter specific types of refugia available to consumers (e.g. those offered by species with prop roots vs those with pneumatophores).

6.1.11.4 Soil structure and nutrients

Ecosystem consequences of impacts: Mangroves, particularly those in the genus *Rhizophora*, have a low decomposition rate of root biomass relative to root production, which results in the accumulation of organic matter in the soil and leads to the development of mangrove peat deposits (Snedaker 1993). Differences in litter quality among mangrove species also affect litter decomposition, leading to nutrient immobilization and accumulation (particularly nitrogen), and hence the fertility of mangrove soils (Twilley *et al.* 1986; Steyer 1988). Mineral accumulation is enhanced by mangrove prop roots and pneumatophores, which trap sediments suspended in the water column during low-velocity flooding. Coastal forested wetlands thereby enrich intertidal soils and retard the forces of erosion along the shoreline (Scoffin 1970; Lynch *et al.* 1989). In areas colonized by benthic calcareous algae (e.g. *Halimeda* and *Penicillus*), mangroves stabilize the new carbonate sediment and promote soil development. This process has led to a significant expansion of mangrove shorelines in southeast Florida along with a rise in sea level equivalent to about 23 cm per 100 years (Maul and Martin 1993; Snedaker *et al.* 1994). Mangrove rookeries are enriched in nitrogen and phosphorus which stimulate the productivity of mangrove vegetation. The density and diversity of herbivores is greater on mangrove island rookeries, compared to proximal islands that lack nutrient enrichment (Onuf *et al.* 1977). The so-called 'soil reclamation' projects in Africa, as well as in parts of Asia (cf. Ponnamperna 1984) for agriculture (and aquaculture) have reduced regional levels of coastal productivity due to loss of mangrove habitats. In many instances the conversion of organic-rich, pyritic mangrove soils leads to the formation of acid sulphate soils that are both extremely difficult to reclaim further, and incapable of supporting the original diversity of the landscape (cf. Dost 1973; Moorman and Pons 1975).

6.1.11.5 Water distribution, balance and quality

Ecosystem consequences of impacts: The conversion of coastal landscapes to agriculture has resulted in the deterioration of water quality in contiguous estuarine ecosystems. In Ecuador, pesticides from banana plantations have been implicated in the morphological deformity of shrimp in the Guayas River estuary (Taura syndrome). Water-borne heavy metals in the coastal regions of Brazil and Malaysia (Peterson *et al.* 1979) influence mangrove biodiversity and have impacts on the biodiversity and response of estuarine ecosystems. In Malaysia, the reduction of mangroves has resulted in increased turbidity of estuarine waters in the affected areas (Nixon *et al.* 1984). The nutrient removal capacity of the mangrove community *sensu lato* has been utilized for waste-water treatment in many tropical localities, particularly for nitrate

removal (Nedwell 1975; Clough *et al.* 1983). This practice is presumed to interfere with the dissolved organic matter (DOM) export from basin mangrove forests that augments aquatic primary production and the dynamics of phytoplankton (Prakash 1971; Prakash *et al.* 1973; Rivera *et al.* 1995).

6.1.11.6 Atmospheric properties

Ecosystem consequences of impacts. Nitrogenase activity has been observed on decomposing leaves, root surfaces (prop roots and pneumatophores), and in sediment. This enzyme makes an important contribution to the nitrogen budget in mangrove systems (Kimball and Teas 1975; Gotto and Taylor 1976; Zuberer and Silver 1978; Potts 1979; Gotto *et al.* 1981). Mangrove sediments in southern Florida fix nitrogen at rates of 0.4 to 3.2 g N/m²/yr (Kimball and Teas 1975; Zuberer and Silver 1978) and most of this fixation occurs in mangrove litter at specific stages of decomposition (Gotto *et al.* 1981; van der Valk and Attiwill 1984). This source of nitrogen can account for some of the nitrogen immobilization in leaf litter (Twilley 1988). Rates of nitrogen fixation in mangrove leaf litter are species-specific, depending on the chemical composition of the leaf. Thus, the contribution of this ecological process to the fertility of mangrove ecosystems may depend on the species composition and diversity of leaf litter, which differs among riverine, fringe, basin and dwarf zones. Mangrove forests also fix and store carbon in wood and organic-rich sediments. The total carbon sequestration in tropical coastal ecosystems is unknown, but it may contribute to the potentially significant carbon sinks in deltaic continental margins (Twilley *et al.* 1992).

6.1.11.7 Landscape and waterscape structure

Ecosystem consequences of impacts. River (and surface runoff) diversions that deprive tropical coastal deltas of fresh water and silt result in losses of mangrove species diversity and organic production, and alter the terrestrial and aquatic food webs that mangrove ecosystems support. Freshwater diversion of the Indus River to agriculture in Sind Province over the last several hundred years has reduced the once species-rich Indus River Delta to a sparse community dominated by *Avicennia marina*; it is also responsible for causing significant erosion of the seafloor due to sediment starvation and the silting-in of the abandoned spill rivers (Snedaker 1984). A similar phenomenon has been observed in southwestern Bangladesh following natural changes in the distributary rivers of the Ganges, and the construction of the Farakka barrage which reduced the dry season flow of fresh water into the mangrove-dominated western Sundarbans. Freshwater starvation, both natural and human-induced, has had negative impacts on the rich vertebrate fauna (e.g. arboreal primates, deer, gaviel, large cats) of the Ganges

River Delta (Hendricks 1975; Das and Siddiqi 1985) and the Santa Marta lagoon (Ciénaga Grande) in Colombia (Botero 1990). Change in the species composition and distribution of mangroves and ecological types, such as fringe and basin forests, alters the quantity and quality of organic matter (DOM vs POC) contributed to adjacent estuaries (Twilley 1988). The effects of land-use changes at the landscape scale of tropical estuaries are also significant because of the dependence of marine organisms on estuarine conditions during the juvenile or adult stages of their life cycles (Yañez-Arancibia *et al.* 1994). The seasonal supply of organic matter by different primary producers, along with seasonal variations in physical constraints of organisms, such as temperature and salinity, provides a unique set of conditions for estuarine-dependent life cycles (Rojas *et al.* 1992). The fragmentation of mangrove-dominated landscapes may create the same types of problems for estuarine-dependent organisms that are associated with the fragmentation of upland forests, yet there has been little, if any, research on this topic.

6.1.11.8 Biotic linkages and species interactions

Ecosystem consequences of impacts. Organisms associated with mangrove forests may play many roles. In Malaysia, for example, bats that visit mangroves are also responsible for pollinating trees bearing the highly valued durian fruit. In Belize, wood-boring insects in mangroves are important to the formation of gaps and the specific architecture of mangrove trees (Feller 1993). Crabs are diverse in mangrove habitats (Jones 1984) with many functions such as contributing to plant zonation by differential seed predation (Smith 1987), to litter dynamics (leaf burrowing; Robertson 1986; Robertson and Daniel 1989; Twilley *et al.* 1993), and to nutrient dynamics (soil aeration from burrows; Smith *et al.* 1991) (see Box 6.1-2). Sponges, tunicates and a variety of other forms of epibionts on prop roots are equally diverse (Ruetzler and Feller 1988; Ellison and Farnsworth 1992) and may be sources of nutrition for higher level predators as well as influencing various processes in mangrove fringe forests. Finfish and macro-invertebrates may exert top-down control of community dynamics in fringe mangrove zones (Robertson and Duke 1990). Also, the diverse avifauna, mainly those that use mangroves for rookeries, control nutrient levels and foliage dynamics through nesting and the associated herbivory (cited above). These keystone guilds have disproportionate effects on the ecological processes of mangrove ecosystems, and illustrate the multiple roles of biodiversity in ecosystem functioning (Ray and McCormick 1992).

6.1.11.9 Microbial activities

Ecosystem consequences of impacts. The production and accumulation of mangrove peat occurs when root

Box 6.1-2: Crabs – a central ecosystem element in mangrove forests.

Crabs are extraordinarily abundant in many mangrove forests. They can make up nearly 80% of the macrofaunal biomass (Golley *et al.* 1962) and can reach densities of 80–90 per m² (Macintosh 1988). Two families of crabs are particularly associated with mangrove ecosystems (mangal) – the Grapsidae with 63 mangrove species, and the Ocypodidae with over 80 species (Jones 1984). These animals can have an enormous impact on ecosystem dynamics:

1. They can process as much as 70% of the leaf litter, and leaf processing by crabs in Australian mangrove systems can turn over litter at a rate in excess of 75 times that of microbial decay. The latter process predominates in New World mangrove ecosystems (Robertson and Daniel 1989).
2. Most of the mangal crabs feed on vascular plant material, including litter, but they also feed on green leaves, including seedlings. Seedling grazing, particularly by members of the genus *Sesarma*, may slow regeneration of these systems (Jones 1984) and crab seed predators greatly influence tree distribution in many mangrove forests. In the forests of Malaysia, Panama and Australia, grapsid crabs are the prime seed predators whereas in Florida snails occupy this functional role (Smith *et al.* 1989).
3. Mangal crabs not only fill every feeding niche but also occupy virtually all spatial dimensions of their habitat, showing species replacements horizontally from the sea inward and from the muddy substrate to the top of the canopy. Most, however, are burrowing forms (Jones 1984).
4. Crabs, through their burrowing activity modify the microtopography of the mangrove forest floor, not only influencing sediment texture distribution but also negatively affecting the abundance of surface algae (Warren and Underwood 1986).
5. Crabs of the mangrove forest positively influence tree productivity, and reproductive output, presumably by aerating the soil through burrowing activity and by decreasing sulphide levels. For this and many of the other activities described here Smith *et al.* (1991) have designated crabs as keystone species in mangrove systems.

production and mortality exceeds decomposition. The relative rate of below-ground production and decomposition in wetland plant communities depends on the presence of sulphate in seawater that is utilized by anaerobic sulphate reducers (Alongi 1988). In this regard, Snedaker (1993) has argued that in terms of climate change, changes in precipitation and freshwater run-off are the most important parameters (see also Pool *et al.* 1975) since each promotes mangrove [root] production and restricts root-peat decomposition by seawater-sulphate reducers. The succession of microbial processes also controls the transformation of nutritionally-poor mangrove leaf litter to a protein-rich food substrate which represents a significant contribution to the energy and nutrient budgets of tropical estuarine ecosystems (Heald 1971; Odum 1971; Fell and Master 1973).

6.1.11.10 Summary and relevance to human activities

A 1991 workshop on the status of mangroves of Southeast Asian coastlines (Sasekumar 1993) reported that the region has lost large areas of mangroves in the Philippines (80%), Thailand (50%), Indonesia (50%) and Malaysia (32%). This pattern is likely to continue as greater demands are placed on forest and fishery resources along with land use-changes along coastlines and in upland watersheds. The result will necessarily cause a change in the ecological characteristics of tropical estuaries. Many of the biodiversity components are sensitive to changes in physical conditions (salinity, turbidity), chemical balances (eutrophication) and biological changes (exotic species). The environmental quality of tropical estuaries relies on the unknown balance of the mosaic of ecosystem functioning, many components of which are still poorly understood. Major restoration projects in countries such as Colombia (Botero 1990), Pakistan (Qureshi 1990), Ecuador (Twilley *et al.* 1993) and Bangladesh (Siddiqi and Khan 1990) will challenge our ability to rebuild tropical estuaries and the dependent fisheries that have collapsed or been altered as a consequence of human interference.

References

- Alongi, D.M. 1988. Bacterial productivity and microbial biomass in tropical mangrove sediments. *Microbiology and Ecology* 15: 59–79.
- Botero, L. 1990. Massive mangrove mortality on the Caribbean coast of Colombia. *Vida Silvestre Neotropical* 2: 77–78.
- Boto, K.G. and Bunt, J.S. 1981. Tidal export of particulate organic matter from a Northern Australian mangrove system. *Estuarine, Coastal and Shelf Science* 13: 247–255.
- Carlson, P.R., Yarbro, L.A., Zimmermann, C.F. and Montgomery, J.R. 1983. Pore water chemistry of an overwash mangrove island. *Florida Scientist* 46: 239–249.
- Chapman, V.J. 1976. *Mangrove Vegetation*. J. Cramer, Germany.

- Cintrón, G., Lugo, A.E., Pool, D.J. and Morris, G. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10: 110-121.
- Clough, B.F., Boto, K.G. and Attiwill, P.M. 1983. Mangroves and sewage: a re-evaluation. In: Teas, H.J. (ed.), *Biology and Ecology of Mangroves*. Vol. 8, 188. Dr W. Junk Publishers, The Hague.
- Das, S. and Siddiqi, N.A. 1985. *The Mangroves and Mangrove Forests of Bangladesh*. Mangrove Silviculture Division Bulletin No. 2, 142. Bangladesh Forest Research Institute, Chittagong.
- Dost, H. (ed.) 1973. *Acid Sulfate Soils*, Vols. I and II. International Institute for Land Reclamation and Improvement, Publication No. 575. Wageningen, The Netherlands.
- Ellison, A.M. and Farnsworth, E.J. 1992. The ecology of Belizean mangrove-root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth. *Hydrobiologia* 247: 871-98.
- Fell, J.W. and Master, L.M. 1973. Fungi associated with the degradation of mangrove (*Rhizophora mangle* L.) leaves in south Florida. In: Stevenson, L.H. and Colwell, R.R. (eds), *Estuarine Microbial Ecology*, 455-465. University of South Carolina Press, Columbia, SC.
- Feller, I.C. 1993. *Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove*. Ph.D. dissertation, Georgetown University, Washington, DC.
- Gilmore, R.G. and Snedaker, S.C. 1993. Mangrove forests. In: Martin, W.H., Boyce, S. and Echemacht, K. (eds), *Biodiversity of the Southeastern United States: Lowland terrestrial communities*, 165-198. John Wiley, New York.
- Golley, F., Odum, H.T. and Wilson, R.F. 1962. The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology* 43: 9-18.
- Gotto, J.W., Tabita, F.R. and Baalen, C.V. 1981. Nitrogen fixation in intertidal environments of the Texas gulf coast. *Estuarine, Coastal and Shelf Science* 12: 231-235.
- Gotto, J.W. and Taylor, B.F. 1976. N_2 fixation associated with decaying leaves of the red mangrove (*Rhizophora mangle*). *Applied and Environmental Microbiology* 31: 781-783.
- Heald, E.J. 1971. The production of organic detritus in a south Florida estuary. *University Miami Sea Grant Technical Bulletin* No. 6.
- Hendricks, H. 1975. The status of the tiger *Panthera tigris* (Linne 1758) in the Sundarbans mangrove forest (Bay of Bengal). *Säingetierkundliche Mitteilungen*, 23 (3):161-199.
- Hicks, D.B. and Burns, L.A. 1975. Mangrove metabolic response to alterations of natural freshwater drainage to southwestern Florida estuaries. In: Walsh, G., Snedaker, S. and Teas, H. (eds), *Proceedings of the International Symposium on the Biology and Management of Mangroves*, 238-255. Institute of Food and Agricultural Sciences, University of Florida, Gainesville.
- Jones, D.A. 1984. Crabs of the mangal ecosystem. In: Por, F.D. and Dor, I. (eds), *Hydrobiology of the Mangal*, 89-110. Dr W. Junk Publishers, The Hague.
- Kimball, M.C. and Teas, H.J. 1975. Nitrogen fixation in mangrove areas of southern Florida. In: Walsh, G., Snedaker, S. and Teas, H. (eds), *Proceedings of the International Symposium on the Biology and Management of Mangroves*, 654-660. Institute of Food and Agricultural Sciences, University of Florida, Gainesville.
- Lugo, A.E. and Snedaker, S.C. 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* 5: 39-64.
- Lugo, A.E., Brown, S. and Brinson, M.M. 1990. Concepts in wetland ecology. In: Lugo, A.E., Brinson, M. and Brown, S. (eds), *Ecosystems of the World 15: Forested Wetlands*, 53-85. Elsevier, Amsterdam.
- Lynch, J.C., Meriwether, J.R., McKee, B.A., Vera-Herrera, F. and Twilley, R.R. 1989. Recent accretion in mangrove ecosystems based on ^{137}Cs and ^{210}Pb . *Estuaries* 12: 284-299.
- Macintosh, D.J. 1988. The ecology and physiology of decapods of mangrove swamps. *Symposia of the Zoological Society of London* 59: 315-341.
- Macnae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Advances in Marine Biology* 6: 73-270.
- McKee, K.L., Mendelssohn, I.A. and Hester, M.W. 1988. Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. *American Journal of Botany* 75: 1352-1359.
- Maul, G.A. and Martin, D.M. 1993. Sea level rise at Key West, Florida, 1846-1992: America's longest instrument record? *Geophysical Research Letters* 20 (18): 1955-1958.
- Moorman, F.R. and Pons, L.J. 1975. Characteristics of mangrove soils in relations to their agricultural land use and potential. In: Walsh, G., Snedaker, S. and Teas, H. (eds), *Proceedings of the International Symposium on the Biology and Management of Mangroves*, 529-547. Institute of Food and Agricultural Sciences, University of Florida, Gainesville.
- Nedwell, D.B. 1975. Inorganic nitrogen metabolism in an eutrophic tropical mangrove estuary. *Water Research* 9: 221-231.
- Nickerson, N.H. and Thibodeau, F.R. 1985. Association between pore water sulfide concentrations and the distribution of mangroves. *Biogeochemistry* 1: 183-192.
- Nixon, S.W., Furnas, B.N., Lee, V., Marshall, N., Jin-Eng, O., Chee-Hoong, W., Wooi-Khoon, G. and Sasekumar, A. 1984. The role of mangroves in the carbon and nutrient dynamics of Malaysia estuaries, 534-544. *Proceedings Symposium on Mangrove Environments - Research and Management*.
- Odum, W.E. 1971. Pathways of energy flow in a south Florida estuary. *University of Miami Sea Grant Bulletin* No. 7.
- Odum, W.E. and Heald, E.J. 1972. Trophic analysis of an estuarine mangrove community. *Bulletin of Marine Science* 22: 671-738.
- Odum, W.E., McIvor, C.C. and Smith, T.J. III. 1982. *The Ecology of the Mangroves of South Florida: A community profile*. Fish and Wildlife Service/Office of Biological Services, Washington, DC. FWS/OBS-81/24.
- Onuf, C., Teal, J. and Valiela, I. 1977. The interactions of nutrients, plant growth, and herbivory in a mangrove ecosystem. *Ecology* 58: 514-526.
- Pannier, F. 1979. Mangrove impacted by human-induced disturbance: A case study of the Orinoco Delta mangrove ecosystem. *Environmental Management* 3: 205-216.

- Peterson, P.J., Burton, M.A.S., Gregson, M., Nye, S.M. and Porter, E.K. 1979. Accumulation of tin by mangrove species in west Malaysia. *Science of the Total Environment* 11: 213-221.
- Ponnamperuma, F.N. 1984. Mangrove swamps in south and southeast Asia as potential rice lands. In: Soepadmo, E., Rao, A.N. and McIntosh, D.J. (eds), *Proceedings Asian Mangrove Symposium*, 25-29 August 1980, Kuala Lumpur, Malaysia. 672-683. Percetakan Ardyas Sdn. Bhd., Kuala Lumpur.
- Pool, D.J., Lugo, A.E. and Snedaker, S.C. 1975. Litter production in mangrove forests of southern Florida and Puerto Rico. In: Walsh, G., Snedaker, S. and Teas, H. (eds), *Proceedings of the International Symposium on the Biology and Management of Mangroves*. 213-237. Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida.
- Potts, M. 1979. Nitrogen fixation (acetylene reduction) associated with communities of heterocystous and non-heterocystous blue-green algae on mangrove forests of Sinai. *Oecologia* 39: 359-373.
- Prakash, A. 1971. Terrigenous organic matter and coastal phytoplankton fertility. *Proceedings of an International Conference on the Fertility of the Sea, Sao Paulo, Brazil*. Gordon and Breach Science Publishers.
- Prakash, A., Jensen, A. and Rashid, M.A. 1973. Humic substances and aquatic productivity. In: Povoledo, D. and Golteman, H.L. (eds), *Humic substances: Their structure and function in the biosphere*.
- Qureshi, M.T. 1990. Experimental plantation for rehabilitation of mangrove forests in Pakistan. In: Field, C.B. (ed.), *Mangrove Ecosystems Occasional Papers No. 4*. COMAR, Unesco, Paris.
- Ray, G.C. and McCormick-Ray, M.G. 1992. Functional coastal-marine biodiversity. *Transactions 57th North American Wildlife and Natural Resources Conference*. 384-397.
- Rivera-Munoy, V.H., Day, J.W., Twilley, R.R., Vera-Herrera, F. and Coronado-Molina, C. 1995. Flux of nitrogen and sediment in a fringe mangrove forest in Terminos Lagoon, Mexico. *Estuarine, Coastal and Shelf Science* 40: 139-160.
- Robertson, A.I. 1986. Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* spp.) in northeastern Australia. *Journal of Experimental Marine Biology and Ecology* 102: 237-248.
- Robertson, A.I. and Daniel, P.A. 1989. The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia* 78: 191-198.
- Robertson, A.I. and Duke, N.C. 1990. Mangrove fish-communities in tropical Queensland, Australia: spatial and temporal patterns in densities, biomass and community structure. *Marine Biology* 104: 369-379.
- Rojas Galaviz, J.L., Yañez-Arancibia, A., Day, J.W. and Vera-Herrera, F. 1992. Estuary primary producers: Laguna de Terminos - a case study. In: Seeliger, U. (ed.), *Coastal Plant Communities of Latin America*. 141-154. Academic Press, New York.
- Ruetzler, K. and Feller, C. 1988. Mangrove swamp communities. *Oceanus* 30: 16-24.
- Saenger, P. and Snedaker, S.C. 1993. Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia* 96: 293-299.
- Saenger, P., Hegerl, E.J. and Davie, J.D.S. 1983. Global Status of Mangrove Ecosystems. *The Environmentalist* 3, Supplement 3.
- Sasekumar, A. 1993. Asian-Australia marine science project: Living coastal resources. *Proceedings of a workshop on mangrove fisheries and connections*, 26-30, August 1991. Australian International Development Assistance Bureau (AIDAB).
- Sasekumar, A., Chong, V.C., Le, M.U. and D'Cruz, R. (spelling) 1992. Mangroves as habitat for fish and prawns. In: Jaccarini, V. and Martens, E. (eds), *The Ecology of Mangroves and Related Habitats*. Development in Hydrobiology 80. 195-207. Kluwer Academic Publishers, Boston.
- Scoffin, T.P. 1970. The trapping and binding of subtidal carbonate sediments by marine vegetation in Bimini Lagoon, Bahamas. *Journal of Sedimentary Petrology* 40: 249-273.
- Siddiqi, N.A. and Khan, M.A.S. 1990. Growth performance of mangrove trees along the coastal belt of Bangladesh. In: Field, C.D. (ed.), *Mangrove Ecosystems Occasional Papers No. 8*. 4-14. COMAR, Unesco, Paris.
- Smith, T.J., III. 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology* 68: 266-273.
- Smith, T.J., III, Chan, H.T., McIvor, C.C. and Robblee, M.B. 1989. Comparison of seed predation in tropical, tidal forests from three continents. *Ecology* 70: 146-151.
- Smith, T.J., III, Boto, K.G., Frusher, S.D. and Giddins, R.L. 1991. Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science* 33: 419-432.
- Snedaker, S.C. 1984a. The mangroves of Asia and Oceania: status and research planning. In: Soepadmo, E., Rao, A.N. and McIntosh, D.J. (eds), *Proceedings, Asian Mangrove Symposium*, 25-29 August 1980, Kuala Lumpur, Malaysia. 5-15. Percetakan Ardyas Sdn. Bhd., Kuala Lumpur.
- Snedaker, S.C. 1984b. Mangroves: A summary of knowledge with emphasis on Pakistan. In: Haq, B.U. and Milliman, J.D. (eds), *Marine Geology and Oceanography of Arabian Sea and Coastal Pakistan*. 255-262. Van Nostrand Reinhold Company, New York.
- Snedaker, S.C. 1986. Traditional uses of South American mangrove resources and the socio-economic effect of ecosystem changes. In: Kunstadter, P., Bird, E.C.F. and Sabhasri, S. (eds), *Proceedings, Workshop on Man in the Mangroves*. 104-112. United Nations University, Tokyo.
- Snedaker, S.C. 1989. Overview of ecology of mangroves and information needs for Florida Bay. *Bulletin of Marine Science* 44 (1): 341-347.
- Snedaker, S.C. 1993. Impact on mangroves. In: Maul, G.A. (ed.), *Climate Change in the Intra-Americas Sea*. 282-305. Edward Arnold, Kent, UK.
- Snedaker, S.C., Meeder, J.F., Ross, M.S. and Ford, R.G. 1994. Discussion of Joanna C. Ellison and David R. Stoddart, Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *Journal of Coastal Research* 10 (2): 497-498.
- Steyer, G. 1988. Litter dynamics and nitrogen retranslocation in three types of mangrove forests in Rookery Bay, Florida. M.S. Degree, University of Southwestern Louisiana, Lafayette.
- Thayer, G.W., Colby, D.R. and Hettler, W.F. Jr. 1987. Utilization

- of red mangrove prop root habitat by fishes in south Florida. *Marine Ecology Progress Series* 35: 25-38.
- Thom, B.G. 1982. Mangrove ecology: a geomorphological perspective. In: Clough, B.F. (ed.), *Mangrove Ecosystems in Australia*, 3-17. Australian National University Press, Canberra.
- Tomlinson, P.B. 1986. *The Botany of Mangroves*. Cambridge University Press, New York.
- Twilley, R.R. 1985. The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. *Estuarine, Coastal and Shelf Science* 20: 543-557.
- Twilley, R.R., Lugo, A.E. and Patterson-Zucca, C. 1986. Production, standing crop, and decomposition of litter in basin mangrove forests in southwest Florida. *Ecology* 67: 670-683.
- Twilley, R.R. 1988. Coupling of mangroves to the productivity of estuarine and coastal waters. In: Jansson, B.O. (ed.), *Coastal-Offshore Ecosystem Interactions*, 155-180. Springer-Verlag, Berlin.
- Twilley, R.R., Chen, R.H. and Hargis, T. 1992. Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water, Air and Soil Pollution* 64: 265-288.
- Twilley, R.R., Boderio, A. and Robadue, D. 1993. Mangrove ecosystem biodiversity and conservation: case study of mangrove resources in Ecuador. In: Potter, C.S., Cohen, J.I. and Janczewski, D. (eds), *Perspectives on biodiversity: Case studies of genetic resource conservation and development*, 105-127. AAAS Press, Washington, DC.
- van der Valk, A.G. and Attiwill, P.M. 1984. Acetylene reduction in an *Avicennia marina* community in southern Australia. *Australian Journal of Botany* 32: 157-164.
- Walsh, G.E. 1967. An ecological study of a Hawaiian mangrove swamp. In: Lauff, G.H. (ed.) *Estuaries*, 420-431. AAAS Press, Washington, DC.
- Warren, J. H., and Underwood, A.J. 1986. Effects of burrowing crabs on the topography of mangrove swamps in New South Wales. *Journal of Experimental Marine Biology and Ecology* 102: 223-235.
- Watson, J. 1928. Mangrove forests of the Malay Peninsula. *Malayan Forest Records* 6. Fraser and Neave, Ltd, Singapore.
- Yañez-Arancibia, A., Sanchez-Gil, P. and Lara-Dominguez, A.L. 1994. Functional groups, seasonality, and biodiversity in Terminos Lagoon a tropical estuary, Mexico. In: *Proceedings, International Workshop Ecosystem Function of Marine Biodiversity in Estuaries, Lagoons and Near-shore Coastal Ecosystems*. IUBS Journal Biology International (in press).
- Yañez-Arancibia, A., Lara-Dominguez, A.L., Rojas Galaviz, J.L., Sanchez-Gil, P., Day, J.W. and Madden, C.J. 1988. Seasonal biomass and diversity of estuarine fishes coupled with tropical habitat heterogeneity (southern Gulf of Mexico). *Journal of Fish Biology* 33 (Suppl. A): 191-200.
- Yañez-Arancibia, A., Lara-Dominguez, A.L. and Day, J.W. 1993. Interactions between mangrove and seagrass habitats mediated by estuarine nekton assemblages: coupling of primary and secondary production. *Hydrobiologia* 264: 1-12.
- Zuberer, D.A. and Silver, W.S. 1978. Biological nitrogen fixation (acetylene reduction) associated with Florida mangroves. *Applied and Environmental Microbiology* 35: 567-575.

6.1.12 Open oceans

6.1.12.1 Introduction

Open-ocean systems include all environments on Earth minus the landmasses and the continental shelf benthos. These systems comprise more than 70% of the Earth's surface, and over 90% of its habitable volume. Open-ocean ecosystems are unique in being almost completely devoid of higher plants, and depauperate in other forms of biogenic structure which is limited to drift-weed, terrigenous flotsam (especially wood) and the surfaces of other, usually motile living creatures. Primary production is dominated by phytoplankton, and averages one-fifth that of the mean terrestrial ecosystem (Valiela 1984), although turnover rates of oceanic plankton may be more than one order of magnitude greater than those of terrestrial vascular plants. Biomes within the open ocean are defined by the intersection of four factors: energy source for primary productivity, physical structure, depth/light attenuation, and latitude (Figure 6.1-10). Approximately 15% of described species are marine (Barnes 1989; May 1992). The diversity of open-ocean taxa is poorly known for both high and low taxonomic levels (Grassle and Maciolek 1992; Fuhrman and Davis 1994). The most conservative estimate for the total number of species in the open ocean - half a million - is still at least twice the number of species thus far described (May 1992), and estimates range up to 10 million (Grassle and Maciolek 1992; Poore *et al.* 1994; but see May 1992; Briggs 1994). Global phyletic diversity is dominated by oceanic taxa: 32 out of the 33 phyla are marine, and 15 of these phyla are marine endemics (Margulis and Schwartz 1988; Ray and Grassle 1991; Angel 1993). The variety of major functional groups in the marine environment also overshadows that found in other biomes. In particular, we must emphasize the significance of biodiversity within the microbial groups at the fundamental biochemical level. These are arguably the most unfamiliar, fundamentally 'different' life-forms in recent discovery (Fuhrman *et al.* 1992; Fuhrman and Davis 1994). And we have barely scratched the surface of the sediments (Grassle and Maciolek 1992; Poore and Wilson 1993; Poore *et al.* 1994). Species diversity is generally higher at low latitudes, with three peaks, dependent upon taxonomic group: photic zone, benthic environments at 2000 to 3000 m depth (mostly on the continental slope), and the abyssal plain (Vinogradova 1979b; Grassle 1991; Alongi 1992; Grassle and Maciolek 1992; Angel 1993; Poore and Wilson 1993; Brey *et al.* 1994). Life in the epipelagic zone is dominated by generalists with a dynamic metapopulation structure (Steele 1985, 1991). The deep benthos harbours a much higher diversity of species (Grassle and Maciolek 1992) and a higher proportion of local or regional endemics. Relationships among species in highly diverse deep-sea communities have not been well studied, and rates of dispersal of deep-sea species among

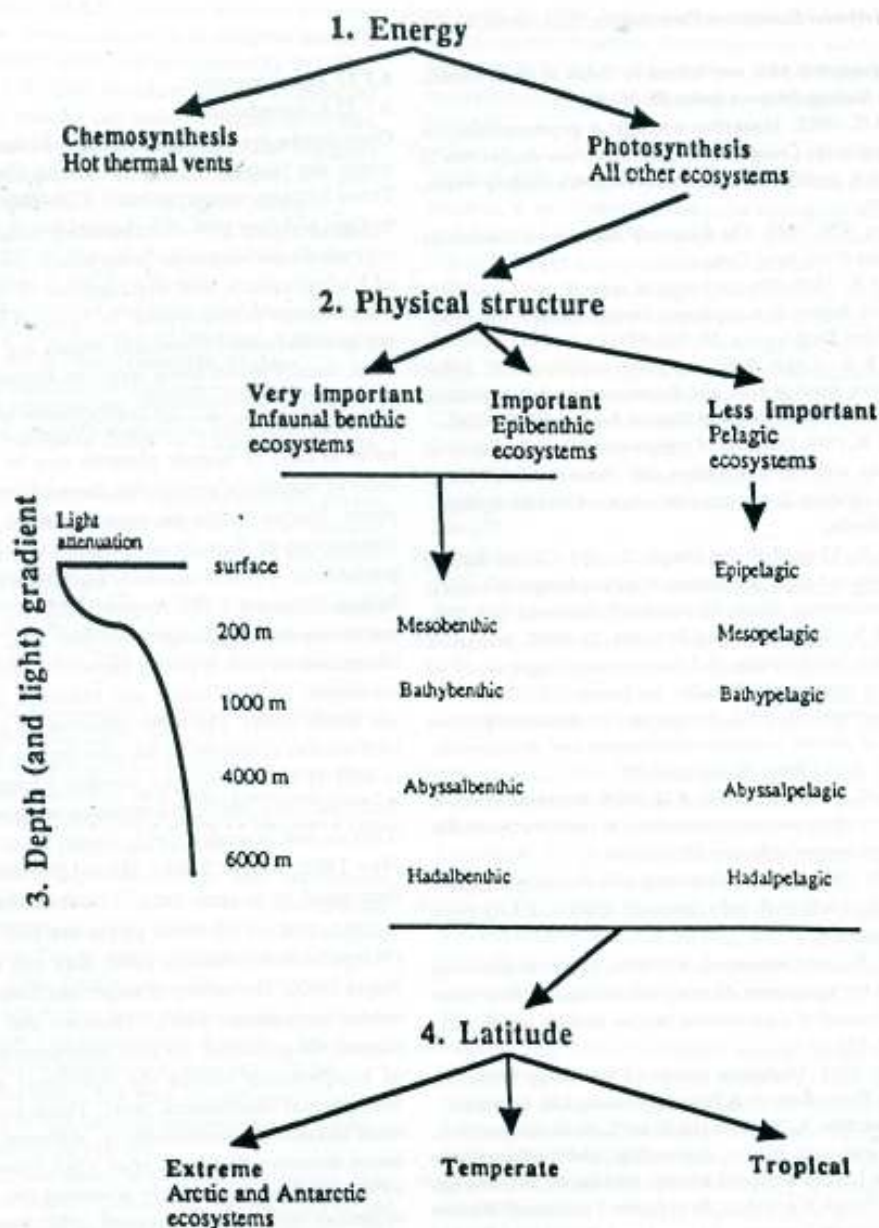


Figure 6.1-10: A heuristic view of the structure of open-ocean ecosystems.

geographic regions are also poorly known. There is an extremely important and dynamic link between the open ocean and coastal pelagic biomes due to the high prevalence of the larvae of many coastal marine organisms dependent upon pelagic dispersal.

6.1.12.2 Threats to the oceans

Increases in ultraviolet radiation may directly affect both phytoplankton and zooplankton in open ocean pelagic

areas. A steady increase in temperature amounting to 0.32 °C over the last 35 years has been observed at abyssal depths (Parrilla *et al.* 1994). Pollutants have been observed on the deep-sea floor in all areas where they have been looked for, and increases from atmospheric sources (LaFlemme and Hites 1978; Takada *et al.* 1994) are inevitable. The greatest flux of pollutants to the deep sea is likely to occur on continental margins where sediments from land sources accumulate. Human impacts on biodiversity in the open-

ocean biomes are summarized in Table 6.1-1. The biodiversity impact of changes in atmospheric gases (i.e. acid rain, global warming and ozone depletion processes) is uncertain, but likely to be significant. The reason for the uncertainty is partly that our knowledge of the biodiversity of the smallest epipelagic organisms is extremely poor. The likelihood of there being direct effects of these processes on the biodiversity of the megafauna is unknown. Fishery collapses in every sector of the world ocean point to a clear human impact on the diversity of top-level carnivores and herbivores in the epipelagic zone (Brown 1993; Norse 1993; Paine 1993; Anon. 1994), and major changes in community structure of oceanic ecosystems following the over-exploitation of dominant vertebrates and invertebrates have been observed in the Antarctic (Laws 1985), North Atlantic (Beddington and May 1982; Weber 1986), and Pacific Oceans (MacCull 1986; Cox 1993). Another human impact is the potential for acoustic noise to disrupt normal social and migratory behaviour of marine mammals and large teleosts.

There is insufficient baseline information about the distribution and abundance of deep-sea species to

determine whether or not major changes are occurring in deep-sea ecosystems (Grassle *et al.* 1990). The number of quantitative samples from the deep sea is minuscule, and increases in pollutants are not monitored in any area of the deep ocean. Furthermore, few scientists are capable of identifying species within even the better-known deep-sea taxa. Present information is insufficient for determining whether introductions or extinctions are taking place in either pelagic or benthic assemblages.

6.1.12.3 Productive capacity, biomass, decomposition and nutrient cycling

Human impacts on biodiversity. Most of the impacts mentioned above should be included here. There is evidence for major intra- and interspecific shifts in life history profiles of the dominant taxa in the open ocean due to over-extraction in fisheries and as by-catch (Nelson and Soule 1987; Rijnsdorp 1993; Stokes *et al.* 1993). Intraspecifically, there is evidence for response to overharvesting of sexually mature individuals, manifested as a reduction in age at first maturity and of maximum adult size. Fisheries have systematically reduced the

Table 6.1-1: Human impacts on the biodiversity of the open-ocean biomass.

Anthropogenic impacts ¹	Coastal ²		Open ocean	
	Benthic and pelagic	Epipelagic ³	Mesopelagic ³	Benthic
Land-based activities				
Air pollution				
Change in atmospheric gases (e.g. CO ₂ , methane, acid rain)	*** ⁴	***	indirect	indirect
Increase UV radiation	***	***	indirect	indirect
Global warming	***	***	indirect	indirect
Land pollution				
Siltation	***	*	indirect	**
Accidental waste disposal (e.g. flotsam)	***	**	*	
Waste disposal	***	**	**	
Ocean-based activities				
Inputs				
Introductions	***	***	?	
Accidental waste disposal (e.g. oil spills)	***	***	***	
Waste disposal	***	**	***	
Outputs				
Resource extraction (harvesting and mining)***		***	**	***

1. References to the impacts are found in text.

2. Coastal systems extend to the limits of the continental shelf.

3. Epipelagic systems occur above 200 m; mesopelagic systems occur below 200 m.

4. Ranking of impact: ***expected serious impact; **expected moderate impact; *expected mild impact; indirect/direct effects may cascade impacts down down to other ocean systems.

abundance of all species of large organisms in the epipelagic zone.

Ecosystem consequences of impacts. Human impacts on productive capacity in the open ocean are predominantly nutrient-loading effects. However, alterations to biodiversity could have important secondary impacts on productive capacity or its spatial distribution. Shifts in the abundances of non-cetacean planktivores in Antarctic waters are probably a consequence of this impact (Valiela 1984). Elimination of large carnivores and herbivores should also have profound effects on the efficiency and form of open-ocean food webs. The effects of removal of large epipelagic species should cascade down to the rest of the water column, as these are significant agents of nutrient transport, both as living individuals undergoing frequent vertical migration, and as deadfall (Smith *et al.* 1989; Pfannkuche and Lochte 1993). Recent simulations of oceanic systems suggest that the effects of altering species composition are very difficult to predict, may be highly counterintuitive, and are dependent on relevant temporal and spatial scales (Yodzis 1988, 1994).

6.1.12.4 Sediment structure and nutrient pools

Human impacts on biodiversity. Removal of manganese nodules eliminates one important type of surface structure exploited by a distinct assemblage of epifauna (Thiel 1982). Reduction in epipelagic megafauna has compromised deadfall, which serves both as a source of nutrients and as a potential stepping-stone for dispersal of rift-associated organisms (Smith *et al.* 1989).

Ecosystem consequences of impacts. It is not known if human activity has yet had any significant impact on the biodiversity that affects sediment structure of infaunal dynamics in the deep sea. The possibility for impact exists through alteration of physical structure, chemical or radiological contamination, and alteration of nutrient inputs from surface waters. As for impact specifically emergent from loss of deep ocean soft sediment species, nothing can be surmised at this time. A cautionary note is in order, however. It is apparent that the diversity of microbial activity in the deep benthos is not only a key attribute of the system, but also of enormous potential value to humanity. The possibility of losing specific taxa or strains as a result of direct human alteration of sections of sea bottom should be taken seriously.

6.1.12.5 Water distribution, balance and quality

Human impacts on biodiversity. Principal concerns for the open ocean include toxic inputs (oil spills, ocean dumping of PCBs, heavy metals, pseudohormones, atmospheric inputs of toxic organic compounds), discharges, and alteration of nutrient regimes (Tanabe *et al.* 1984; Tanabe 1988; Cox, 1993). Although these are currently thought of as principally coastal phenomena

(GESAMP 1990), this is almost certainly a product of ignorance rather than an accurate reflection of fact. Even the most distant oceanic ecosystems have traces of human activities (Flegal *et al.* 1993).

Ecosystem consequences of impacts. The pervasive nature of chemical pollution suggests that open-ocean organisms and ecosystems are likely to experience levels of disruption at least as great as those observed in coastal systems. Existing data suggest, however, that substantially longer time scales are likely to be needed for recovery from such impacts. The biomagnification of toxins up through the food web could lead to significant changes in community structure if the larger apex organisms are negatively affected (Tanabe *et al.* 1984; Tanabe 1988; Addison 1989).

6.1.12.6 Feedbacks to atmospheric properties

Human impacts on biodiversity. Human impact on the biodiversity that influences atmospheric processes is difficult to ascertain because of our ignorance of which biogenic products are most important in regulating climate. Dimethyl sulphide, carbonyl sulphate and bromoform are gases that potentially can have an important impact on cloud formation or the greenhouse effect. All three gases are known to be produced by marine organisms (primarily the diatoms and non-calcifying coccolithophorids) (Charlson *et al.* 1987; Turner *et al.* 1988; Iverson *et al.* 1989; Kiene and Bates 1990). The relative abundance of these species and their distributions are poorly known, although anthropogenic activities (see Table 6.1-1 and above) will most likely alter their current status, because different taxa respond differently to eutrophication, chemical pollution, UV radiation and species introduction. Recent studies have suggested that oceanic phytoplankton may act as a carbon sink for globally increasing levels of carbon dioxide.

Ecosystem consequences of impacts. To the extent that the relative abundances of plankton producing carbonyl sulphate and dimethyl sulphide are impacted by human activities in the open ocean, change in at least the regional climate is likely to occur (Fuhrman and Capone 1991). This is a largely unexplored yet important field with possible wide-ranging ramifications given the potential ability of climate models to predict effects of global weather.

6.1.12.7 Landscape and waterscape structure

Human impacts on biodiversity. Patch dynamics are very important to the way open-ocean ecosystems function. Pelagic systems are heterogeneous at all scales (Steele 1985; Colebrook 1991; Kawasaki 1991): hydrodynamic structure predominates and is provided to oceanic systems principally by currents and waves from small-scale eddies, through warm-core rings of water moving across ocean basins, to trans-oceanic currents. Open-ocean biomes are not dominated by a biogenic physical structure, such as

angiosperms, that humans can alter. The extent of large floating mats of raftweed, such as *Sargassum*, may, however, have declined. Much of the benthic environment is very distant to most human activities, although mining and fish trawling in benthic habitats may differentially impact significant members of the benthic community (Watling and Langton 1994).

Ecosystem consequences of impacts. Physical structure is important to the functioning of the deep benthos, primarily because of the tunnelling activities and mixing of the sediments by specific biota, which alter biogeochemical cycling of nutrients and oxygen availability. Recent interest in mining and harvesting the deep sea will probably impact the structure of the seascape, although this effect has not been quantified.

6.1.12.8 Biotic linkages and species interactions

Human impacts on biodiversity. The decline of many marine fish stocks and the complete closure of many formerly productive marine fisheries signifies an important depletion in many top-level predators and herbivores in the open ocean. As one species becomes depleted, another is exploited until it, too, is scarce. Many of the formerly common fishes and marine mammals are now already rare, and two attributes of ocean systems may make them especially vulnerable. The first is pelagic recruitment. These species are subject to highly stochastic determinants and when disrupted sufficiently at large scales the outcome is highly unpredictable. Second, these systems are ordinarily very resilient so that a shift in the dominant species may be extremely difficult to reverse. This resilience is predicted from the prevalence of pelagic larval dispersal plus the likelihood that many adults can prey on the juveniles of many other species. Another important human impact comes from the introduction of marine species into novel environments via tanker ballast water, etc. (Carlton 1993; Carlton and Geller 1993; see 6.1.12.3). It is often assumed that open-ocean taxa are more cosmopolitan in distribution and that open-ocean systems should be less prone to the introduction of novel organisms, but this has yet to be tested.

Ecosystem consequences of impacts. Many of the organisms exploited by humans play pivotal roles in the food web, and because many of the top-level species are being exploited simultaneously, substantial changes in the composition of oceanic communities can be expected. The change in Antarctic communities due to whale harvesting, and the shift from a community dominated by bony fish to one dominated by cartilaginous fish in the Northwestern Atlantic are two examples of the transformation of open-ocean communities (Laws 1985; Weber 1986). Introduction of new organisms into an environment may result in the exposure of key organisms to novel diseases or predators (Carlton 1993; Carlton and Geller 1993), which can result

in dramatic shifts in community structure. These effects have been noticed most dramatically in coastal and coral reef systems. The lack of quantitative sampling over any time period in the open ocean precludes any firm conclusion on whether the effects of novel diseases or predation are more or less important in oceanic systems. The recent mortalities of marine mammals along the Atlantic coastlines from viral epidemics (Visser *et al.* 1993) may reflect only the most visible outcome of some of the changes currently occurring in ocean ecosystems.

6.1.12.9 Microbial activities

Human impacts on biodiversity. The microbial world of both the pelagic and the benthic open ocean are poorly understood, in part because only now are molecular techniques revealing surprising information about the relatively high abundances of certain organisms (e.g. Archaea in surface waters) (Bergh *et al.* 1989; Giovannoni *et al.* 1990; Bolliger *et al.* 1991; Fuhrman *et al.* 1992, 1993). Its importance cannot be denied: the heterotrophic microbial loop accounts for over 70% of the total carbon and nitrogen in the euphotic zone (Fuhrman and Capone 1991). Chemical pollution could have a serious effect on microbial diversity by differentially impacting particular species.

Ecosystem consequences of impacts. Very little is known about the consequences of changing microbial communities because of the difficulty of identifying micro-organisms, and the dearth of knowledge about their ecology. Circumstantial evidence suggests that microbial processes such as degradation and the utilization of specific nutrients are most efficiently performed by specific microbes. Changes in the abundance of these organisms would thus alter the microbial loop. A high diversity of bacteria may be important in stabilizing microbial loops, given the large numbers of parasitic viruses found in open oceans (Bergh *et al.* 1989).

6.1.12.10 Summary and relevance to human activities

Although a great deal is known in principle about open-ocean biodiversity and potential human impacts, the empirical database is small, and our capacity to monitor and trace cause-effect relationships extremely limited. Many oceanic taxa are generalists, with a well-distributed population structure characterized by boom-and-bust cycles (Steele 1991). This may suggest that for many species, removal would have little overall effect on oceanic ecosystem processes; however, humans have simultaneously reduced the abundance of many organisms in higher trophic levels. This is predicted to cause a substantial change in the community structure and productivity of oceanic systems. Novel diseases and predators that will substantially change the functioning of certain oceanic ecosystems are likely to occur at some point

if the redistribution and introduction of organisms by humans continues. Changes in planktonic communities because of greenhouse effects, increased UV radiation, or food-web structural alterations may have large effects on our global climate because several of the climate-modulating gases are produced by relatively few plankton taxa. That we have overlooked open-ocean biodiversity in the past is understandable. That we should continue to do so is indefensible.

References

- Addison, R.F. 1989. Organochlorines and marine mammal reproduction. *Canadian Journal of Fisheries and Aquatic Science* 46: 360-368.
- Alongi, D.M. 1992. Bathymetric patterns of deep-sea benthic communities from bathyal to abyssal depths in the western South Pacific (Solomon and Coral Seas). *Deep Sea Research: A Oceanographic Research Papers* 39: 549-565.
- Angel, M.V. 1993. Biodiversity of the pelagic ocean. *Conservation Biology* 7: 760-772.
- Anon. 1994. The tragedy of the oceans. *The Economist*, 19 March 1994.
- Barnes, R.D. 1989. Diversity of organisms: How much do we know? *Amer. Zool.*, 29: 1075-1084.
- Beddington, J.R. and May, R.M. 1982. The harvesting of interacting species in a natural ecosystem. *Scientific American* 247 (5): 62-69.
- Bergh, Ø., Børsheim, K.Y., Bratbak, G. and Heldal, M. 1989. High abundance of viruses in aquatic environments. *Nature* 340: 462-468.
- Bolliger, R., Hanselmann, K.W. and Bachofen, R. 1991. Microbial potential in deep-sea sediments. *Experientia* 47: 517-523.
- Briggs, J.C. 1994. Species diversity: land and sea compared. *Systematic Biology* 43: 130-135.
- Brey, T., Klages, M., Dahn, C., Gomey, M., Cull, J., Hain, S., Stiller, M. and Arntz, W.F. 1994. Antarctic benthic diversity. *Nature* 368: 297.
- Brown, L.R. 1993. A new era unfolds. In: Starke, L. (ed.), *State of the World. A Worldwatch Institute report on progress toward a sustainable society*. W.W. Norton and Co., New York.
- Carlton, J.T. and Geller, J.B. 1993. Ecological roulette: The global transport of nonindigenous marine organisms. *Science* 261: 78-82.
- Carlton, J.T. 1993. Neoextinctions of marine invertebrates. *American Zoologist* 33: 499-509.
- Charlson, R.J., Lovelock, J.E., Andreae, M.O. and Warren, S.G. 1987. Oceanic phytoplankton, atmosphere sulfur, cloud albedo and climate. *Nature* 326: 655-661.
- Colebrook, J.M. 1991. Continuous plankton records: from seasons to decades in the plankton of the north-east Atlantic. In: Kawasaki, T., Tanaka, S., Tobu, Y. and Taniguchi, A. (eds), *Long-term Variability of Pelagic Fish Populations and their Environment*. 29-45. Pergamon Press, New York.
- Cox, G.W. 1993. *Conservation Ecology*. W.C. Brown Publishers, Dubuque, Iowa.
- Flegel, A.R., Maring, H. and Niemeyer, S. 1993. Anthropogenic lead in Antarctic sea water. *Nature* 365: 242-244.
- Fuhrman, J.A. and Capone, D.G. 1991. Possible biogeochemical consequences of ocean fertilization. *Limnology and Oceanography*, 36 (8): 1951-1959.
- Fuhrman, J.A. and Davis, A.A. 1994. Unexplored marine prokaryotic biodiversity. *Abstract Ocean Sciences Meeting, February*.
- Fuhrman, J.A., McCallum, K. and Davis, A.A. 1992. Novel major archaeobacterial group from marine plankton. *Nature* 356: 148-149.
- Fuhrman, J.A., McCallum, K. and Davis, A.A. 1993. Phylogenetic diversity of subsurface marine microbial communities from the Atlantic and Pacific Oceans. *Applied Environmental Microbiology* 59: 1294-1302.
- GESAMP (Joint group of experts on the Scientific Aspects of Marine Pollution). 1990. *The State of the Marine Environment*. Blackwell Scientific, Cambridge, Mass.
- Giavannoni, S.J., Britschgi, T.B., Moyer, C.L. and Field, K.G. 1990. Genetic diversity in Sargasso Sea bacterioplankton. *Nature* 345: 60-63.
- Grassle, J.F. 1989. Species diversity in deep-sea communities. *Trends in Ecology and Evolution* 4: 12-15.
- Grassle, J.F. 1991. Deep-sea benthic biodiversity. *BioScience* 41: 464-469.
- Grassle, J.F. and Maciolek, N.J. 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139: 313-341.
- Grassle, J.F., Maciolek, N.J. and Blake, J.A. 1990. Are deep-sea communities resilient? In: Woodwell, G.M. (ed.), *The Earth in Transition: Patterns and processes of biotic impoverishment*. 386-394. Cambridge University Press, New York.
- Iverson, R.L., Nearhoof, F.L. and Andreae, M.O. 1989. Production of dimethylsulphide propionate and dimethylsulphide by phytoplankton in estuarine and coastal waters. *Limnology and Oceanography* 34: 53-67.
- Kawasaki, T. 1991. Long-term variability in the fish populations. In: Kawasaki, T., Tanaka, S., Tobu, Y. and Taniguchi, A. (eds), *Long-term variability of Pelagic Fish Populations and their Environment*. 29-45. Pergamon Press, New York.
- Kiene, R.O. and Bates, T.S. 1990. Biological removal of dimethylsulphide from seawater. *Nature* 345: 702-705.
- La Flamme, R.E. and Hites, R.A. 1978. The global distribution of polycyclic aromatic hydrocarbons in recent sediments. *Geochimica Cosmochimica Acta* 41: 289-303.
- Laws, R.M. 1985. The ecology of the southern ocean. *American Scientist* 73: 26-40.
- MacCall, A.D. 1986. Changes in the biomass of the California Current ecosystem. In: Sherman, K. and Alexander, L.M. (eds), *Variability and Management of Large Marine Ecosystems*. 33-54. American Association for the Advancement of Science, Washington, DC.
- Margulis, L. and Schwartz, K.V. 1988. *Five Kingdoms*. W.H. Freeman, New York.
- May, R.M. 1992. Bottoms up for the oceans. *Nature* 357: 278-279.
- Nelson, K. and Soule, M. 1987. Genetical conservation of exploited fishes. In: Ryman, N. and Utter, F. (eds) *Population*

- Genetics and Fisheries Management*. Washington Sea Grant Program, 345-368. University of Washington Press, Seattle.
- Norse, E.A. 1993. *Global Marine Biological Diversity: A strategy for building conservation into decision making*. Island Press, Washington, DC.
- Paine, R.T. 1993. A salty and salutary perspective on global change. In: Kareiva, P.M., Kingsolver, J.G. and Huey, R.B. (eds), *Biotic Interactions and Global Change*. 347-363. Sinauer Associates, Sunderland, Mass.
- Parilla, G., Lavin, A., Bryden, H., Garcia, M. and Millard, R. 1994. Rising temperatures in the subtropical North Atlantic Ocean over the past 35 years. *Nature* 369: 48-51.
- Pfannkuche, O. and Lochte, K. 1993. Open ocean pelago-benthic coupling: Cyanobacteria as tracers of sedimenting salp faeces. *Deep Sea Research I. Oceanography Research Paper* 40: 727-733.
- Poore, G.C.B. and Wilson, G.D.F. 1993. Marine species richness. *Nature* 361: 597-598.
- Poore, G.C.B., Just, J. and Cohen, B.F. 1994. Composition and diversity of Crustacea, Isopoda of the southeastern Australian continental slope. *Deep-Sea Research I*, 41: 677-693.
- Ray, G.C. and Grassle, J.F. 1991. Marine biological diversity. *Bioscience* 41: 453-457.
- Rijnsdorp, A.D. 1993. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North sea plaice, *Pleuronectes platessa* L. *Oecologia* 96: 391-401.
- Smith, C. R., Kukert, H., Wheatcoff, R.A., Jumars, P.A. and Deming, J.W. 1989. Vent fauna on whale remains. *Nature* 341: 27-28.
- Steele, J.H. 1985. A comparison of marine and terrestrial ecological systems. *Nature* 313: 355-358.
- Steele, J.H. 1991. Marine functional diversity. *BioScience* 41: 470-474.
- Stokes, T.K.A., Law, R., and McGlade, J. 1993. *The Exploitation of Evolving Populations*. Springer-Verlag, Berlin.
- Takada, H., Farrington, J.W., Bothner, M.H., Johnson, C.G. and Tripp, B.W. 1994. Transport of sludge-derived organic pollutants in deep-sea sediments at Deep Water Dump Site 106. *Environmental Science and Technology* 28: 1062-1072.
- Tanabe, S. 1988. PCB problems in the future: Foresight from current knowledge. *Environmental Pollution* 50: 5-28.
- Tanabe, S., Tanaka, H. and Tatsukawa, R. 1984. Polychlorophenyls, DDT, and hexachlorocyclohexane isomers in the western North Pacific ecosystem. *Archives of Environmental Contamination and Toxicology* 13: 731-738.
- Thiel, H. 1982. Deep-sea environment disturbance and recovery potential. *Int. Rev. Gesamt. Hydrobiol.* 77: 331-339.
- Turner, S.M., Malin, G., Liss, P.S., Harbour, D.S. and Holligan, P.M. 1988. The seasonal variation of dimethylsulphide and dimethylsulfonio-propionate concentrations in near shore waters. *Limnology and Oceanography* 33: 364-375.
- Valiela, I. 1984. *Marine Ecological Processes*. Springer-Verlag, New York.
- Vinogradova, N.G. 1979a. Vertical zonation in the distribution of deep-sea benthic fauna in the ocean. *Deep-Sea Research* 8: 245-250.
- Vinogradova, N.G. 1979b. The geographical distribution of the abyssal and the hadal (ultra-abyssal) fauna in relation to vertical zonation of the oceans. *Sarsia* 64: 41-50.
- Visser, I.K.G., van Bresse, M.F., Barrett, T. and Osterhaus, A.D.M.E. 1993. Morbillivirus infections in aquatic mammals. *Veterinary Record* 24: 169-178.
- Walling, L. and Langton, R. 1994. Fishing, habitat disruption, and biodiversity loss. *Abstract, Ocean Sciences Meeting*, February.
- Weber, M. 1986. Federal marine fisheries management. In: DiSilvestro, R.L. (ed.), *Audubon Wildlife Report* 1986, 267-344 National Audubon Society, New York.
- Yodzis, P. 1988. The indeterminacy of ecological interactions, as perceived by perturbation experiments. *Ecology* 69: 508-515.
- Yodzis, P. 1994. Food webs, dynamics and perturbations. *Abstract at Canadian Society of Zoologists Meeting Bulletin* 25 (2): 111.
- ### 6.1.13 Lakes and rivers
- #### 6.1.13.1 Introduction
- Freshwater ecosystems (lakes and rivers) cover about 2.5×10^6 km², less than 2% of the Earth's surface (Wetzel 1983). Only 0.014% of Earth's water occurs in the soils, rivers and lakes of the biosphere (la Riviere 1989): freshwater lakes contain 1.25×10^5 km³ of water (Wetzel 1983), while rivers contain about 1.2×10^3 km³ (Wetzel 1983). Combined, lakes and rivers contain about 0.009% of Earth's water (Wetzel 1983). Fresh water is a crucial resource for terrestrial ecosystems and human life. In addition, extensive riparian areas associated with rivers and lakes include some of the most productive ecosystems of the landscape. The small pool of water available for life is distributed irregularly, and water often limits terrestrial productivity and economic development (Gleick 1993). Climate and geomorphology determine the global distribution and diversity of fresh waters. Diversity of fresh waters across landscapes depends in part on regional geochemistry and land use. At the species level, diversity is best known for fishes (8400 species, 40% of the world's total fish diversity; WCMC 1992) and aquatic vascular plants (1022 species, Sculthorpe 1967). Other groups are less well known. For example, phytoplankton diversity may be in the order of 10^5 species, but only 10% or so of these are known (WCMC 1992).
- Human impacts on biodiversity.* A few common drivers account for virtually all human impacts on freshwater biodiversity components (Moyle and Leidy 1992; National Research Council 1992; Allan and Flecker 1993). The most important and widespread of these are:
1. Habitat loss and degradation, driven mainly by land transformations such as agriculture and forestry (Naiman *et al.* 1993) and by direct transformations of freshwater bodies by large water projects (Allan and Flecker 1993).
 2. Species invasions and introductions (Lodge 1993).

3. Overharvesting (Moyle and Leidy 1992; Allan and Flecker 1993; Persson 1993).
4. Secondary effects, or cascading consequences of the loss of a native species, addition of an exotic, or overharvesting (Carpenter and Kitchell 1993).
5. Chemical pollution (National Research Council 1992).

Climate change is a potential driver with implications that are less certain than those of drivers 1–5 (Firth and Fisher 1991; Carpenter *et al.* 1992).

Methods for restoring damaged freshwater ecosystems are currently an area of active research (National Research Council 1992; Cooke *et al.* 1993). Rates of recovery are variable, and as a rule of thumb, are proportional to the water renewal time and the generation times of the longest-lived keystone organisms (see Box 5.2-1) (which are usually fishes or higher plants, including riparian trees). Water renewal times of the world's rivers are about 0.05 year and lake renewal times range up to 100 years (Wetzel 1983). Generation times of the keystone organisms are typically about a decade or longer.

Ecosystem consequences of impacts. Scientific certainty is relatively high for the following effects, except where noted otherwise.

6.1.13.2 Productivity, biomass, decomposition and nutrient cycling

Agriculture and construction activity promote erosion and nutrient loading which cause eutrophication of fresh waters. Input of sewage or household wastes can also result in eutrophication. Eutrophication involves increased primary production (especially of nuisance plants which reduce water quality; Cooke *et al.* 1993), increased storage of organic matter, and decreased decomposition due to anaerobiosis (National Research Council 1992). Dams can also increase primary production and storage of organic matter, while decreasing decomposition. In many cases exotic species, overharvesting, and their secondary effects have led to reduction of valuable fishery resources. Some kinds of chemical pollution can reduce fish stocks.

Eutrophication is generally associated with increased nutrient availability and retention in freshwater ecosystems (Wetzel 1983). Exotic species and overharvesting have complex effects on sediments and nutrients. Exotic macrophytes alter sediment accumulation rates and biogeochemistry (Lodge *et al.* 1988), while changes in fish communities affect recycling rates of limiting nutrients (Lamarra 1975; Kitchell *et al.* 1979) and can shift the limiting nutrient between nitrogen and phosphorus (Elser *et al.* 1988; Carpenter and Kitchell 1993). Species composition, size distribution, and migratory behaviour of zooplankton and fishes largely determine the rates and spatial patterns of nutrient recycling in lakes (Carpenter *et al.* 1992; Schindler *et al.* 1993).

6.1.13.3 Water distribution, balance and quality

Eutrophication reduces water quality (Peierls *et al.* 1991, National Research Council 1992). Exotic species, overexploitation, and their secondary consequences, can either improve or degrade water quality. For example, exploitation of large fishes leads to increases in the numbers of small zooplanktivorous fishes, decreases in herbivorous zooplankton, excess algal growth and reduced water quality (Carpenter and Kitchell 1993). On the other hand, invasions of the zebra mussel in Eurasia and North America may improve water quality by filtering particles from the water. In rivers, the impacts of invasion or over-exploitation may depend very much on spatial scale and the elapsed time since last major flood (Grimm 1992). Chemical pollution reduces water quality.

6.1.13.4 Atmospheric properties

Anoxia, which has significant impacts on aquatic life, is a common consequence of eutrophication that is in a sense 'atmospheric'. Regional climates are affected by large freshwater bodies (Firth and Fisher 1991). Scientific certainty is relatively low for the following atmospheric effects.

Carbon dioxide: Most lakes have high pCO_2 relative to the atmosphere and therefore outgas CO_2 (Cole *et al.* 1994). However, the direction of gas exchange with the atmosphere can be reversed by adding nutrients or by adding fish that eat herbivorous zooplankton (Schindler 1977; Cole *et al.* unpublished). In either case productivity rises and uses the excess CO_2 , decreasing pCO_2 in the lake and causing CO_2 to invade from the atmosphere.

Methane: Anoxic sediments of wetlands, lakes and ponds produce considerable amounts of CH_4 at rates linked to landscape biodiversity and the biogeography of beaver (Carpenter *et al.* 1992). Beaver distributions control water retention, soil hydration and oxygenation, nutrient cycling and gas flux over vast continental areas (Naiman *et al.* 1993).

6.1.13.5 Landscape and waterscape structure

For ecosystem consequences of habitat loss and degradation, see 6.1.13.2 and 6.1.13.3.

Landscape and waterscape structures have been altered by river canalization, damming, reservoir construction, sedimentation and saltwater encroachment. Land-use practices that remove or alter riparian vegetation decrease the inputs of large woody debris to rivers and lakes, affecting cover, food resources and spawning habitat of fishes (Maser and Sedell 1994). Impacts of these structural changes are relatively well known scientifically.

6.1.13.6 Biotic linkages and species interactions

Because of the insularity of fresh waters, species introductions, overharvesting and management actions targeted on particular species can have effects that ramify throughout freshwater systems, affecting production, decomposition and nutrient recycling as well as other species (Power 1990; Carpenter *et al.* 1992; National Research Council 1992; Carpenter and Kitchell 1993; Lodge 1993; Persson 1993). These changes may also affect wildlife and waterfowl that use freshwater systems for drinking, habitat and food. Biodiversity of functional guilds in fresh waters can stabilize process rates in stressed ecosystems (Schindler 1990). This resistance to stress depends on the capacity of more tolerant species to replace the contributions of less tolerant ones (Frost *et al.* 1994). The resilience of freshwater ecosystems (i.e. their rate of recovery from perturbation) depends in part on biotic linkages and species interactions (Cottingham and Carpenter 1994). However, there is considerable scientific uncertainty about the responses of freshwater systems to changes in biodiversity. Species invasions have had a wide range of impacts on freshwater communities and ecosystems (Lodge 1993). For a given freshwater system, the nature and consequences of future invasions by exotic species may be difficult to predict.

6.1.13.7 Microbial activities

Eutrophication affects microbial activity, the biodiversity of microbial metabolic pathways, and the biodiversity of biogeochemical pathways through anaerobiosis (Wetzel 1983). Effects of species introductions and overharvesting on microbial activity are poorly resolved (Porter *et al.* 1988). Pelagic microbial activity closely tracks the productivity of phytoplankton, which can be effected by food-web structure (Pace 1993). Chemical pollution can directly and selectively affect crucial biogeochemical transformations (e.g. nitrification and sulphate reduction; Schindler 1990).

6.1.13.8 Summary and relevance to human activities

Landscapes and freshwater bodies are linked by powerful feedbacks. Terrestrial landscape diversity affects fresh waters by determining rates of erosion, siltation and nutrient input. Freshwater bodies are a magnet for human settlement and use, and human activities determine landscape biodiversity in the watersheds. Freshwater bodies are insular habitats in which biotic interactions can have major consequences. Species introductions and fish manipulations have significantly changed productivity, nutrient cycling and physical characteristics of fresh waters, and the net consequence of land-use changes and species introductions has been to increase the similarity among fresh-water ecosystems through eutrophication and community change.

Humans need fresh water for drinking, fishing, industry, irrigation, recreation and transportation (Schindler and Bayley 1990). These uses are impaired by landscape changes that fill, eutrophicate or pollute lakes and rivers, and by exotic species introductions and overharvesting that displace or eliminate living resources. A diversity of freshwater systems on the landscape is valuable as insurance against fluctuations in the productivity of, or need for, particular freshwater resources. Freshwater ecosystem diversity requires a diversity of riparian vegetation that buffers freshwater systems from upland erosion or other disturbances. Species management is a component of many methods for restoring fresh waters that have become degraded (National Research Council 1992). Species diversity guarantees a range of options for restorations that are potentially self-sustaining and consequently less costly. A major reason for sustaining freshwater biodiversity is to preserve options for maintaining high-quality water resources under different environments in the future.

References

- Allan, J.D. and Flecker, A.S. 1993. Biodiversity conservation in running waters. *BioScience* 43: 32-43.
- Carpenter, S.R., Cottingham, K.L. and Schindler, D.E. 1992. Biotic feedbacks in lake phosphorus cycles. *Trends in Ecology and Evolution* 7: 332-336.
- Carpenter, S.R., Fisher, S.G., Grimm, N.B. and Kitchell, J.F. 1992. Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics* 23: 119-139.
- Carpenter, S.R., Frost, T.M., Kitchell, J.F. and Kratz, T.K. 1992. Species dynamics and global environmental change: a perspective from ecosystem experiments. In: Kareiva, P.M., Kingsolver, J. and Huey, R. (eds), *Biotic Interactions and Global Change*, 267-279. Sinauer Associates, Sunderland, Mass.
- Carpenter, S.R. and Kitchell, J.F. (eds), 1993. *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge.
- Cole, J.J., Caraco, N.F., Kling, G.W. and Kratz, T.K. 1994. Carbon dioxide supersaturation in the surface waters of lakes. *Science* 265: 1568-1570.
- Cooke, G.D., Welch, E. B., Peterson, S.A. and Newroth, P.R. 1993. *Restoration and Management of Lakes and Reservoirs*, 2nd edn. Lewis Publishers, Boca Raton, Fla.
- Cottingham, K.L. and Carpenter, S.R. 1994. Predictive indices of ecosystem resilience: consistency and testability in models of North Temperate lakes. *Ecology* 75: 2127-2138.
- Elser, J.J., Elser, M.M., MacKay, N.A. and Carpenter, S.R. 1988. Zooplankton-mediated transitions between N- and P-limited algal growth. *Limnology and Oceanography* 33: 1-14.
- Firth, P. and Fisher, S.G. 1991. *Climate Change and Freshwater Ecosystems*. Springer-Verlag, New York.
- Frost, T.M., Carpenter, S.R., Ives, A.R. and Kratz, T.K. 1994. Species compensation and complementarity in ecosystem function. In: Jones, C. and Lawton, J. (eds), *Linking Species and Ecosystems*. Chapman and Hall, New York.

- Gleick, P.H. 1993. *Water in Crisis: A guide to the world's fresh water resources*. Oxford Science Publications, London.
- Grimm, N.B. 1992. Implications of climate change for stream communities. In: Kareiva, P.M., Kingsolver, J. and Huey, R. (eds), *Biotic Interactions and Global Change*. 293-314. Sinauer Associates, Sunderland, Mass.
- Kitchell, J.F., O'Neill, R.V., Webb, D., Gallepp, G., Bartell, S.M., Koonce, J.F. and Ausmus, B.S. 1979. Consumer regulation of nutrient cycling. *BioScience* 29: 28-34.
- Lamarra, V. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. *Verh. Int. Verein. Limnol.* 19: 2461-2468.
- la Riviere, J.W.M. 1989. Threats to the world's water. *Scientific American*, September 1989: 80-94.
- Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* 8: 133-137.
- Lodge, D.M., Burko, J.W., Strayer, D., Meluck, J.M., Mittelbach, G.G., Howarth, R.W., Menge, B. and Titus, J.E. 1988. Spatial heterogeneity and habitat interactions in lake communities. In: Carpenter, S.R. (ed.), *Complex Interactions in Lake Communities*. 181-208. Springer-Verlag, New York.
- Maser, C. and Sedell, J.R. 1994. *From the Forest to the Sea: The ecology of wood in streams, rivers, estuaries and oceans*. St Lucie Press, Delray Beach, Fla.
- Moyle, P.B. and Leidy, R.A. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. In: Fiedler, P.L. and Jain, S.K. (eds), *Conservation Biology: The theory and practice of nature conservation, preservation, and management*. 128-169. Chapman and Hall, New York.
- Naiman, R.J., DeCamps, H. and Pollock, M. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3: 209-212.
- National Research Council 1992. *Restoration of Aquatic Ecosystems*. National Academy Press, Washington, DC.
- Pace, M.L. 1993. Heterotrophic microbial processes. In: Carpenter, S.R. and Kitchell, J.F. (eds), *The Trophic Cascade in Lakes*. 252-277. Cambridge University Press, Cambridge.
- Peierls, B.L., Caraco, N.F., Pace, M.L. and Cole, J.J. 1991. Human influence on river nitrogen. *Nature* 350: 386-387.
- Persson, L. 1993. Natural patterns of shifts in fish communities - mechanisms and constraints on the sustenance of mass removals. In: Cox, I.G. (ed.), *Rehabilitation of Freshwater Fisheries*. 421-434. Blackwell, London.
- Porter, K.G., Paerl, H., Hodson, R., Pace, M., Prisco, J., Riemann, B., Scavia, D. and Stockner, J. 1988. Microbial interactions in lake food webs. In: Carpenter, S.R. (ed.), *Complex Interactions in Lake Communities*. 209-228. Springer-Verlag, Berlin.
- Power, M.E. 1990. Effects of fish in river food webs. *Science* 250: 411-415.
- Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes: natural mechanisms compensate for deficiencies of nitrogen and carbon in eutrophied lakes. *Science* 195: 260-262.
- Schindler, D.W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* 57: 25-41.
- Schindler, D.W. and Bayley, S.E. 1990. Fresh waters in cycle. In: Mungall, C. and McLaren, D.J. (eds), *Planet Under Stress*. 149-167. Oxford University Press, Oxford.
- Schindler, D.W., Kitchell, J.F., He, X., Carpenter, S.R., Hodgson, J.R. and Cottingham, K.L. 1993. Food web structure and phosphorus cycling in lakes. *Transactions of the American Fisheries Society* 122: 756-772.
- Sculthorpe, C.D. 1967. *The Biology of Aquatic Vascular Plants*. Edward Arnold, London.
- World Conservation Monitoring Centre 1992. *Global Biodiversity: Status of the earth's living resources*. Chapman and Hall, London.
- Wetzel, R.G. 1983. *Limnology*. Saunders, Philadelphia, Pa.

6.2 Cross-biome comparisons

6.2.1 Productive capacity and biomass accumulation

6.2.1.1 Introduction

The response of ecosystem net primary production (plant growth) to biodiversity has two major components. One reflects the role of diversity in providing genotypes or species adapted to the full range of habitats within a biome, over the long term, including year-to-year climate variation and cycles of disturbance and recovery. The other concerns the response of production to diversity in a single year and at a single site. Because the relevant evidence, the underlying principles, and the feasible approaches for studying these two components are quite different, they are treated here in sequence.

Here, when referring to biodiversity, we generally refer to genetic and species diversity of the primary producers with the dominant life-form, i.e. trees in forests, grasses in grasslands, macro-algae in nearshore habitats and so on. Whole ecosystem biodiversity has additional dimensions, some of which may be critical determinants of production. For example, a relatively uncommon insect that preys on insect herbivores can have a major impact on production. At present, general tools for identifying species with a functional impact much larger than their biomass are not available (see Section 5.2.2). A focus on consequences of the diversity of primary producers in the dominant life form provides a starting point for understanding the functional role of biodiversity, but it clearly does not address the entire range of potentially important interactions.

6.2.1.2 Lessons from agriculture

Modern agriculture and plantation forestry are based on the premise that low-diversity ecosystems can be highly productive. While this premise is broadly validated in intensively managed ecosystems, the experience of agriculture highlights the critical sensitivity of low-diversity ecosystems to variation in climate and soils as well as outbreaks of pests and pathogens. Across all of the world's biomes, temporal and spatial variation in climate, soils, disturbance (e.g. fire, hurricanes) and biotic influences (e.g. pests, pathogens, dispersers, pollinators) are the rule rather than the exception. This variability,

much of which modern practices in agriculture and forestry are designed to suppress, establishes important constraints on the productivity of low-diversity natural ecosystems, especially over long time periods.

Lessons from agriculture provide useful guideposts for understanding the role of biodiversity in regulating production. First, when the genetic diversity of agricultural crops is severely limited, as when single hybrids are planted over large areas, pests and pathogens can be devastating. The outbreak of *Helminthosporium maydis* on CMS-T hybrid corn in 1969 and 1970 is an extreme example (Williams and Levings 1992). Second, maintaining productivity across a mixture of good and bad years is one of the most common motivations for multi-crop agriculture (Francis 1986; Vandermeer 1988; Swift and Anderson 1993). Third, progressive losses of productivity in some intensively farmed regions demonstrate that high productivity in low diversity ecosystems may be transient, depleting the accumulated capital of soil nutrients rather than operating on the sustainable supply.

6.2.1.3 Habitat variation in space and time

The role of biodiversity in modulating the sensitivity of production in natural ecosystems to variation in climate, soils and biotic factors is far from completely understood, but several lines of evidence establish its importance. Some of the evidence is very direct. For example, Tilman and Downing (1994) observed that biomass production was less drought-sensitive in high-diversity grassland plots than in low-diversity plots in the American Midwest (see Section 6.1.7.3). Year-to-year variations in climate can strongly favour different species in different years (Hobbs and Mooney 1991), a pattern that appears to result in higher productivity than occurs with continuous dominance by a single species.

Much of the evidence for the links between production and the biodiversity sufficient to provide species that thrive across a biome and over time is indirect and comes more from studies of pattern than of process. For example, vegetation differences between north- and south-facing slopes, drier upland and moister lowland sites, or sites on different soil types, are very common (Chabot and Mooney 1985). Whenever biodiversity falls below the minimum representing the suite of species or genotypes best adapted to each of the major habitat types within a biome, the overall vegetation becomes less well adapted to local conditions. With variation in slope, aspect, elevation, soils, moisture, temperature and wind, most biomes include several habitats that support distinctive local ecosystems. While these broad patterns do not necessarily maximize production in any particular year, they consistently yield solid compromises between short-term productivity and long-term persistence (Grime 1979; Chapin 1980). In

general, a single species does not thrive over the entire range of habitats in a biome. The uniform dominance of the tree *Metrosideros polymorpha* in natural Hawaiian habitats is an exception, though the recent history of biological invasions in Hawaii (Vitousek *et al.* 1987) points to the sensitivity of this pattern. Except in intensively managed systems, parallel changes in the habitat and in functional characteristics of the dominant plants make it likely that production increases with biodiversity, at least until each major habitat within a biome is occupied by least one species that thrives in it (Figure 6.2-1).

In many biomes, the vegetation on a patch depends on the time since disturbance, and the distinctions between early successional and late successional species are often striking (Tilman 1988). The failure of late successional species to thrive in early successional habitats and vice versa has been tested in many cases and supported experimentally in some, but not all, studies (e.g. Chapin *et al.* 1994). To the extent that the dominant species of one successional stage fail to thrive in others, production tends to increase with biodiversity whenever the increased biodiversity represents a specialist on an empty successional stage or time since disturbance (Figure 6.2-1).

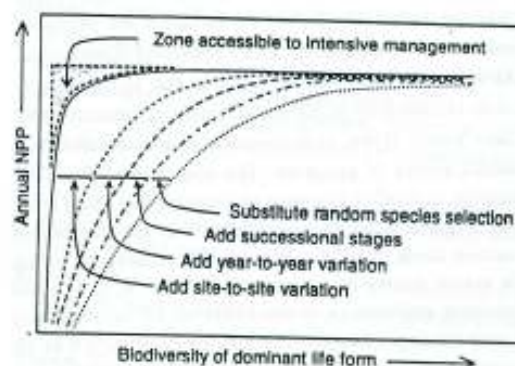


Figure 6.2-1: A conceptual schematic of the response of average annual net primary production (NPP) to the biodiversity of plant species or genotypes in the dominant life-form, showing how mechanisms are likely to combine. The basic idea is that, at one site and in one year, low-diversity ecosystems subjected to intensive management can achieve nearly the same NPP as highly diverse ecosystems. In real biomes, however, spatial variation in climate and resources, temporal variation in climate, and successional dynamics related to disturbance history all increase the range of biodiversity over which NPP changes. NPP of any suite of species not skillfully chosen to provide plants adapted to the full range of habitats probably saturates even more slowly with biodiversity.

Vegetation production and persistence often reflect a balance between highly competitive species that use resources efficiently, and less competitive species that effectively colonize disturbed sites (Tilman 1993). A loss