

# Marine biodiversity: patterns, threats and conservation needs

JOHN S. GRAY

*Biological Institute, University of Oslo, Pb 1064 Blindern, 0316 Oslo, Norway*

Received 7 November 1995; revised and accepted 3 February 1996

Marine biodiversity is higher in benthic rather than pelagic systems, and in coasts rather than the open ocean since there is a greater range of habitats near the coast. The highest species diversity occurs in the Indonesian archipelago and decreases radially from there. The terrestrial pattern of increasing diversity from poles to tropics occurs from the Arctic to the tropics but does not seem to occur in the southern hemisphere where diversity is high at high latitudes. Losses of marine diversity are highest in coastal areas largely as a result of conflicting uses of coastal habitats. The best way to conserve marine diversity is to conserve habitat and landscape diversity in the coastal area. Marine protected areas are only a part of the conservation strategy needed. It is suggested that a framework for coastal conservation is integrated coastal area management where one of the primary goals is sustainable use of coastal biodiversity.

*Keywords:* patterns of diversity; threats; habitat and landscape conservation; integrated coastal area management.

## Introduction

Although there are a number of general reviews of biodiversity, such as the Global Biodiversity Assessment (Heywood and Watson, 1995) and Huston's (1994) more theoretical approach, there is no concise synthesis of marine biodiversity in relation to conservation needs. Short general reviews cover coastal-zone biodiversity patterns (Ray, 1991), deep sea benthic diversity (Grassle, 1991), marine benthic biodiversity research (Lambshead, 1993), marine functional diversity (Steele, 1991), coral reefs (Jackson, 1991), foraminifera (Buzas and Culver, 1991), fish diversity in the Caribbean (Robbins, 1991) and whale and dolphin diversity (Perrin, 1991).

Angel (1993) reviews possible causes for the patterns of the pelagic biodiversity in the ocean and Suchanek (1994) temperate coastal marine biodiversity showing that temperate systems are among the most productive and diverse. Coral reefs, with their associated flora and fauna, although highly diverse, are still relatively poorly described and their functioning is not well understood (Sebens, 1994). However, not all coral reefs are highly diverse, inshore shallow habitats on the Pacific rim have physically tolerant species to elevated temperatures and surface irradiance (B.E. Brown, pers. comm.) and are threatened by exploitation, dredging and removal. Such low diversity areas are also in need of conservation. Rao (1991) has reviewed the threats to mangroves and states the objectives for their conservation as: maintenance of genetic resources, sustainable utilization and conservation or re-creation of suitable habitats.

The research agenda for biodiversity has been fully expounded by Solbrig (1991) and Grassle *et al.* (1991), and more recently for marine biodiversity by the US National

Research Council (1995). These set out priority research problems yet do not deal with conservation aspects of marine biodiversity. The purpose of this paper is to give a concise review of marine biodiversity, explaining why it is different from terrestrial and freshwater diversity, analyse the threats and suggest conservation needs.

### **What is biodiversity?**

At the UN Conference on Environment and Development in Rio in 1992 the Convention on Biological Diversity was concluded. Subsequently it has been signed by the requisite number of nations and has now come into effect. In the Convention, *biological diversity* is defined as: 'The variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species and of ecosystems'.

Biological diversity is often written in shorthand as 'biodiversity', and here the two terms are taken to be synonymous.

#### *Genetic diversity*

The most basic level of biological diversity is that found within a species and is known as *genetic diversity*. Genetic diversity encompasses the variation among individuals within a population in their genetic make-up and the genetic variation among populations. Each species consists of one or more populations of individuals. A population is usually defined as a group of individuals that can interbreed and, if sexually reproducing, can interchange genetic material. Different populations tend to diverge genetically due to their having limited genetic mixing or mutations, natural selection, genetic drift and the accumulation of selectively neutral mutations. Thus, there are genetic differences both among individuals and among populations. Populations with higher genetic diversity are more likely to have some individuals that can withstand environmental change and thereby pass on their genes to the next generation, (Nevo *et al.*, 1987). On an evolutionary time scale, (over many generations) genetic diversity is higher in species which characterize unstable, stressed environments when compared with counterparts from more stable environments (Nevo *et al.*, 1984). However, on an ecological time scale (few generations), stress reduces genetic diversity. Gillespie and Guttman (1988) showed that long-term exposure to contaminants decreased genetic diversity and the remaining population was more vulnerable to extinction. Alberte *et al.* (1994) have shown that stressed eelgrass has lower genetic diversity than non-stressed populations. Commercial fishing, concentrating on specific size ranges, has significantly altered of the genetic composition of populations (Elliott and Ward, 1992).

In general, marine species have higher genetic diversity than freshwater and terrestrial species. In a comparative study of fish Ward *et al.* (1994) showed that average heterozygosity was similar in marine and freshwater species subpopulations, but was considerably less in freshwater species. High genetic diversity is found in marine algae, (Wood, 1989) and *Pinctada margaritifera* an exploited tropical bivalve (Durand and Blanc, 1988). Elliott and Ward (1992) found that a minimum of only 200 migrants per year were enough to maintain the genetic diversity of the Orange Roughy (*Hoplostethus atlanticus*) which suggests that marine populations probably exchange between 10 and 100 times more migrants per generation than freshwater species. Not all marine populations have high numbers and Scudder (1989) argues that for marginal populations the best way to

maintain genetic (and species) diversity is by 'marginal habitat conservation'. This is an alternative strategy to the conservation of high biodiversity 'hot spots' advocated by some.

Much work has been done on the genetics of species used in aquaculture: on clams (Bushek and Allen, 1989); Manila clam (Mattoccia *et al.*, 1991); oysters (Blanc and Jaziri, 1990; Hedgecock and Sly, 1990; Hedgecock *et al.*, 1991; Jaziri *et al.*, 1987; Sly and Hedgecock, 1989); penaid shrimps (Qiu, 1991; Benzie *et al.*, 1992); salmonids (Gall *et al.*, 1992); and the Orange Roughy (Elliott and Ward, 1992). Doyle *et al.* (1991) have reviewed genetic aspects of aquaculture and conclude that current practices lead to reductions in genetic diversity and maintenance of many breeds and meta-populations of marine species is needed (see also reviews by Cataudella and Crosetti, 1993, and Blanc and Bonhomme, 1987).

Grassle (1991) argues that a considerable proportion of the genetic diversity of the planet is probably found in deep sea organisms and recommends genetic studies of hydrothermal vent fauna which are naturally tolerant of high concentrations of toxic elements produced by the vents.

### *Species diversity*

The most common usage of diversity is the number of species found in a given area, *species diversity*. Most ecologists would regard a community comprising of 50 individuals of species A and 50 of species B as more diverse than a community comprising 99 individuals of species A and 1 individual of B. Thus, in addition to the number of species in a given area diversity indices have been proposed that take into account the distribution of individuals among species (see Magurran, 1988, for a review).

The number of species currently described on Earth is between 1.4 and 1.7 million (Stork, 1988), but the Global Diversity Assessment suggests a conservative estimate of 1.75 million (Heywood and Watson, 1995). However, this figure does not include microbial species. Little is known about microbial diversity in general. New genetic techniques will change this. For example, Giovannoni *et al.* (1990) using ribosomal RNA techniques found a completely novel group of bacteria in the Sargasso Sea.

On land there are more species known than in the sea. This is due largely to the extraordinary diversity of beetles (Coleoptera); 400 000 species are described (Heywood and Watson, 1995). Recently, in a highly controversial paper, Grassle and Maciolek (1992) have suggested that there may be 10 million undescribed species in the deep sea. Briggs (1991) and May (1992) disagree with the methods used and May suggests that a more realistic estimate may be around 500 000 undescribed deep sea species. Nevertheless, even this lower figure would be a substantial increase in the approximate figure of 300 000 known marine species.

Over geological time there has been a large change in the ratios of orders of families to genera to species. A rapid increase occurred in higher taxa (orders and families) until the Ordovician when diversity levelled off. In the Permian, some 50% of marine families became extinct (Raup, 1979; Sepkoski, 1979, 1984, 1991). The number of species has increased enormously in recent geological time more than doubling compared to those present 100 million years ago (Signor, 1994).

Most of marine species diversity is benthic rather than pelagic (Angel, 1993). This is a consequence of the fact that the marine fauna originated in benthic sediments. The pelagic realm has an enormous volume compared with the inhabitable part of the benthic realm. Yet there are only 3500–4500 species of phytoplankton (Sournia and Chretiennot-Dinet,

1991) compared with the 250 000 species of flowering plants on land. Angel estimates that there are probably only 1200 oceanic fish species against 13 000 coastal species. In the pelagic realm, diversity is higher in coastal rather than oceanic areas (Angel, 1993) and therefore, efforts should be concentrated in coastal areas.

Another highly important aspect of species diversity is endemism, (that is the species occurring in a restricted locality). The Antarctic has a higher degree of endemism than the Arctic. In the Red Sea 90% of some groups of fishes are endemic. Overall however, only 17% of Red Sea fishes are endemic (Sheppard, 1994). In a survey of 799 pan-tropical fish species Roberts *et al.* (in Sheppard, 1994) showed that 17% occupied only one grid square (223 × 223 km). In the Indian Ocean, of the 482 coral species recorded, 27% occur only at one site (Sheppard, 1994) and of the 1200 species of echinoderms found at 16 sites 47% occurred at only one site (Clark and Rowe, 1971). High degrees of endemism pose particularly severe problems for development of conservation strategies. Questions that need to be raised are: are all species equally important for conservation purposes? Do some endemic species play more significant roles than others in the structuring or functioning of the habitat concerned?

The urgency of the need for assessments of species diversity has led to the development of a number of new 'rapid assessment' techniques. Non-specialists have been trained in a few days to sort samples into taxonomic groups with a high degree of precision (Oliver and Beattie, 1993). While the identification of the actual species must be done later by specialists, these techniques allow rapid assessment of the species diversity of areas that have not been fully studied. These methods need to be further tested in tropical marine areas but show great promise.

#### *Phyletic diversity*

In the marine domain there are more animal phyla than on land. Thirty-five phyla are marine and of these 14 are endemic whereas only 14 occur in freshwater, where none are endemic, 11 are terrestrial, with one phylum being endemic and 15 phyla are symbiotic with four being endemic (Briggs, 1994; Ray and Grassle, 1991). This figure includes the newly described phylum Cyclophora found in the gills of the Norway lobster (Funch and Kristensen, 1995). Thus *phyletic diversity* is highest in the sea. Of the 35 marine phyla only 11 are represented in the pelagic realm (Angel, 1993); most phyla occur in the benthos, which is the archetypal habitat. Despite the fact that there are some rare phyla containing only a few species, it is extremely unlikely that present environmental threats will lead to reduction of phyletic diversity.

#### *Functional diversity*

Functional diversity is the range of functions that are performed by organisms in a system. The species within a habitat or community can be divided into different functional types such as feeding guilds or plant growth forms or into functionally similar taxa such as suspension feeders or deposit feeders. Functionally similar species may be from quite different taxonomic entities.

One of the major current topics of debate is that of functional redundancy (di Castri and Younes, 1990; Walker, 1991) where it is suggested that there are more species present in communities than are needed for efficient biogeochemical and trophic functions. Recent data, however, show that this is not the case and the higher the number of species in a community the greater the efficiency of biogeochemical processes (Naeem *et al.*, 1994;

Tilman and Downing, 1994). Such experiments, however, have not been done in the marine environment.

Steele (1991) defines functional diversity in a different and idiosyncratic way as ‘the variety of different responses to environmental change, especially the diverse space and time scales with which organisms react to each other and to the environment’. Steele’s main point is that marine organisms are closely linked to physical processes at decadal scales whereas on land undisturbed systems change at scales of centuries to millennia.

#### *Community and ecosystem diversity*

Biodiversity can also be considered at levels other than that of taxonomic organization, for example at the level of the community or/and ecosystem. In fact, when biodiversity is measured quantitatively it is usually as the number of species or the value of a diversity index for a given community or area of habitat.

A great ecological debate started in the 1930s on whether or not species occurred in distinct groups which could be classified as communities. Today the generally accepted view is that species are distributed along environmental gradients in approximately log-normal abundance patterns (Mills, 1969). However, interactions between species (predator–prey, commensal, symbiotic and competitive) lead to there being co-occurring groups of species under given environmental conditions. Thus communities are convenient groupings of species which merge gradually into other groupings unless there are sharp boundaries in environmental conditions. Recently, another term has found favour, assemblage, which is a more neutral term and does not imply the tight inter-species organization that is implied in the term ‘community’, with its anthropomorphic connotations. The diversity of a *community* (or assemblage) is often measured.

In the Biodiversity Convention an ecosystem is defined as ‘A dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit’.

Terms such as ‘estuarine ecosystem’, or ‘coral reef ecosystem’ are used commonly. Yet the boundaries of such systems are loosely defined and are especially difficult to demarcate in the sea since the fluxes of energy and material within and exported from a system are rarely known. It is perhaps significant that in the Research Agenda for Biodiversity (Solbrig, 1991) no mention is made of ecosystem diversity. Huston (1994) in his book uses the terms ‘community’ and ‘ecosystem’ interchangeably, and a recent textbook on ecology (Begon *et al.*, 1990) states that ‘Traditionally ...the ecosystem... comprises the biological community together with its physical environment. However, while the distinction between community and ecosystem may be helpful, in some ways the implication that communities and ecosystems can be studied as separate entities is wrong. No ecological system, whether individual, population or community, can be studied in isolation from the environment in which it exists. Thus we will not distinguish a separate ecosystem level of organization’. Also ‘...knowledge of the role that communities play in biogeochemical cycling is essential if we are to understand and combat the effects of acid rain, or increasing levels of atmospheric carbon dioxide or radioactivity...’. Accordingly, I will not use the term ‘ecosystem diversity’ here.

#### *Habitat diversity*

The most frequently used quantitative measure of biodiversity is for a given area rather than for a given biological community. In ecological terms, physical areas and the biotic

components they contain are termed habitats. *Habitat diversity* is a more useful term than that of ecosystem diversity since habitats are easy to envisage (e.g. a mangrove forest, a coral reef, an estuary). Furthermore, habitats often have clear boundaries. Habitats have been termed 'the template for ecology' (Southwood, 1977).

There are strong relationships between sampling scale and the processes that influence diversity (Huston, 1994). At small scales all species are presumed to interact with each other and to be competing for similar limiting resources. Ecologists have called this *within-habitat* (or alpha) *diversity* (Fisher *et al.*, 1943; Whittaker, 1960, 1967). At slightly larger scales habitat and/or community boundaries are crossed and sampling covers more than one habitat or community. This scale has been called *between-habitat* (or beta) *diversity* (Whittaker, 1960, 1975, 1976). At an even larger scale (regional scale) where evolutionary rather than ecological processes operate the pattern has been called gamma diversity or, more recently, 'landscape diversity' (Whittaker, 1960; Cody, 1986). *Landscape diversity* can be defined as the mosaic of habitats over larger scales often hundreds of kilometres. Franklin (1993) discusses landscape diversity in relation to biodiversity conservation. (Ray (1991) calls the marine equivalents seascapes). Much attention has been given to ways of conserving landscape diversity on land. Clearly, a given habitat can be maintained but landscape diversity can be reduced if the mosaic of habitats is altered. It is clearly important, therefore, to specify what scale (and hence type of diversity) is being studied.

In an important recent paper Tuomisto *et al.* (1995) have shown from an analysis of satellite images followed by extensive ground truthing that beta diversity has been greatly underestimated in tropical rain forests. Since the between habitat (beta) diversity has been underestimated then the landscape diversity will also be underestimated. The authors point out that the conservation value of different areas depends on a sound estimate of between habitat and landscape diversity. This is a topic that will need thorough consideration and discussion in any future conservation strategy.

Within coastal areas there are a wide variety of habitats with known high species diversity such as sea grass beds (McRoy, 1981), coastal sedimentary habitats (Gray, 1994), mangal (MacNae, 1968; Walsh, 1974) and coral reefs (Loya, 1972; Huston, 1985; Shepard, 1980). Ray and Gregg (1991) have analysed the coastal wetland areas of Virginia and the Carolinas, USA, and conclude that there are large differences in the proportions of salt and freshwater marshes, forest/scrub-shrub and tidal flat areas which lead to differences in biodiversity between the two areas. Ray classifies marine habitats into 20 categories as a basis for characterizing coastal areas, (Ray, 1991). Coral reefs are themselves highly variable with large differences between the reef flat, reef crest and reef slope both in coral and associated species and each component is probably best considered as between habitat  $\beta$  diversity. Hard rocky surfaces have a rich encrusting flora and fauna, for example in clumps of mussels Suchanek (1992) found over 300 species in Washington, USA, and within kelp holdfasts (*Laminaria digitata*) in boreal areas Moore (1973) found over 350 species on the species-poor East Coast of UK.

Yet it is not only the high diversity areas that are in need of conservation. It is often in low diversity areas that productivity is highest and humans exploit these systems (e.g. upwelling areas and estuaries) for food resources and other uses. Estuaries with low species numbers due to salinity stress are habitats that are under severe threats from urbanisation and industrialization. Arctic marine systems have relatively low diversity and there are low-diversity coral habitats that are subject to a variety of threats. Thus one cannot set priorities for marine diversity conservation based simply on habitats with high diversity.

Ray (1991) argues cogently that biodiversity assessments need to be made at the community, habitat and landscape levels if we are to predict changes over time. In a review (by WWF, IUCN and UNEP) of ways of conserving genetic diversity of freshwater fish it was recommended that the best way to conserve species diversity is to conserve habitats (Nyman, 1991). Ogden (1988) and Ray and Ray (1992) give examples showing species that use a coral reef during the day and migrate to seagrass beds or mangroves at night. Often sea grass beds are an integral part of the coral reef system. Thus it is the mosaic of habitats, that must be protected if a complete protection of biodiversity is to be achieved. It is primarily the loss of habitats that leads to the loss of both genetic and species diversity.

### **What are the characteristic patterns of marine biodiversity?**

#### *The latitudinal pattern of diversity*

In terrestrial systems species, genera and families increase in diversity from poles to tropics. A good example is that of tree species diversity where the highest diversity values are shown in tropical rain forests, (Pianka, 1983; Woodward, 1987).

In the marine domain, there is an apparent increase in species diversity of hard substratum epifauna from the Arctic to tropics (Thorson, 1957; Kendall and Aschan, 1993). The Arctic is much younger and has low biodiversity and low endemism compared with the older Antarctic (Dayton, 1994). The longer period of geographic isolation of the Antarctic is also important for biodiversity generation. Production processes also differ and whereas the Arctic is dominated by many commercial fish species the Antarctic is characterized by invertebrates (krill and squid) which support birds and mammals and only a small fishery.

Stehli and Wells 1971 showed that bivalve molluscs at species, genus and family levels show increased diversity towards the tropics in the Indo-Pacific. Recent data from the deep sea (Etter *et al.*, 1992) purports to confirm this principle. However, in the latter data there is much scatter and if one removes the data from the Norwegian Sea, which has low diversity the trends are far less clear, if evident at all. The Norwegian Sea is a recently glaciated area and it is therefore not surprising that diversity is low. Not all groups show such trends. Seaweed (macroalgal) diversity is higher in temperate latitudes than the tropics and lowest at the poles (Silva, 1992).

In the Southern hemisphere, the pole-to-tropic gradient is far less clear since the Antarctic has high diversity for many taxa (Clarke, 1992). Data from Australia show that in a coastal area 800 species have been recorded from just 10 m<sup>2</sup> of sediment in Bass Strait and 700 species occur in sediments of Port Phillip Bay (Poore and Wilson, 1993). These values are as high as the highest values for soft sediments found anywhere.

In summary, it seems probable that there is a cline of increasing diversity from the Arctic to the tropics but the cline from the Antarctic to the tropics is far less well established if it occurs at all. There is clearly a need to better document diversity patterns in other areas of the Southern hemisphere such as the African and American continents.

#### *The longitudinal pattern of tropical diversity*

Probably the most well-known diversity pattern in the marine domain is that of coral genera and species, which show highest values in the Indonesian archipelago and falling values radiating westwards across the Pacific Ocean (Stehli and Wells, 1971). Across the

Indian Ocean diversity decreases irregularly from the high diversity epicentre, dipping and then rising in the Red Sea and Africa in some groups and with lowest diversity in the Caribbean. Similar patterns have been shown for mangroves, and gastropod snails (see Huston, 1994). It appears that the Indonesian archipelago is the 'epicentre' for evolution of marine tropical biodiversity (Veron, 1995). Using rRNA techniques Palumbi (1995) has recently shown that species have indeed radiated out into the Indo-Pacific region from the centre.

The reason for this high level of diversity in the Indo-Pacific region is thought not to be solely the result of a long period of evolutionary stability, but rather due to the fact that there is a large diversity of types of islands and archipelagos which differ in size, in their geological history and in distance from sources of colonising species. There have been periods of isolation over evolutionary time, which have given rise to allopatric speciation, (speciation caused by the erection of physical boundaries between populations) followed by periods of reunification which has given sympatric speciation (speciation within a population, usually caused by competitive interactions). Throughout geological time there have been massive extinctions followed by rapid evolution and speciation (Kauffman and Fagerstrom in Huston, 1994).

#### *Other marine biodiversity patterns*

Another pattern that has received much attention is that in soft sediments with increasing diversity from shallow areas to the deep sea (Sanders, 1968). This has recently been confirmed by Grassle and Maciolek (1993) in a study along a transect of 176 km off the US East coast at depths of between 1500 m and 2100 m. A total of 798 species was found among 90 677 individuals from an area sampled of 21 m<sup>2</sup>.

It has been assumed that the data presented by Sanders are representative of a general pattern of low species diversity in shallow coastal areas. Surprisingly no-one has questioned whether or not this is the case. This is all the more remarkable since there are very large numbers of studies done in coastal areas. Using data obtained from the Norwegian continental shelf in the North Sea, Gray (1994) found over a distance of 1200 km a total of 620 species from 39 582 individuals. These data together with those of Poore and Wilson (1993) raise the question of whether coastal biodiversity shows values as high as that of the deep sea. More quantitative information from coastal areas is needed particularly from tropical coasts and from the Southern hemisphere.

#### **Threats to marine biodiversity**

With the exception of ocean dumping and UV-B radiation there are probably few human activities posing major threats to oceanic diversity. However, long-transported materials enter the open ocean system and there are concerns about effects of organochlorine compounds on planktonic and benthic systems. The oceanic system is open and continuous and it is unlikely that contaminants will lead to measurable effects on diversity, such as local or regional extinctions. Organisms that live near tectonically active zones where plates are diverging have high diversity and naturally high levels of heavy metals and derive their primary energy from chemosynthesis rather than from sedimenting products of photosynthesis.

Most of the threats to biodiversity are in the coastal zone and are a direct result of human population and demographic trends. The world population has more than doubled

since World War II and is expected to increase from 5.5 billion in 1992 to 8.5 billion by 2025 (UN Population Bureau, Anon, 1993). More important however, are the demographic trends of increased population densities in coastal areas. It is estimated that 67% of the global population lives on the coast or within 60 km of the coast and the percentage is increasing (Hammond, 1992). Within 30 years this population will double (Norse, 1994). Furthermore, many of the largest cities in the world, where population growth rates are highest, are near the coast (e.g. Sao Paulo, Shanghai, Hong Kong, Manila, Jakarta). These burgeoning populations increase pressures on utilization of resources in coastal areas and in addition lead to habitat degradation, fragmentation and destruction. This is a special problem in Indonesia where the highest marine diversity is found near to centres of high human population growth.

There are a number of recent reviews of threats to coastal systems (Lundin and Linden, 1993; Fluharty, 1994; Norse 1994; Sebens 1994; Suchanek 1994). These threats are: habitat loss; global climate change; overexploitation and other effects of fishing; pollution (including direct and indirect effects of inorganic and organic chemicals; eutrophication and related problems such as pathogenic bacteria and algal toxins; radionuclides); species introductions/invasions; water-shed alteration and physical alterations of coasts; tourism; marine litter; and the fact that humans have little perception of the oceans and their marine life. The threats are frequently interlinked. All the reviews agree that the most critical threat is habitat loss. This is echoed in the recent Global Biodiversity Assessment (Heywood and Watson, 1995) which states (p. 920) 'The most effective way to conserve biodiversity, by almost any reckoning is to prevent the conversion or degradation of habitat'.

#### *Habitat degradation, fragmentation and loss*

Complete loss of habitat is the most serious threat to marine biodiversity, especially if contiguous but different habitats forming landscape diversity are lost. Southeast Asia contains 30% of the world's coral reefs. Based on studies of coral cover, which is not a good indicator of reef condition, Wilkinson and Chou (1993) claim that 60% are already destroyed or on the verge of destruction and make the prediction that unless drastic action is taken immediately most of the reefs will be eradicated during the next 40 years. The loss of the reefs is due to increased sedimentation, overexploitation by dynamite and chemical fishing and by sewage pollution. In an analysis of data on coral reefs in Japan Veron (1992) found that over 37% of species are at some risk of regional extinction and 29% at a substantial risk of extinction.

In Sri Lanka reef cover is declining by 10% annually (Rajasuriya, 1993) and in the Gulf of Thailand by 20% annually, (ASEAN, 1992). In the Philippines studies show that almost 70% of 735 studied reefs are seriously damaged (Gomez *et al.*, 1990; Lundin and Linden, 1993) and in Eastern Indonesia 80% of the reefs have been damaged by dynamite fishing (Lundin and Linden, 1993). There is reason to believe that similar damage is occurring in East Africa and in the Caribbean. Recently the US State Department (1995) has launched an International Coral Reef Initiative which is endorsed by scientists, policy makers, donor organizations and national representatives. This concludes that 'human activity is the primary agent of degradation' of reefs either from direct impacts or by inadequate planning and management of coastal land and upland activities. All these impacts are exacerbated by human population growth, increased pollution.

Mangrove forest destruction is occurring on an equally alarming rate. Indonesia has by far the largest areas of mangroves (21 011 km<sup>2</sup>) and 45% have been lost and the rates of loss are increasing rapidly, (Primavera, 1991). Data from the World Resources Institute (Hammond, 1992; Heywood and Watson, 1995) show losses of between 40 and 70% in Africa, almost 70% in Asia, 85% in India and 87% in Thailand. In both the Philippines and Ecuador over 70% of the forest has been destroyed to make way for shrimp farms, (Primavera 1991). The primary source of shrimp larvae to stock the farm is the mangrove forest and thus the long-term sustainability of farms is jeopardised by destruction of mangrove. Other problems such as soil erosion often accompany mangrove destruction.

While losses of coral reefs and mangrove habitats are probably the most significant in terms of losses of biodiversity it should not be forgotten that other critical coastal habitats are also disappearing. Wetland areas, estuaries and seagrass beds are known to be key nursery areas for coastal fisheries and yet are being destroyed rapidly without there being full ecological and economical appraisal of the consequences even in developed countries. Estuaries pose particular problems globally since there are often conflicting interests such as industrial development, shipping and associated harbour development, fishing, tourism and the needs for conservation.

There are few published data on the loss of landscape diversity in the marine environment (e.g. the mosaic of wetland, estuary and sand and mud flats as a combined system). It is relatively straightforward to record and document habitat loss on land and in shallow and/or tidal areas using for example remote sensing and Geographical Information Systems (GIS). Regional scale assessments are urgently needed.

Biodiversity will also be lost if habitats become degraded so that species can no longer survive. Assessing the degree of degradation needs monitoring over space and time and this is a major task. GESAMP has recently (1995a) produced a report on Biological Indicators and their Use in the Measurement of the Condition of the Marine Environment. This report describes the indicators that can be used to measure exposure to contaminants and their effects, sets out a tiered approach for a field assessment programme and discusses sampling designs which are appropriate to the measurement of the condition of a given habitat or area and finally discusses the types of managerial action that are needed to complete an assessment.

Another severe problem is that, while habitats may be ostensibly maintained, they become divided into small fragments. There is a large ecological literature on these so-called 'habitat islands' with theories of maintenance and loss of diversity within such islands (MacArthur and Wilson, 1967; Williamson, 1983). Huston (1994) discusses this in a general context. Small 'habitat islands' that are remote from the main pool of species have higher rates of species extinctions and lower immigration rates than larger 'habitat islands' or 'habitat islands' that are nearer the main pool of species. Fragmentation of habitats is expected to lead to losses of species diversity. However, in marine coastal areas few studies have been done that quantify species loss with loss of a given area of habitat.

Horn (1975) and Connell (1978) have shown that diversity is often higher in habitats that are subjected to some disturbance than in undisturbed habitats, 'the intermediate disturbance hypothesis'. This is due to the disturbance creating space for new species to colonize. The spatial and temporal scales of the disturbance determine whether or not diversity increases or decreases. The species within a given habitat are adapted to the

natural disturbance scales and are not necessarily adapted to man-made disturbances so that one cannot assume that man-made disturbance will increase diversity.

One important aspect that also needs to be considered is habitat restoration. On land there is a long tradition of restoring habitats, such as mining waste tips. There are some examples of habitat restoration in the marine environment, such as the well-publicized clean-up of the River Thames in the UK where salmon can now be found in London. The developing science of restoration ecology should be a part of a strategy for conservation of coastal biodiversity.

#### *Global climate change*

Pernetta (1993) has reviewed the potential implications of climate change for a number of tropical areas. The most publicised consequence of global climate change is that of sea level rise with severe effects likely in the Maldives and Tuvalu which are only 2 m and 4.5 m respectively above sea level. Bangladesh is expected to lose 12 to 28% of its total land area over the next century as a consequence of predicted sea-level rise. Coastal wetland habitats are likely to suffer since wetland subsistence and formation probably cannot occur at rates of sea level rise above 10 mm per year (Norse, 1994). Wetland areas are important not only for the species they contain, their function as nursery areas, but also for stabilizing coastlines and for protection against hurricanes and storm surges.

The most significant effect of global climate change on coastal systems is, however, likely to be altered storm events and rainfall patterns. It is predicted that the return period of storms will alter so that the 100-year storm occurs every 10 years and the 10-year storm annually (Houghton and Jenkins, 1990). Such events are likely to be highly significant for nutrient transport to the coasts, for mixing processes in coastal areas and for current and frontal systems. As yet, models available are not able to make sufficiently accurate predictions of likely consequences at regional levels mainly due to the lack of data. A Global Ocean Observing System (GOOS) has been proposed to redress this lack of data and its implementation is being planned by UNESCO-IOC, UNEP and WMO. There are component modules on the Health of the Oceans (HOTO) and on the coasts.

The warming of the coastal ocean is known to lead to severe effects on corals. In 1983, 1989 and 1990 the surface temperature of the Caribbean increased by 2°C from 28–29 to 30–31°C with massive bleaching followed by death of corals. The species that died were important in structuring the reef so that the consequences were severe and extended over wide areas (see Sebens, 1994, for a review). Similar events have been recorded in Panama and Indonesia but not with the widespread effects found in the Caribbean (Glynn, 1990).

#### *UV-B radiation*

As a consequence of ozone depletion (which is not related to climate change) UV-B radiation is increasing. There are few data that predict effects on marine systems (but see GESAMP, 1995c). It has been suggested that there will be reduced productivity of phytoplankton in surface waters, which includes the open ocean (Hader and Worrest, 1991). Effects on the symbiotic zooxanthellae in corals have been predicted by Gleason and Wellington (1993) but this is still controversial (Dunne, 1994; Gleason and Wellington 1994). There are also concerns about impacts on diatoms on sand and mud flats. More research is needed before reliable predictions can be made of effects on marine biodiversity.

*Effects of fishing and other forms of overexploitation*

Despite the fact that most fisheries resources are now within the jurisdiction of coastal states nearly all the world's fish resources are overexploited (FAO, 1991). Between 1988 and 1990 the marine fish catch declined in nine key fishing areas and especially off Peru, pelagic fish off Japan, off the Northeast coast of the US and in European seas. The consequences of heavy fishing pressure on commercial species is that the size distribution changes and this leads to loss of genetic diversity, e.g. Orange Roughy (Elliott and Ward, 1992).

In many areas of the Northwest Atlantic there have been dramatic changes in the composition of fish stocks as a consequence of fishing. Highly important commercial species have declined (e.g. herring and Arctic cod) and other less valuable species have increased e.g. sandeels, (Sherman and Alexander, 1990), and sharks. Several studies show that changes in fish species composition have dramatic effects on other species dependent on fish such as sea birds and mammals (Monaghan, 1992; Hamre, 1994).

Exploitation of fish resources can lead to local or regional species extinctions. The Blue Walleye (*Stizostedion vitreum glaucum*) was overfished in Lake Erie and became locally extinct (Scott and Crossman, 1973). The Coelacanth (*Latimeria chalumnae*), which lives in caves in the Cormora islands, has a total world population of under 500 individuals and is being harvested accidentally as a bycatch of fishing for other species (Mackenzie, 1995) and is in real danger of becoming extinct. Local extinctions of fish can also occur where estuaries are made unfit for spawning.

Trawling for bottom-living fish species is having a major effect on the habitat for species other than target species. It has been estimated that all of the sea bed of the North Sea is trawled over at least twice per year and the gear is getting heavier over time (Sydow, 1990). Trawls have destroyed long-lived species of molluscs and echinoderms in the North Sea. Since these species play important functional roles in biogeochemical cycling the consequences may be far-reaching. There are plans to designate trawl-free areas where by comparison with trawled areas effects of trawling can be assessed.

Fishing using explosives on coral reefs (Lundin and Linden, 1993) occurs globally in areas where reefs are not properly protected. The ensuing destruction of the reef habitat, which sustains not only the fish but all other species dependent on the reef, has catastrophic consequences for biodiversity. In the Phillipines in addition to dynamite fishing, and fishing for the aquarium industry there is a further serious problem that of the widespread and increasing use of cyanide to obtain live fish for restaurants. Although the fish recover when placed in clean water the cyanide has major effects on the reefs. It is not known what effects the loss of large numbers of reef fish will have on the reef system as a whole.

There are relatively few quantitative data on local species extinctions. A few known examples are the Red Coral (*Corallium* spp.) and Black Corals (*Anthiparia* spp.) which are heavily exploited for jewellery in the Mediterranean and throughout the tropics and are listed by IUCN on the Red Data list (IUCN, 1994) as species in danger of extinction, as are Triton's trumpet snail (*Caronia tritonis*) and the Knysna sea horse (*Hippocampus capensis*) (Wells *et al.*, 1983). Predatory gastropod snails are sought as souvenirs in many tropical areas and since they play key roles in controlling prey populations, their local extinction can lead to major changes in diversity (e.g. Paine's 1966 classic study on effects of removing keystone predators, but see Mills *et al.*, 1993, for a critique of the keystone species idea). Many other species are heavily exploited and may be in danger but there is

far too little information on which to make a proper evaluation. There is an urgent need for better information.

Marine mammal and sea turtle exploitation are well documented (see Norse, 1994, for an introduction) and will not be treated in detail here. The species that are in danger are listed in the appendices to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

#### *Pollution and marine litter*

The GESAMP State of the Marine Environment Report (GESAMP, 1990) is still the most authoritative statement of the threats to marine life. The report emphasizes that coastal areas are affected by man almost everywhere and stresses that habitat losses from a wide variety of causes if unchecked will lead to a global deterioration of the environment. There is little that has happened since 1990 to suggest that things have changed for the better.

In recent years there has been a recognition that heavy metals seldom pose a threat to marine biodiversity, although there are local areas where high concentrations are still cause for concern, such as areas subjected to mining waste run-off and industrialized estuaries or fjords. There are major concerns about the long-term effects on marine populations of organic chemicals. PCBs and dioxins have been much in focus and there are recent concerns about the fact that many organic chemicals of quite different structures seem to mimic the effects of female oestrogenic hormones and have led to severe reproductive changes in terrestrial species (see review of Müller *et al.*, 1995). Clearly this is a topic where more research is needed before the threats to marine biodiversity can be quantified.

GESAMP states that eutrophication caused by excess nutrients and/or sewage discharged into coastal waters is an expanding problem and incidents are known from almost every coastal state. The initial effects are of altered species compositions both in the water columns and in benthic communities. This may lead to local changes in biodiversity. More severe effects due to low oxygen concentrations are mass mortalities (see Gray, 1994). Other effects that have been linked to eutrophication are harmful algal blooms, but causal links to eutrophication are not yet proven. Nutrient abatement is recommended where eutrophication symptoms occur.

Ciguatera, a disease affecting the nervous and cardio-vascular systems is caused by eating tropical fish that have bio-accumulated toxins from natural algae. Where algal biomasses are significantly elevated, such as in nutrient/sewage enriched areas, the risks of ciguatera are high and it is a common problem in Asia and the Pacific and affects 50 000 people per year (Hammond, 1992). Other toxins produced by algal blooms affect coastal aquaculture and occasionally human health in both developed and developing countries.

Although oil is a highly visible pollutant and when spilled in large quantities can cause severe local effects (GESAMP, 1993) it is not regarded as a significant pollutant on global scales.

Marine litter is an increasing problem for marine life and tourism. In the Mediterranean there are three main sources: litter from drainage sources on land; litter left on beaches; and litter discarded from ships, including discarded nets and other materials from fishing vessels (UNEP, 1991). Almost 75% of litter is plastic with Styrofoam, metal, glass and wood as the other major components. Turtles are particularly vulnerable to discarded litter. Of 51 carcasses stranded in Florida, 6% were entangled in nets and over 50% of

Green Turtles (*Chelonia mydas*) had ingested debris which was thought to have been a major contributor to their deaths (Bjorndal, 1994).

#### *Species introductions/invasions*

The ctenophore *Mnemiopsis leidyi* was imported from the US East coast to the Black Sea, probably in ballast water, and has led to a catastrophic alteration in the whole trophic web and contributed to a huge reduction in stocks of commercial fisheries (GESAMP, 1995b). Other concerns covered by GESAMP are the transport of species of algae that may cause toxic blooms in new areas and other introductions which have led to dramatic effects at regional levels. Alterations in biodiversity are also highly likely although this is poorly documented.

#### *Watershed alteration and physical alterations of coasts*

GESAMP has reviewed how altered watershed use has led to significant changes in both nutrient, (GESAMP, 1987) and sediment transport to the coasts (GESAMP, 1994). Construction of dams for hydroelectricity generation or for irrigation purposes has led to dramatic reductions in sediment loads with severe consequences for coastal ecosystems. The Nile delta is sinking at the rate of tens of centimeters per year due to a combination of lack of sediment input and enhanced erosion and in addition nutrient loads have been so severely reduced that the fisheries have collapsed in much of the Eastern Mediterranean.

Deforestation and mining, often many hundreds of kilometres inland have led to large increases in sediment loads which have smothered coral reefs and other coastal habitats in the Philippines, Malaysia, Indonesia, Sri Lanka, Pacific Islands, the Gulf of Thailand, the Caribbean, Columbia, Costa Rica and Cuba (Lundin and Linden, 1993). It is thought from remote-sensing that the sediment loads come principally from small streams, although quantitative data from the streams are lacking, (Milliman and Meade, 1983).

#### *Tourism*

There are greatly increasing stresses on coasts caused by tourism even in Antarctica and the Arctic. The most serious threats are those of habitat destruction. Mangroves are often removed, wetland areas filled in and estuaries reclaimed to make way for touristic complexes without there being any evaluation of the benefits of the intact systems. Once built the resort may lead to effects on adjacent habitats through sewage discharge and other threats and ultimately to the loss of habitats and their resources. Establishment of hotels on coral reefs is becoming popular and often leads to the destruction of the habitat that was the reason for the development in the first place. Coral reefs are vulnerable to trampling and in the Cayman Islands the one-day visit of a tourist ship to a coral reef led to 3000 m<sup>2</sup> of a previously intact reef being destroyed (Smith, 1988). What is needed is a better understanding by policy makers and planners of the value and requirements for maintenance of the integrity of the natural habitat.

#### *Human perceptions of the oceans*

'Most people are familiar with terrestrial habitats and can relate to a walk in the woods. Few, however, have experienced the wonders of a coral reef except for occasionally viewing a Jacques Cousteau special. Whilst it is easy to capture images of rain forests being cut down and to collect data to quantify the magnitude of habitat destruction on land, it is

more difficult to study and document coral reef processes and degradation' (Richmond, 1994). This view is echoed by Suchanek (1994) who lists three reasons why marine conservation is less developed than that of the terrestrial environment. These are that the populations and communities are not normally visible; our knowledge of them is limited; and we are maintaining no ongoing monitoring.

Thus, apart from efforts devoted to protect marine mammals, turtles and sea birds, there is a very limited public response to the needs for marine biodiversity conservation compared with conservation of terrestrial habitat conservation. In North America it is only recently and after considerable efforts that the coastal zone has been highlighted as in need of conservation (Hildebrand, 1989; Wells and Ricketts, 1994).

### *Summary of threats*

From this analysis it is clear that there are few threats to the open ocean and the threats are concentrated in coastal areas. Habitat destruction is particularly pervasive in tropical areas where mangroves, coral reefs and wetland areas are being destroyed at alarming rates. In temperate areas there are severe threats to wetland areas and estuaries and conflicts between industrial and tourist development and conservation are universal. The threats from commercial fishing on biodiversity of coastal areas has been neglected.

### **The legal framework of biodiversity conservation**

Apart from the Biodiversity Convention itself, the UN's Convention on the Law of the Sea (UNCLOS III 1982), which came into force in November 1994, is of major significance in relation to biodiversity. IUCN has recently produced a comprehensive analysis of the Law of the Sea and other legal issues relating to marine conservation (Kimball, 1995). UNCLOS establishes a comprehensive framework for use of the ocean and its resources. In addition to UNCLOS, Kimball lists other international agreements that relate to fishing and conservation of marine resources, such as conventions on whaling, marine mammal conservation, regional seas, Antarctic resources, transboundary fisheries (e.g. salmon and tuna) etc.

Other important conventions include:

The 1971 Convention on Wetlands of International Importance Especially as Waterfowl Habitat, Ramsar (1971), and (1982) Protocol (RAMSAR).

Convention Concerning the Protection of the World Cultural and Natural Heritage, Paris (1972). (UNESCO)—this includes the Great Barrier Reef and the Galapagos Islands.

The 1973 Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES).

The 1979 Convention on the Conservation of Migratory Species of Wild Animal (CMS).

There are many regional conventions and agreements protecting given coastal areas and Kimball (loc. cit.) lists these.

Application of these conventions alone will not lead to protection of coastal biodiversity. Most problems lie at national and local community levels where there are conflicting uses of coastal areas.

### **How can marine biodiversity best be conserved?**

Beatley (1991) reviews briefly how biodiversity can be protected in coastal environments, but the review lacks detail and contains no clear conservation strategy. Norse (1994) has produced 'A strategy for building conservation into decision making'. This covers the topic in a general way, but includes neither a strategy for conservation, nor an indication of the types of concrete action that are needed.

A number of national and regional assessments of biodiversity which suggest conservation needs have been made (e.g. Canada, Biodiversity Science Assessment Team, 1994; California, Jensen *et al.*, 1993). The creation of marine protected areas is the general strategy adopted (see Sobel, 1993; McNeely, 1994; Heywood and Watson, 1995) and the International Union for the Conservation of Nature (IUCN) has been heavily involved (Salm and Clark, 1984; Kelleher and Kenchington, 1992). It has been estimated that <1% of the coasts are covered by marine protected areas and often these are isolated habitats. If marine biodiversity is to be conserved better protection of the coasts outside marine protected areas is needed.

Habitats themselves occur as a mosaic of interconnected units thus the mosaic of habitats, the landscape, must be considered. Perrings *et al.* (1992) state 'Understanding and managing the habitats, as well as the landscape matrix of ecosystems—including greenways and corridors to counteract habitat fragmentation—is therefore likely to be more effective than focusing on species and populations alone, and it has been argued that in order to sustain biodiversity over multiple human generations biodiversity policy should in fact be set at the landscape level..'

The economic value of coastal habitats is often not estimated. Barbier (1994a, b, c) describes examples of the indirect benefits of wetlands which are often not taken into account, such as storm protection and groundwater recharge of floodplains. There are many similar 'ecological services' that are provided by coastal habitats that need full economic appraisal. Barbier *et al.* (1994) have given an overview of the economics of biodiversity conservation.

Hodgson and Dixon (1988) evaluated the advantages of logging versus tourism on the coast of Palawan, Phillipines. They found that there were economic benefits of maintaining the forest and concentrating on tourism, an option that the authorities had not considered.

In a comprehensive study Ruitenbeek (1994) has analysed the competing options for exploiting the mangrove forests in Bintuni Bay, Indonesia. His analysis shows that the preferred economic option for sustainable use of the forest is to selectively cut 25% of the harvestable mangrove as this option will allow alternative uses of the coast for among others offshore shrimp production, as well as maintaining biodiversity. He emphasises that an important aspect is how this work relates to policy, planning and decision-making processes. From inception through field work to analysis and input to the decision process took just 6 months, a time frame that fits well within a single government administration.

The greatest levels of marine biodiversity are found in tropical countries which are developing. Being poorer than their developed country counterparts in general they have less facilities, equipment, trained staff and resources available to devote to marine biodiversity conservation. In addition it is natural that their priorities focus more on food production and development than on conserving biodiversity. There is a need to explore the economic and other practical benefits of conservation of biodiversity (such as that by Ruitenbeek, 1994), so that policy decisions are made in the full knowledge of the benefits

that can be gained from biodiversity conservation. A strategy should be made partly for protection of biodiversity, but also to ensure sustainable use of coastal habitat resources which includes biodiversity. Sustainable use of these resources will require that all stakeholders are involved in the assessments and the decision-making processes that follow. In addition to natural scientists users of the habitats, managers, planners, economists and policy makers must be included if marine biodiversity is to be conserved. A framework for integration of this type is that of Integrated Coastal Management (ICM).

### Acknowledgements

I thank the following experts for helpful comments: Barbara Brown, Carleton Ray, Charles Sheppard, Richard Warwick, Jack Uthe and GESAMP members Mike Bewers, Rick Boelens, Peter Wells and Helen Yap.

### References

- Alberte, R.S., Suba, G.K., Procaccini, G., Zimmerman, R.C. and Fain S.R. (1994) Assessment of genetic diversity of seagrass populations using DNA fingerprinting: Implications for population stability and management. *Proc. Natl Acad. Sci. USA* **91**, 1049–53.
- Angel, M.V. (1993) Biodiversity of the pelagic ocean. *Conserv. Biol.* **7**, 760–72.
- Anon. (1993) *World Population Prospects: the 1992 Revision*. New York: United Nations.
- ASEAN-Australia Marine Science Project. (1992) *ASEAN Marine Science Project: Living Coastal Resources*. Townsville: Australian Institute of Marine Science.
- Barbier E.B. (1994a) National capital and the economics of environment and development. In *Investing in Natural Capital: the Ecological Economics Approach to Sustainability* (A.M. Jansson, M. Hammer, C. Folke, R.A. Constanza eds). New York: Island Press.
- Barbier, E.B. (1994b) Tropical wetland values and environmental functions. In *Biodiversity Conservation: Policy Issues and Options* (Perrings C, C. Folke, K-G. Mäler, C.S. Holling and B-O. Jansson, eds) Dordrecht: Kluwer Academic Press.
- Barbier, E.B., (1994c) Valuing environmental functions: Tropical wetlands. *Land econ.* **70**, 155–73.
- Barbier, E.B., Burgess, J.C. and Folke, C. (1994) *Paradise Lost?: the Ecological Economics of Biodiversity*. London: Earthscan, pp 267.
- Beatley, T. (1991) Protecting biodiversity in coastal environments: introduction and overview. *Coast Manage.* **19**, 1–19.
- Begon, M., Harper J.L. and Townsend C.R. (1990) *Ecology: Individuals Populations and Communities*. Oxford: Blackwell Scientific Publications.
- Benzie, J.A.H., Frusher, S. and Ballment, E. (1992) Geographical variation in allozyme frequencies of populations of *Penaeus monodon* (Crustacea: Decapoda) in Australia. *Aust. J. Mar. Freshwat. Res.* **43**, 715–25.
- Biodiversity Science Assessment Team (1994) *Biodiversity in Canada: a Science Assessment*. Ottawa: Environment Canada, pp 245.
- Bjorndal, K.A. (1994) Effects of marine debris on sea turtles (abstract). 3rd International Conference on Marine Debris, Miami, Florida, 1994.
- Blanc, F. and Bonhomme, F. (1987) Generic polymorphism in natural mollusk populations of aquacultural interest. Selection, Hybridization and Genetic Engineering In *Aquaculture*, vol. 1. (K. Tiews, ed.) FAO European Inland Fisheries Advisory Committee, Rome, Italy: **18/19**, 59–78.
- Blanc, F. and Jaziri, H. (1990) Variation of allozymic polymorphism in *Ostrea angasi* and *O. edulis*. In *Genetics in Aquaculture*. (T.Gjedrem, ed.) pp. 331–2.
- Briggs, J.C. (1994) Species diversity: land and sea compared. *Syst. Biol.* **43**, 130–5.

- Bushek, D. and Allen, S.K. (1989) Effective population size for shellfish broodstock management: Conflicts between theory and practice. *J. Shellfish. Res.* **8**, 446–7.
- Buzas, M.A. and Culver, S.J. (1991) Species diversity and dispersal and benthic foraminifera. *Bioscience* **47**, 483–9.
- Cataudella, S. and Crosetti, D. (1993) Aquaculture and conservation of genetic diversity. In *Environment and Aquaculture in Developing Countries* (R.S.V. Pullin, H. Rosenthal, and J.L. Maclean, eds) International Cent for Living Aquatic Resources Management, Manila, Philippines. *ICLARM* **31**, 60–73.
- Clark, A.M. and Rowe, F.W.E. (1971) *Monograph of Shallow Water Indo-West Pacific Echinoderms*. London: British Museum (Nat. Hist.), pp 238.
- Clarke, A. (1992) Is there a latitudinal diversity cline in the sea? *Trends Ecol. Evolut.* **7**, 286–7.
- Cody, M.L. (1986). Diversity, rarity, and conservation in Mediterranean-climate regions. In *Conservation Biology: the Science of Scarcity and Diversity*. (M.E. Soulé, ed.) pp. 122–52. Sunderland, Massachusetts: Sinauer.
- Connell, J.H. (1978) Diversity in tropical rainforests and coral reefs. *Science* **199**, 1302–10.
- Dayton, P.K. (1994) Polar marine Communities. *Amer. Zool.* **34**, 90–9.
- di Castri, F. and Younes, T. (1990) Ecosystem function of biological diversity. *Biol. Int. Spec. Issue.* **22**, 1–20.
- Doyle, R.W., Shackell, N.L., Basiao, Z., Urawain, S., Matricia T. and Talbot A.J. (1991) Selective diversification of aquaculture stocks: a proposal for economically sustainable genetic conservation. In *Ecological and Genetic Implications of Fish Introductions* (N. Billington, P.D.N. Herbert, eds) pp. 148–54.
- Dunne, R.P. (1994) Radiation and coral bleaching. *Nature* **368**, 697.
- Durand, P. and Blanc, F. (1988) Genetic diversity in a tropical marine bivalve: *Pinctada margaritifera* (Linne, 1758). *Bull. Soc. Zool. France* **113**, 293–304.
- Elliott, N.G. and Ward, R.D. (1992) Enzyme variation in orange roughy, *Hoplostethus atlanticus* (Teleostei: Trachichthyidae), from southern Australian and New Zealand waters. *Aust. J. Mar. Freshwat. Res.* **43**, 1561–71.
- Etter, R.J. and Grassle, J.F. (1992) Patterns of species diversity in the deep-sea as a function of sediment particle size. *Nature* **360**, 576–8.
- FAO (1991) *Environment and the Sustainability of Fisheries*. Rome: FAO.
- Fisher, R.A., Corbet, A.S. and Williams, C.B. (1943) The relationship between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* **12**, 42–58.
- Fluharty, D.L. (1994) Coastal management: new global concern. *Forum Appl. Res. Public Policy.* **9**, 53–8.
- Franklin, J. (1993) Preserving biodiversity: species, ecosystems or landscapes? *Ecol. Applic.* **3**, 202–5.
- Funch, P. and Kristensen, R.M. (1995) Cycliophora is a new phylum with affinities to Entoprocta and Ectoprocta. *Nature* **378**, 711–4.
- Gall, G.A.E., Bartley, D., Bentley, B., Brodziak, J., Gomulkiewicz, R. and Mangel, M. (1992) Geographic variation in population genetic structure of chinook salmon from California and Oregon. *Fish Bull.* **90**, 77–100.
- GESAMP (1987) Land-sea boundary flux of contaminants: contributions from rivers. *Rep. Stud. GESAMP* **32**, 1–172.
- GESAMP (1990) The State of the Marine Environment. UNEP Regional Seas. *Rep. Stud. GESAMP* **39**, 1–111.
- GESAMP (1991) Global strategies for marine environmental protection. *Rep. Stud. GESAMP* **45**, 1–36.
- GESAMP (1993) Impact of oil and related chemicals and wastes on the marine environment. *Rep. Stud. GESAMP* **50**, 1–180.

- GESAMP (1994) Anthropogenic influences on sediment discharge to the coastal zone and environmental consequences. *Rep. Stud. GESAMP* **52**, 1–67.
- GESAMP (1995a) Biological indicators and their use in the measurement of the condition of the marine environment. *Rep. Stud. GESAMP* **55**, 1–56.
- GESAMP (1995b) The invasion of the ctenophore *Mnemiopsis leidyi* in the Black Sea. *Rep. Stud. GESAMP* **58**, (in press).
- GESAMP (1995c) The seasurface microlayer. *Rep. Stud. GESAMP* **59**, (in press).
- Gillespie, R.B. and Guttman, S.I. (1988) Relationships between genetic structure of electrophoretically-determined allozymes in fish populations and exposure to contaminants. (Meserve, L. ed.) 97th Annual Meeting: The Ohio Academy Of Science. **88**, 46.
- Giovannoni, S.J., Britschgi, T.B., Moyer C.L. and Field, K.G. (1990) Genetic diversity in Sargasso Sea bacterioplankton. *Nature* **345**, 60–3.
- Gleason, D.F. and Wellington, G.M. (1993) UV radiation and coral bleaching. *Nature* **366**, 836–8.
- Gleason, D.F. and Wellington, G.M. (1994) Radiation and coral bleaching. *Nature* **368**, 697.
- Glynn, P.W. (1990) Experimental evidence for high temperature stress as the cause of El Nino coincident coral mortality. *Coral Reefs* **8**, 181–91.
- Gomez, E.D., Deocadiz, E., Hungpreugs, M., Jothy, A.A., Kuan Kwee Jee, Soegiarto, A. and Wu, R.S.S. (1990) State of the marine environment in the East Asian Region. *UNEP Regional Seas Rep. Stud.* **126**.
- Grassle, J.F. (1991) Deep-sea benthic biodiversity. *Bioscience* **41**, 464–9.
- Grassle, J.F. and Maciolek, N.J. (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* **139**, 313–41.
- Grassle, J.F., Lasserre, P., McIntyre, A.D. and Ray, G.C. (1991) Marine biodiversity and ecosystem function. *Biol. Intern.* **23**, 1–19.
- Gray, J.S. (1994) Is the deep sea really so diverse? Species diversity from the Norwegian continental shelf. *Mar. Ecol. Progr. Ser.* **112**, 205–9.
- Gray, J.S., Calamari, D., Duce, R., Portmann, J.E., Wells, P.G. and Windom, H.L. (1991) Scientifically based strategies for marine environmental protection and management. *Mar. Pollut. Bull.* **22**, 432–40.
- Hader, D-P. and Worrest, P. (1991) Environmental effects of ozone depletion: 1991 update. (J.C. van der Leun, M. Tevini, eds) Nairobi, UNEP, 33–40.
- Hammond, A. (1992) *World Resources 1992–1993: Towards Sustainable Development*. Oxford University Press.
- Hamre, J. (1994) Biodiversity and exploitation of the main fish stocks in the Norwegian–Barents Sea ecosystem. *Biodiv. Conserv.* **3**, 473–92.
- Hedgecock, D. and Sly, F. (1990) Genetic drift and effective population sizes of hatchery-propagated stocks of the Pacific oyster, *Crassostrea gigas*. *Aquaculture* **88**, 21–38.
- Hedgecock, D., Nelson, K. and Banks, M.A. (1991) Does variance in reproductive success limit effective population sizes of marine organisms? A proposed test in the Dabob Bay population of Pacific oysters, using enzymatic amplification of mitochondrial DNA. *J. Shellfish Res.* **10**, 234–237.
- Heywood, V.H. and Watson, R.T. (eds) (1995) *Global Biodiversity Assessment*. Cambridge: Cambridge University Press, pp 1140.
- Hildebrand, L.P. (1989) *Canada's Experience with Coastal Zone Management*. Halifax: Oceans Institute of Canada.
- Hodgson, G. and Dixon, J.A. (1988) Logging versus tourism in Palawan: an environmental and economic analysis. *East-West Env Pol. Inst. Honolulu*, 1–95.
- Horn, H.S. (1975) Markovian processes of forest succession. In. *Ecology and Evolution of Communities* (M.L. Cody and J.L. Diamond, eds) pp. 196–213. Cambridge, USA: Belknap Press.
- Houghton, J.T. and Jenkins, A. (1990) *Climate Change: the IPCC Scientific Assessment*. Cambridge, UK: Cambridge University Press.

- Huston, M.A. (1985) Patterns of species diversity in relation to depth at Discovery Bay, Jamaica. *Bull. Mar. Sci.* **37**, 928–35.
- Huston, M. (1994) *Biological Diversity: the coexistence of Species in Changing Landscapes*. Cambridge: Cambridge University Press.
- IUCN (1994) *IUCN Red List Categories*. Gland, Switzerland: IUCN.
- Jackson, J.B.C. (1991) Adaptation and diversity of reef corals. *Bioscience* **41**, 475–82.
- Jaziri, H., Durand, P. and Pichot P. (1987) Genetic diversity between and within populations of the European oyster, *Ostrea edulis*. Selection, Hybridization and Genetic Engineering. In *Aquaculture*, vol 1. (K.Tiews, ed.) FAO European Inland Fisheries Advisory Committee, Rome, Italy **18/19**, 177–87.
- Jensen, D.B., Torn, M.S. and Harte, J. (1993) *In our Own Hands: a Strategy for Conserving California's Biological Diversity*. Berkeley: University of California Press, pp 302.
- Kelleher, G. and Kenchington, R. (1992) *Guidelines for Establishing Marine Protected Areas*. Gland, Switzerland: IUCN.
- Kendall, M.A. and Aschan, M. (1993) Latitudinal gradients in the structure of macrobenthic communities: a comparison of Arctic, temperate and tropical sites. *J. Exp. Mar. Biol. Ecol.* **172**, 157–69.
- Kimball, L.A. (1995) *The Law of the Sea: Prorities and Responsibilities in Implementing the Convention*. Part 1. *The United Nations Convention on the Law of the Sea: a Framework for Marine Conservation*. Gland, Switzerland: IUCN.
- Lambshead, J. (1993) Recent developments in marine benthic biodiversity research. *Océanis* **19**, 5–24.
- Loya, Y. (1972) Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Mar. Biol.* **13**, 100–23.
- Lundin, C.G. and Lindén O. (1993) Coastal ecosystem: attempts to manage a threatened resource. *Ambio* **22**, 468–73.
- MacArthur, R.A. and Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton, New Jersey: Princeton University Press.
- Mackenzie, D. (1995) End of the line for the living fossil. *New Sci.* **1978**, 14–5.
- MacNae, W. (1968) A general account of the fauna and flora of mangrove swamps and forests of the Indo-West-Pacific region. *Adv. Mar. Biol.* **6**, 73–270.
- McNeely, J.A. (1994) Introduction to a special issue on protected areas. *Biodiv. Conserv.* **3**, 387–9.
- McRoy, P.C. and Lloyd, D.S. (1981) Comparative function and stability of macrophyte-based ecosystems. In: *Analysis of Marine Ecosystems*. (A.R. Longhurst ed.) New York: Academic Press, pp. 473–90.
- Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Croom Helm.
- Mattoccia, M., Cesaroni, D. and Matarazzo, P. (1991) Genetic changes in the Manila clam, *Tapes philippinarum*: temporal and spatial variation. In *Aquaculture and the Environment* (N. Depauw and J. Joyce, eds) pp. 210–1.
- May R.M. (1992) Bottoms up for the oceans. *Nature* **357**, 278–9.
- Milliman, J.D. and Meade, R.H. (1983) World-wide delivery of river sediment to the oceans. *J. Geol.* **91**, 1–21.
- Mills, E.L. (1969) The community concept in marine zoology, with comments on continua and instability in some marine communities: a review. *J. Fish. Res. Bd. Canada* **26**, 1415–28.
- Mills, L.S., Soulé, M.E. and Doak, D.F. (1993) The keystone-species concept in ecology and coconservation. *Bioscience* **43**, 219–24.
- Monaghan, P. (1992) Seabirds and sandeels: the conflict between exploitation and conservation in the northern North Sea. *Biodiv. Conserv.* **1**, 98–111.
- Moore, P.G.M. (1973) The kelp fauna of northeast Britain. II. Multivariate classification: turbidity as an ecological factor. *J. Exp. Mar. Biol. Ecol.* **13**, 127–63.

- Müller, A.M.F., Makropoulos, V. and Bolt, H.M. (1995) Toxicological aspects of oestrogen. mimetic xenobiotics present in the environment. *Toxicol. Ecotox. Nova* **2**, 68–73.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734–7.
- National Research Council (1995) *Understanding Marine Biodiversity*. Washington, DC: National Academy of Sciences, PP. 114.
- Nevo, E., Beiles, A. and Ben-Shlomo, R. (1984) The evolutionary significance of genetic diversity: ecological, demographic and life history correlates. In *Evolutionary Dynamics of Genetic Diversity. Lecture Notes in Biomathematics* (G.S. Mani, ed.) **53**, 13–213.
- Nevo, E., Noy, R. and Lavie, B. (1987) Levels of genetic diversity and resistance to pollution in marine organisms. FAO/UNEP Meeting On The Effects Of Pollution On Marine Ecosystems, Blanes, Spain, 7–11 October, 1985, pp. 175–82.
- Norse, E.A. (1994) *Global Marine Biological Diversity*. Washington: Island Press, pp. 383.
- Norse, E.A. (1995) Maintaining the world's marine biological diversity. *Bull. Mar. Sci.* **57**, 10–13.
- Nyman, L. (1991) Conservation of freshwater fish: protection of biodiversity and genetic variability in aquatic ecosystems. *Fish Dev. Serv. Natl. Bd. Fish.*, Gothenberg, Sweden **56**, 38.
- Ogden, J.C. (1988) The influence of adjacent systems on the structure and function of coral reefs. *Proc. 2nd. Intl. Coral Reef Symp.* **1**, 87–96.
- Oliver, L. and Beattie, A.J. (1993) A possible method for the rapid assessment of biodiversity. *Conserv. Biol.* **7**, 562–8.
- Paine, R.T. (1966) Food web complexity and species diversity. *Am. Nat.* **100**, 65–75.
- Palumbi, S.R. (1995) A molecular view biogeography of the Indo-West Pacific. *J. Exp. Mar. Biol. Ecol.* (in press).
- Pernetta, J.C. (1993) *Monitoring Coral Reefs for Global Change*. Gland, Switzerland: IUCN.
- Perrin, W.F. (1991) Why are there so many kinds of dolphins? *Bioscience* **47**, 460–1.
- Perrings, C., Folke, C. and Mäler, K-G. (1992) The ecology and economics of biodiversity loss: the research agenda. *Ambio* **21**, 201–11.
- Pianka, E.R. (1983) *Evolutionary Ecology*. New York: Harper & Row.
- Poore, G.C. and Wilson, G.D.F. (1993) Marine species richness. *Nature* **361**, 597–8.
- Primavera, J. and Honculada (1991) Intensive prawn farming in the Phillipines: ecological, social and economic implications. *Ambio* **20**, 28–33.
- Qiu, Y. (1991) Utility of protein and mtDNA markers in penaeid shrimp: a review. *Aquacult. Env.* **14**, 270.
- Rajasuriya, A. (1993) *Global Aspects of Coral Reefs: Health, Hazards and History*. University of Miami.
- Rao, A.N. (1991) Evaluation, utilisation and conservation of mangroves. In *A Global Network Of Mangrove Genetic Resource Centres Project Formulation*. (S.V. Deshukh and R. Mahalingam, eds) Workshop, January 15– 19, 1991, Madras, India, pp. 1–13.
- Raup, D.M. (1979) Size of the Permo-Triassic bottleneck and its evolutionary implications. *Science* **206**, 217–8.
- Ray, G.C. (1991) Coastal-zone biodiversity patterns. *Bioscience* **41**, 490–8.
- Ray, G.C. and Grassle, J.F. (1991) Marine biological diversity. *Bioscience* **41**, 453–61.
- Ray, G.C. and Gregg, W.P. Jr (1991) Establishing biosphere reserves for coastal barrier ecosystems. *Bioscience* **41**, 301–9.
- Ray, G.C. and McCormick-Ray, M.G. (1992) Functional coastal-marine biodiversity. *Trans 57th N A Wildl & Nat Res Conf*, 384–97.
- Richmond, R.H. (1994) Coral reef resources: Pollution's impacts. *Forum. App. Re. Publ. Pol.* **9**, 54–7.
- Robbins, C.R. (1991) Regional diversity among Caribbean fish species. *Bioscience* **47**, 458–9.
- Ruitenbeek, H.J. (1994) Modelling economy-ecology linkages in mangroves: economic evidence for promoting conservation in Bintuni Bay, Indonesia. *Ecol. Econ.* **10**, 233–47.

- Salm, R.V. and Clark J.R. (1984) Marine and coastal protected areas: a guide for planners and managers. Gland, Switzerland: IUCN.
- Sanders, H.L. (1968) Marine benthic diversity: a comparative study. *Am. Nat.* **102**, 243–82.
- Scott, W.B. and Crossman, E.J. (1973) Freshwater fishes of Canada. *Bull. Fish. Res. Bd. Canada.* **752**, 996.
- Scudder, G.G.E. (1989) The adaptive significance of marginal populations: a general perspective in *Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks*, (C.D. Levings, L.B. Holtby and M.A. Henderson, eds) pp. 180–5.
- Sebens, K.P. (1994) Biodiversity of coral reefs: What are we losing and why? *Am. Zool.* **34**, 115–33.
- Sepkoski, J.J.J. (1979) A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria. *Palaebiol.* **5**, 222–51.
- Sepkoski, J.J.J. (1984) A kinetic model of Phanerozoic taxonomic diversity. III. Post-Palaeozoic families and mass extinctions. *Palaebiol.* **10**, 246–67.
- Sepkoski, J.J.J. (1991) In *The Unity of Evolutionary Biology* (E.C. Dudley, ed.) Poraand, Diosorides Press, pp. 210–36.
- Sheppard, C.R.C. (1980) Coral cover, zonation and diversity on reef slopes of Chagos Atolls, and population structures of major species. *Mar. Ecol. Progr. Ser.* **2**, 193–205.
- Sherman, K. and Alexander, L. (1990) Large marine Ecosystems: patterns processes and yields. Washington D.C. USA: *Am. Assoc. Adv. Sci. Select. Symposium* **111**, pp. 493.
- Signor, P.W. (1994) Biodiversity in geological time. *Am. Zool.* **34**, 23–32.
- Silva, P.C. (1992) Geographic patterns of diversity in benthic marine algae. *Pac. Sci.* **46**, 429–37.
- Sly, F. and Hedgecock, D. (1989) Genetic drift and effective population sizes in commercial stocks of the Pacific Oyster, *Crassostrea gigas*, on the U.S. West Coast. *J. Shellfish Res.* **8**, 324–34.
- Smith, S.H. (1988) Cruise ships: a serious threat to coral reefs and associated organisms. *Ocean Shorel. Manage.* **113**, 231–48.
- Sobel, J. (1993) Conserving biological diversity through marine protected areas. *Oceanus* **36**, 19–26.
- Solbrig, O.T. (ed.) (1991) IUBS/SCOPE/UNESCO *From Genes to Ecosystems: a Research Agenda for Biodiversity*. IUBS.
- Sournia, A. and Chretiennot-Dinet, G. (1991) Marine phytoplankton: how many species in the world ocean? *J. Plankton. res.* **13**, 1093–9.
- Southwood, T.R.E. (1977) Habitat, the templet for ecological strategies? *J. Anim. Ecol.* **30**, 1–8.
- Steele, J.H. (1991) Marine functional diversity. *Bioscience* **41**, 470–4.
- Stehli F.G. and Wells, J.W. (1971) Diversity and age patterns in hermatypic corals. *Syst. Zool.* **20**, 115–26.
- Stork, N. (1988) Insect diversity: facts, fiction and speculation. *Biol. J. Linn. Soc.* **35**, 321–37.
- Suchanek, T.H. (1992) Extreme biodiversity in the marine environment: mussel bed communities of *Mytilus californianus*. *Northwest Environ. J.* **8**, 150–2.
- Suchanek, T.H. (1994) Temperate coastal marine communities: biodiversity and threats. *Am. Zool.* **34**, 100–14.
- Sydow, J.S. (1990) Cruise report experiments on the interaction fishing gear (beamtrawl)-benthos with R.V. Mitra. *BEON Rapport* **8**, 1–57.
- Thorson, G. (1957) Bottom Communities (sublittoral and shallow shelf). In *Treatise on marine ecology and palaeoecology*. Vol 1, Ecology (J.W. Hegpath, ed) Memoirs of the Geological Society of America **67**, 461–534.
- Tilman, D. and Downing, J.A. (1994) Biodiversity and stability in grasslands. *Nature* **367**, 363–5.
- Tuomisto, H., Ruokolainen, K., Kalliola, R., Liina, A., Danjoy, W. and Rodriguez, Z. (1995) Dissecting Amazonian biodiversity. *Science* **269**, 63–6.
- UNEP (1991) *Bibliography on Marine Litter*. Athens: UNEP Mediterranean Action Plan.
- US State Department (1995) *International Coral Reef Initiative*. June, 1995, pp 3.
- Veron, J.E.N (1992) Conservation of biodiversity: a critical time for the hermatypic corals of Japan. *Coral Reefs* **11**, 13–21.

- Veron, J.E.N. (1995) *Corals in Time and Space*. Sydney: University of New South Wales Press.
- Walker, B.H. (1991) Biodiversity and ecological redundancy. *Cons. Biol.* **6**, 18–23.
- Walsh, G.E. (1974) In *Ecology of Halophytes* (R.J. Reimold and W.H. Queen, eds) pp. 51–174. New York: Academic Press.
- Ward, R.D., Woodwark, M. and Skibinski, D.O.F. (1994) A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. *J. Fish. Biol.* **44**, 213–32.
- Wells, P.G. and Ricketts, P.J. (1994) Coastal Zone Canada. *Coastal Zone. Conf. Proc.* **5**, pp 604.
- Wells, S.M., Pyle R.M. and Collins, N.M. (1983) *The IUCN Invertebrate Red Data Book*. Gland, Swizerland: IUCN.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* **30**, 279–338.
- Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biol. Rev.* **42**, 207–64.
- Whittaker, R.H. (1975) *Communities and Ecosystems*, 2nd edn. New York: Macmillan.
- Whittaker, R.H. (1977) Evolution of species diversity in land communities. *Evol. Biol.* **10**, 1–67.
- Wilkinson, C.R., Chou, L.M., Gomez, E., Ridzwaan, A.R., Soekano, S. and Sudra, S. (1993) *Global Aspects of Corals: Health, Hazards and History*. University of Miami.
- Williamson, M. (1983) *Island Populations*. Oxford, UK: Oxford University Press.
- Wood, A.M. (1989) Population genetic studies of algae. *J. Phycol.* **25**, 11.
- Woodward, I. (1987) *Climate and Plant Distribution*. Cambridge, UK: Cambridge University Press.