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ANALYSIS

Ecological goods and services of coral reef ecosystems

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Abstract

This article identifies ecological goods and services of coral reef ecosystems, with special emphasis on how they are generated. Goods are divided into renewable resources and reef mining. Ecological services are classified into physical structure services, biotic services, biogeochemical services, information services, and social/cultural services. A review of economic valuation studies reveals that only a few of the goods and services of reefs have been captured. We synthesize current understanding of the relationships between ecological services and functional groups of species and biological communities of coral reefs in different regions of the world. The consequences of human impacts on coral reefs are also discussed, including loss of resilience, or buffer capacity. Such loss may impair the capacity for recovery of coral reefs and as a consequence the quality and quantity of their delivery of ecological goods and services. Conserving the capacity of reefs to generate essential services requires that they are managed as components of a larger seascape-landscape of which human activities are seen as integrated parts.

Keywords: Coral reefs; Ecological services; Management; Biodiversity; Resilience; Valuation

1. Introduction

Coral reefs are among the most productive and biologically diverse ecosystems on Earth (e.g. Odum and Odum, 1955; Connell, 1978). They supply vast numbers of people with goods and services such as seafood, recreational possibilities, coastal protection as well as aesthetic and cultural

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benefits (e.g. Smith, 1978; Kühlmann, 1988; Spurgeon, 1992; Done et al., 1996; Peterson and Lubchenco, 1997).

Estimates of coral reef cover range from approximately 0.1–0.5% of the ocean floor (Spalding and Grenfell, 1997: 255 000 km^2; Smith, 1978: 617 000 km^2; and Copper, 1994: 1 500 000 km^2). Nevertheless, almost a third of the world's marine fish species are found on coral reefs (McAllister, 1991) and the catch from reef areas constitutes around 10% of the fish consumed by humans (Smith, 1978). More than 100 countries have coastlines with coral reefs. In those countries at least tens of millions of people depend on coral reefs for part of their livelihood or for part of their protein intake (Salvat, 1992). For example, Jennings and Polunin (1996) calculate that 1 km^2 of actively growing reef could support over 300 people if no other protein sources were available.

Unfortunately, many coral reefs are in serious decline (Brown, 1987; Richmond, 1993; Wilkinson, 1993; Bryant et al., 1998). This is particularly true for coral reefs in embayments and near shallow shelves in densely populated areas and for coral reefs affected by deforestation, intensive agriculture, urbanization, and consequent increases of nutrient and sediment loads as well as other kinds of pollution. Other human-associated factors that degrade coral reefs are overharvesting of reef organisms, destructive fishing methods, uncontrolled tourism, new diseases, and possibly global climate change (e.g. Johannes, 1975; Grigg and Dollar, 1990; Wilkinson and Buddemeier, 1994; Roberts, 1995; Peters, 1997).

There are different views on how the degradation and loss of biological diversity affect the functions of coral reef ecosystems and their generation of system services (cf. Done et al., 1996; Paulay, 1997). Moreover, the ecological services of reef ecosystems are generally poorly perceived and the studies dealing specifically with these issues are surprisingly few (McAllister, 1988; de Groot, 1992; Birkeland, 1997a; Costanza et al., 1997).

In this article we describe a diversity of ecological goods and services of coral reef ecosystems, and discuss the value of coral reefs as life-support systems to society. In particular, we focus on how goods and services are generated and sustained by biological communities of coral reefs in different regions of the world. Needless to say, this is not a simple task since reefs come in a great variety of forms, and are considered as one of the most complex systems of all marine ecosystems. The understanding of their dynamic interactions is by no means complete (Hughes et al., 1992; Done et al., 1996).

The consequences of human impacts on coral reefs are also addressed; for example, how loss of resilience, or the buffer capacity that maintains options for recovery and development (Holling, 1973, 1986) may be followed by a shift from coral-dominated to macroalgae-dominated systems (e.g. Done, 1992). Such loss of resilience is affecting the capacity for renewal of coral reefs and thereby the quality and quantity of their delivery of ecological goods and services. Since coral reefs to a large extent are passive receivers of decisions taken elsewhere, their conservation and sustainable use requires a landscape-seascape perspective.

2. Ecological goods and services of coral reefs

The four main types of coral reefs are fringing reefs, barrier reefs, atolls and platform reefs (Table 1). There are many functional differences among these reef types, and they are connected in varying degree to other systems, such as mangrove forests, seagrass beds, and the open ocean (see Fig. 1). Mangroves and seagrass beds interrupt freshwater discharge, are sinks for organic and inorganic materials as well as pollutants, and can generate an environment with clear, nutrient poor water that promotes the growth of coral reefs offshore (e.g. Kühlmann, 1988; Ogden, 1988), but see also Szmant (1997) hypothesising that reefs may have the ability to utilise and benefit from higher nutrient fluxes than the present paradigms imply. Coral reefs in turn serve as physical buffers for oceanic currents and waves, creating, over geologic time, a suitable environment for seagrass beds and mangroves. In addition to these physical interactions there are several biological and biogeochemical interactions between these interconnected ecosystems.

Ogden (1988) called this large biome of the tropical coastal zone the seascape, consisting of a complex mosaic of mangroves, seagrass beds and coral reefs interacting in a dynamic fashion, all influenced by terrestrial as well as open ocean activities (Fig. 1). In the following we have collected information on ecological goods and services of coral reefs (Table 2). In doing so it is important to keep in mind that this life-support to humans is dependent on complex interactions in the seascape as a whole, and also that the supply of these goods and services differs among biogeographic regions, reef types, individual reefs, and even among zones in the individual reefs.

3. Ecological goods

3.1. Renewable resources

Reefs generate a variety of seafood products such as fish, mussels, crustaceans, sea cucumbers and seaweeds (e.g. Craik et al., 1990; Birkeland, 1997a). Reef-related fisheries constitute approximately 9–12% of the world's total fisheries (Smith, 1978) and in some parts of the Indo-Pacific region, the reef fishery constitutes up to 25% of the total fish catch (Cesar, 1996). However, overfishing of coral reefs or reef associated fish populations is a major problem (e.g. Roberts, 1995; Jennings and Polunin, 1996; Jackson, 1997).

The pharmaceutical industry has discovered potentially useful substances with anticancer, AIDS-inhibiting, antimicrobial, antiinflammatory and anticoagulating properties among the seaweeds, sponges, molluscs, corals (e.g. soft-corals (order Alcyonacea) and gorgonians (order Gorgonacea)) and sea anemones of the reefs (e.g. Sorokin, 1993; Carté, 1996; Birkeland, 1997a). It has been claimed that the discovery of prostaglandins in many of the gorgonians in the early 1970s was responsible for the expansion of marine natural products (Carté, 1996).

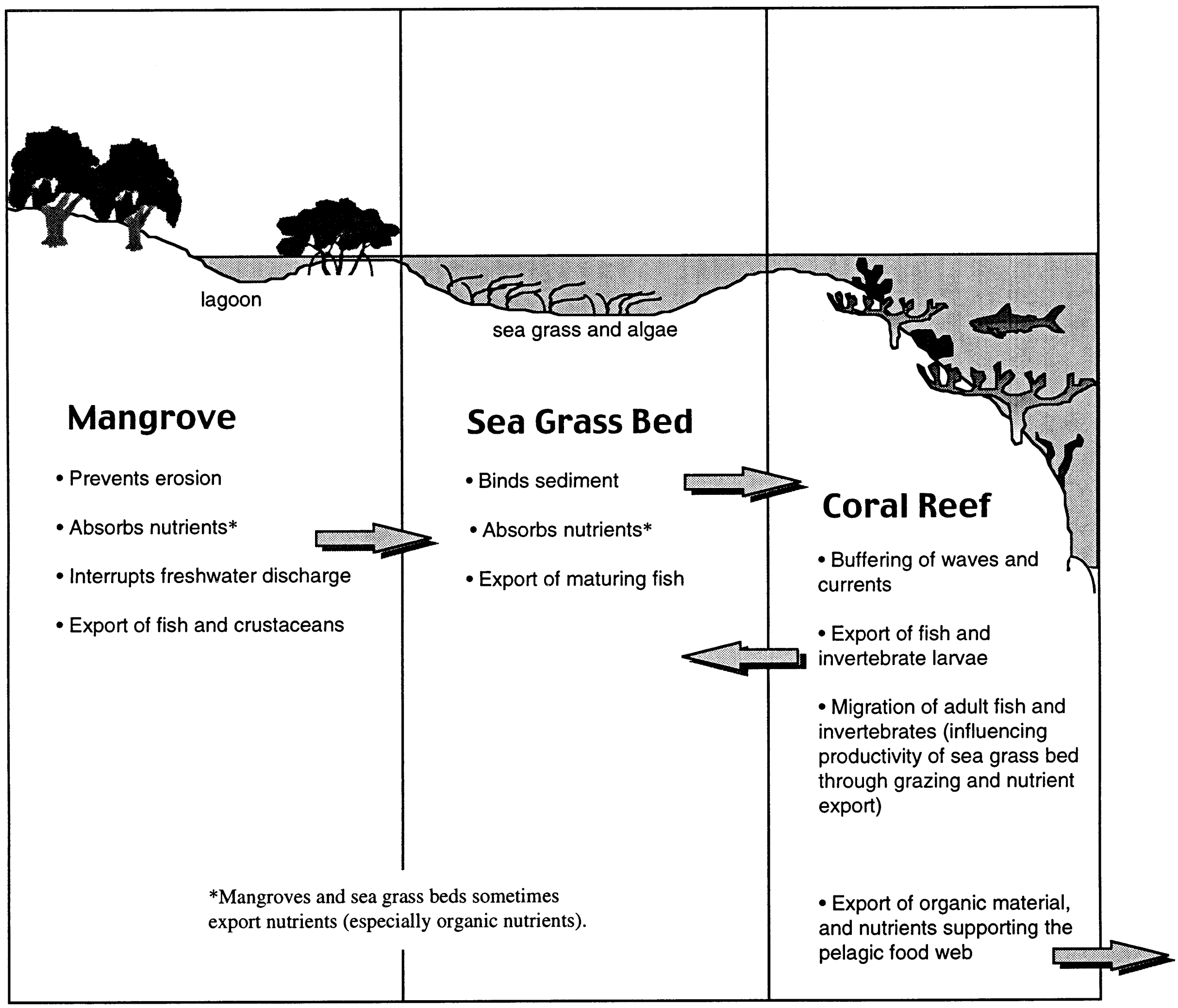
Many species of seaweed are collected from reefs to be used in the production of agar and carrageenan (Birkeland, 1997a) and as manure (Craik et al., 1990), and coral skeletons have proven to be promising in bone graft operations (Spurgeon, 1992).

Mother-of-pearl shells (*Trochus* spp.) and giant clams (*Tridacna* spp.) are collected not only as food but also to sell as jewellery and as souvenirs. In 1978 more than 5000 tons of mother-of-pearl from the gastropod *Trochus niloticus* was collected for the curio trade (Craik et al., 1990). Another example from the ornamental trade is the red coral *(Corallium rubrum)* that was sold for US$ 900 per kg in 1980 (Goh and Chou, 1994). In 1988, almost 1500 tons of corals were imported to the United States for the souvenir market (Wells and Hannah, 1992).

The marine aquarium market in 1985 was a 24–40 million dollar per year industry (Wood, 1985). Unfortunately, live fish collection involves pumping hundreds of tons of toxic cyanide per year into coral communities to stun reef dwelling fishes (Johannes and Riepen, 1995). According to Wells and Hannah (1992) about 250 000 live

Table 1
The four main reef types

Platform reefs	Fringing reefs	Barrier reefs	Atolls
Frequently found in the lagoons created by atolls and barrier reefs	Closely follow shorelines, narrow shallow lagoon	Separated from land by a relatively wide, deep lagoon	Horseshoe shaped or circular reef surrounding a central lagoon (often far from land in the open ocean)
In the Great Barrier Reef lagoon, Belize, Red Sea, Bahamas	Red sea, East Africa, Seychelles and other Indo-Pacific islands, most Caribbean reefs	The Great Barrier Reef in Australia, Belize Barrier Reef, off Mayotte in the Western Indian Ocean	>95% of the atolls are in the Indo-Pacific, others are found outside Belize and in Western Atlantic



Adopted from White (1986) and Ogden (1988).

Fig. 1. Interactions in the tropical seascape, showing the connections between mangroves, sea-grass beds and coral reefs.

corals were imported to the United States in 1991.

The use of the natural resources described above could perhaps be sustainable, but there is a tendency for their overexploitation, especially when world market prices rise (e.g. Cesar, 1996; Birkeland, 1997b). Further, the dynamic complexity of coral reef ecosystems implies that it is extremely difficult to estimate sustainable harvest rates of reef organisms (Sorokin, 1993; Hodgson, 1997).

3.2. Mining of reefs

Among the obviously destructive coral reef uses are the exploitation of hard corals for building materials and for the production of lime, mortar and cement (Dulvy et al., 1995). In the Maldives, coral blocks, rubble and sands serve as the main construction materials with approximately 20 000 m^3 corals mined every year (Cesar, 1996). Lime is also used as a pH regulator in agriculture (Cesar 1996), and in some regions coral debris is also

Table 2
Goods and ecological services of coral reef ecosystems identified in this article

Goods		Ecological services					
Renewable resources	Mining of reefs	Physical structure services	Biotic services		Biogeochemical services	Information services	Social and cultural services
			Within ecosystems	Between ecosystems			
Sea food products	Coral blocks, rubble and sand for building	Shoreline protection	Maintenance of habitats	Biological support through 'mobile links'	Nitrogen fixation	Monitoring and pollution record	Support recreation
Raw materials for medicines	Raw materials for production of lime and cement	Build up of land	Maintenance of biodiversity and a genetic library	Export of organic production, and plankton to pelagic food webs	CO_2/Ca budget control	Climate record	Aesthetic values and artistic inspiration
Other raw materials (seeweed and algae for agar, manure, etc.)	Mineral oil and gas	Promoting growth of mangroves and seagrass beds	Regulation of ecosystem processes and functions	–	Waste assimilation	–	Sustaining the livelihood of communities
Curio and jewellery	–	Generation of coral sand	Biological maintenance of resilience		–	–	Support of cultural, religious and spiritual values
Live fish and coral collected for the aquarium trade	–	–	–	–	–	–	–

collected and crushed to be used as fertilizer (Kühlmann, 1988).

Physicochemical processes acting over millions of years convert biomass of reef organisms into mineral oils and gas. These resources are thought to exist in large quantities below living reefs. Ancient reef structures in Siberia, Saudi Arabia, USA and Canada are potentially rich in oil, stored in the porous limestone (Sorokin, 1993; Hodgson, 1997). As a consequence, the petroleum industry is subsidizing more and more research in finding mineral oils (Kühlmann, 1988), and studies of the ecology and geomorphology of modern reefs help to locate oil deposits in ancient reef structures (Sorokin, 1993). Exploitation of these resources conflicts with all the other uses of reefs and can by no means be considered as sustainable (e.g. Hodgson, 1997).

4. Ecological services

4.1. Physical structure services

Without coral reefs protecting the shoreline from currents, waves, and storms there will be loss of land due to erosion. In Indonesia, Cesar (1996) estimated that between US$ 820–1 000 000 per km of coastline was lost due to decreased coastal protection as a consequence of coral destruction (based on 0.2 m $year^{-1}$ of coast erosion, 10% discount rate and a 25-year period). In the Maldives an artificial substitute breakwater (a 1 km pier) cost around US$12 000 000 to construct (Weber, 1993).

Coral reefs build up land. Many tropical, nations in the Indian and Pacific oceans with large human populations are situated on islands built by coral reefs (e.g. Stoddart, 1973).

The capacity of coral reefs to dissipate wave energy creates lagoons and sedimentary environments. Coral reefs thus physically create favourable conditions for the growth of sea-grasses and mangrove ecosystems (Birkeland, 1985; Ogden, 1988).

Coral reefs generate the fine coral sand supplying shores with the white sand characteristic of tropical islands and one of the main attractions in beach tourism (e.g. Richmond, 1993). It is not only generated from physical forces but also by the biota. Bioeroders, such as algae, sponges, polychaetes, crustaceans, sea urchins, and fishes are important in producing the reef sediments (rubble, sand, silt, and clay) (Trudgill, 1983). For sea urchins, erosion rates have been reported to exceed 20 kg $CaCO_3$ m^{-2} $year^{-1}$ in some reefs, whereas the highest figure reported for fishes (parrotfish) is 9 kg $CaCO_3$ m^{-2} $year^{-1}$ (Glynn, 1997).

4.2. Biotic services

These are in essence the services listed by Holmlund and Hammer (this issue) under the subtitle 'fundamental services', and also very similar to what de Groot (1992) named 'regulation functions'. These services are essentially the prerequisites for a functioning ecosystem. Here we also include the biotic services supporting the adjacent systems in the seascape.

4.2.1. Biotic services within the ecosystems

Coral reefs function as important spawning, nursery, breeding and feeding areas for a multitude of organisms. Being one of the most species-rich habitats of the world, coral reefs are important in maintaining a vast biological diversity and genetic library for future generations. The extremely high habitat heterogeneity of reef systems created by the complex three-dimensional structure facilitates niche diversification and thus also possibilities for evolution of new species (Birkeland, 1997a; Paulay, 1997). Up to 60 000 reef living animals and plants have been described to date (Reaka-Kudla, 1994).

Among these species are keystone process species that regulate ecosystem processes and functions, for example through grazing and predation (Hughes, 1994; McClanahan et al., 1994; Done et al., 1996). Others species and groups of species are important in maintaining resilience of coral reef ecosystems (McClanahan et al., in press). In most reefs there are many species within each functional group (cf. Choat and Bellwood, 1991; Roberts, 1995). Many of those species do not appear to perform key functions but may be able to take over such functions (Peterson and

Lubchenco, 1997) if the keystone process species within a functional group is lost (McClanahan et al., in press). This has been seen, for example, in East African reefs where overfishing has resulted in a loss of the dominant fish predator on sea urchin (red-line triggerfish). Its role in controlling grazing has been replaced by species of wrasses and scavengers (McClanahan, unpubl. data). However, these sea urchin predators did not fully substitute the control function of the red-line triggerfish, since they could not suppress the sea urchin population to levels of undisturbed reefs. Although the qualitative function was maintained, resilience may have been impaired.

4.2.2. Biotic services between ecosystems

Some coral reef organisms migrate back and forth between adjacent ecosystems. Examples of such 'mobile links', i.e. species that link one ecosystem to another, are fish that migrate to mangroves and sea-grass beds and use them as nursery grounds (Ogden and Gladfelter, 1983; Ogden, 1988; Parrish, 1989). Herbivorous fishes and sea urchins from the reefs move to sea-grasses for grazing and influence plant community structure there (e.g. Birkeland, 1985), and may serve as a food source for predators in other systems, as well as food for humans (Parrish, 1989; Spurgeon, 1992). The net result of migration is a transfer of energy from the system where feeding or development occurs to the system that shelters the adults (Ogden and Gladfelter, 1983). In addition the pelagic juvenile stages of many reef organisms that drift into these adjacent ecosystems serve as a food source for commercially important fishes, or they may settle and mature until harvested by fishermen (Spurgeon, 1992).

Herbivorous fishes and invertebrates from coral reefs can also indirectly control the productivity of benthic algae and sea-grass assemblages by reducing self-shading, weeding out large algae with low productivity, and enhancement of nutrient exchange with the water (Hatcher, 1983; McRoy, 1983). Moreover, fishes migrating from the coral reef ecosystem may also influence the nutrient cycles of the sea-grass beds and mangroves through their excretion and defecation (Ogden and Gladfelter, 1983). Coral reefs thus not only provide physical protection but also biological support to sea-grass beds, mangroves, and the open ocean. Another biological link is input to the reef of excretory and fecal products from migrating fish. This input of nutrients and organic matter from migrating white grunts, which feed in seagrass beds at night and rest over coral colonies during the day, may enhance the growth of reef corals (Meyer and Schultz, 1985).

Coral reefs appear to support the pelagic food web with export of excess of organic production such as mucus, wax esters, and dissolved organic matter as well as bacterioplankton, phyto- and zooplankton (Hatcher, 1988; Sorokin, 1990). This net flow to surrounding waters enhances the productivity of local planktonic communities and consequently also supports local fisheries (Sorokin, 1990).

4.3. Biogeochemical services

Coral reefs function as nitrogen fixers in nutrient poor environments (Sorokin, 1993). Reefs would probably not have been able to become so productive and diverse without the capacity of microbial and cyanobacterial associations in reef-bottom biotopes, and also cyanobacteria in the water column, to assimilate atmospheric nitrogen. Compared with other marine ecosystems, nitrogen fixation on coral reefs occurs at a considerably high rate. The nitrogen fixing ability is not only of local importance to the reef system itself but also to the productivity of the adjacent pelagic communities due to the release of excess nitrogen fixed in the reefs (D'Elia 1988; D'Elia and Wiebe, 1990; Sorokin, 1990). However, reefs near high islands may receive enough nutrients via run-off or groundwater inputs (D'Elia and Wiebe, 1990). Furthermore, because eutrophication is a major problem in many tropical coastal areas (e.g. Hunter and Evans, 1995; Goreau et al., 1997), the relative importance of nitrogen fixation, with regard to community requirements, may be larger in isolated reefs such as ocean atolls (Sorokin, 1993).

Reefs appear to act as sinks for carbon dioxide over geological time scales, but are net sources of carbon dioxide in time perspectives relevant for humans (Gattuso et al., 1996; Hallock, 1997).

This net source seems to be of minor significance in the current global carbon budget (Gattuso et al., 1996), as it has been estimated that the release of CO_2 to the atmosphere from human activities the last 100 years is larger than release from reefs in 15 000 years (Hallock, 1997). Buddemeier (1996) claims that those reefs which are sinks for carbon dioxide are subject to human impact, and have an increased ratio of organic production to calcification compared with normal reefs.

Biochemical processes on coral reefs play a significant role in the world's calcium balance (e.g. Kühlmann, 1988). Reefs precipitate approximately half of the 1.2×10^{13} mol of calcium delivered to the sea each year (Smith, 1978). In addition to the reef building corals there are also algae and foraminifera on coral reefs that produce $CaCO_3$ (Wiebe, 1988). This ability of reefs to bind calcium and construct massive calcium carbonate frameworks is the basis for reef development and makes reefs unique. It is essentially the prerequisite for the rest of the services.

Coral reefs can transform, detoxify, and sequester wastes released by humans, thus providing a cleansing service. For instance, petroleum products in the marine environment are detoxified by microbes, turning hydrocarbons into carbon dioxide and water (Peterson and Lubchenco, 1997). More persistent pollutants can be immobilised or sequestered. Such waste assimilation services of reefs are described in a Galapagos case study by de Groot (1992), and was estimated as having a value of US$ 58 per ha and year (replacement cost). However, the waste assimilation capacity of reefs seems limited to us. This is particularly true when there are persistent or chronic quality and quantity emissions of waste that reduce the window for recovery after disturbance.

4.4. Information services

Reef organisms are used in monitoring and as pollution records. Skeletons of reef building corals act as long-term chemical recorders of levels of metals in seawater (e.g. Dodge and Gilbert, 1984; Howard and Brown, 1984). Coral reefs are highly sensitive systems and extensively used in monitoring the recent changes in the marine environment and the effects of human disturbances (e.g. Wilkinson, 1993; Eakin et al., 1997).

Reef corals function as climate records. The chemical composition of coral skeletons can been used to reconstruct the sea surface temperature of the tropics and to track variations in salinity (de Villiers et al., 1995; Swart and Dodge, 1997; Gagan et al., 1998). Long-lived, massive corals deposit layers of skeleton which vary in width and density depending on the environmental conditions (season etc.) (e.g. Barnes and Lough, 1996). These bands can be counted like the growth rings of trees and as such give indications of past conditions. Moreover, it is possible to trace the periods of monsoonal floodings in the past by looking at fluorescent bands in nearshore corals (Isdale, 1984; Veron, 1993).

4.5. Social/cultural services

Coral reefs support recreation. The recreational value of reefs, as indicated by income from tourism is enormous (Dixon et al., 1993; Pendleton, 1995; Cesar, 1996). The financial value of tourism in the Great Barrier Reef World Heritage Area (WHA) was estimated by Driml (1994) to be AUS$ 682 000 000 annually. In 1990 Caribbean tourism earned US$ 8 900 000 000 and employed over 350 000 people (Dixon et al., 1993).

Coral reefs hold aesthetic values (cf. de Groot, 1992). Countless films, photos, and paintings with reefs or reef organisms as motifs are produced every year. The monetary value of all books, films and paintings produced using coral reefs as inspiration is undoubtedly huge.

Coral reefs sustain the livelihood of many local communities. For example, it has been estimated that damages to reefs in Philippines caused by overfishing and pollution have led to the loss of at least 100 000 fishermen's jobs (McAllister, 1988).

Another important and often forgotten service of reefs is their support of cultural and spiritual values. For instance religious rituals have developed around reefs in southern Kenya, where traditional management with the primary purpose to appease spirits has also served to regulate fish stocks (McClanahan et al., 1996). Similar systems of traditional management was developed by

Pacific islanders centuries ago to regulate the use of reef resources (Johannes, 1992; Ruddle et al., 1992). Thus, many local communities living in the tropical coastal zone seem to have gone through a process of co-evolution (Gadgil et al., 1993; Norgaard, 1994), where their cultural traditions have developed in synergy with adjacent reefs. Reefs are in this sense important when it comes to stabilizing the social and institutional structures that underlie cooperative fishing activities in more traditional coastal communities (Birkeland, 1997a).

5. Economic valuations of coral reef ecological goods and services

Illuminating economic values of coral reefs, their goods, and their services may contribute to improved management and conservation. Valuation studies of reefs have predominantly focused on the economic values of tourism and fisheries (Hodgson and Dixon, 1988; Dixon et al., 1993; Barton, 1994; Driml, 1994; Cesar, 1996). The focus of the bulk of valuation studies that exist is shown in Table 3 in relation to ecological goods and services. The table reveals that only some of the reefs' goods and services have been captured in valuation studies.

Monetary values of the environment are directly or indirectly derived from consumer preferences, and generally defined in terms of small or marginal changes. Marginal values are context specific, i.e. they belong to a given decision situation of alternative policy options (Barbier et al. 1994). Since they are context specific marginal values cannot easily be transferred to another area, region, or be applied in economic valuation of the same area in the future (Brookshire and Neill, 1992). Therefore, an estimated economic value of an ecological good or service is not an absolute value, but a relative value on the margin founded on people's preferences.

However, people do not always perceive their dependence on critical goods, ecological services, and ecosystem support. And even if they do, they may not value them: preferences are not necessarily linked to biophysical realities. We have argued elsewhere that there are many ecological goods and services that meet the criteria of having economic value (they contribute to well-being and are scarce), but for which humans have not yet developed preferences (Costanza and Folke, 1997). Making decisions based on economic valuations of people's preferences alone may, therefore, lead to devastating results. Decision-making has to incorporate information and understanding of essential ecological life-support conditions for human well-being. Institutions are critical in this context as they provide the framework, the norms, and rules for individuals (e.g. Ostrom, 1990; Hanna et al., 1996). In the following sections we will address the work of coral reefs, including the role that biological diversity plays, in the generation of life-support conditions and ecological goods and services of value to society.

6. Biodiversity, ecosystem function and ecological services

The coral reef ecosystem is open and complex, its structure, function, biodiversity, and resilience prone to influence by human alterations of water quality and biogeochemical and hydrological flows (locally or at distance). The bulk of ecological goods and services of reef ecosystems are dependent on a vast variety of complex and dynamic interactions between networks of species within and between ecosystems. Although biodiversity in coral reefs and its influence on maintenance of ecosystem function is highlighted in the literature, comparatively little is known about the diversity of these systems and how changes in diversity might result in system instability and potential threshold effects (Done et al., 1996).

6.1. The reef building framework

The existence of a reef framework which creates a three-dimensional, complex habitat is the basis for the diversity of fishes and other reef dwelling animals (e.g. Sutton, 1983; Sale, 1991). The structure also breaks waves and generates a diversity of ecological services (e.g. McAllister, 1991; Done et al., 1996). Corals are the main builders of the

Table 3
Articles with economic valuation of ecological goods and/or ecological services of coral reef ecosystems

Authors, year	Goods	Ecological Services				
		Physical structure	Biotic	Biogeochemical	Information	Social/cultural
Andersson and Ngazi, 1995	Fishery, lime prod, construction	–	–	–	–	Tourism
Berg et al., 1998	Fishery, Mining	Coastal protection	–	–	–	Tourism
Cesar, 1996	Fishery, Mining,	Coastal protection	–	–	–	Tourism
de Groot, 1992	Fishery, ornaments, construction	Coastal protection	Biological control, habitat	Waste assimilation	Research/education	Artistic inspiration, Spiritual values
Dixon et al., 1993	–	–	–	–	–	Tourism
Driml, 1994	Fishery	–	–	–	Research	Tourism
Hoagland et al., 1995[a]	Aquarium trade	–	–	–	–	Tourism, recreation
Hodgson and Dixon, 1988	Fishery	–	–	–	–	Tourism
Hundloe, 1990[b]	–	–	–	–	–	Tourism, recreation
Johannes and Riepen, 1995	Live fish	–	–	–	–	–
Mattson and DeFoor, 1985[b]	Live coral	–	–	–	–	Tourism
McAllister, 1988	Fishery	–	–	–	–	Livelihood
McAllister, 1991[c]	–	Coastal protection	–	–	–	–
Pendleton, 1995	–	–	–	–	–	Tourism
van't Hof, 1985	–	–	–	–	–	Tourism
Wood, 1985	Aquarium trade	–	–	–	–	–

[a] In Costanza et al. (1997).
[b] In Spurgeon (1992).
[c] McAllister (1991) also includes a value based on a court settlement for damage to a whole coral reef.

reef framework through the accumulation of limestone (calcification), but a diversity of other organisms, e.g. encrusting coral line algae, foraminifera, molluscs, and echinoderms are also needed in the building of the reef (e.g. Smith, 1983).

The calcifying process of the main reef builders, the hermatypic corals, is heavily dependent on the internal symbiosis with the microalgae zooxanthellae. These unicellular algae living inside the tissue of hermatypic corals not only provide oxygen, sugars, lipids, and amino acids to the coral host, but also facilitate skeletal growth via the 'light-enhanced calcification' which is two to three times as fast as dark calcification (Goreau, 1959; Muscatine, 1990; Muller-Parker and D'Elia, 1997). Without reef building corals, no proper framework would exist (e.g. Davies, 1983), and as a consequence there would be no porous three-dimensional structures that provide habitat for so many other organisms. All the goods and services of the reef are thus directly or indirectly dependent on one group of species: the reef building corals (e.g. Johannes, 1975; Done et al., 1996).

However, the symbiosis between corals and their microalgae is also the reason why reef corals are relatively sensitive to changes in environmental conditions (Kühlmann, 1988; Birkeland, 1997a; Muller-Parker and D'Elia, 1997). The symbiosis requires sufficient light and good water circulation, and exists in a rather narrow range of water temperature and salinity, with low nutrient and sedimentation loads.

6.2. Keystone process species

Reef building corals drive critical processes for ecosystem functioning, physically shaping their own community (Baskin, 1997). In the Caribbean, the sea urchin *Diadema antillarum* has proven to be a keystone species (Paine, 1966) or keystone process species through its role in facilitating coral growth and settlement by grazing down algae (Hay, 1984; Lessios et al., 1984; Carpenter, 1986; Hughes, 1994). In the Indo-West Pacific region, other species are important in structuring the coral communities, including the crown-of-thorns starfish *Acanthaster planci*, the asteroids *Culcita* sp., the gastropod *Drupella* sp. and coral eating parrotfishes (Done et al., 1996; Paulay, 1997).

Without herbivores, the main reef builders, corals and crustose coral line algae would be overgrown and excluded by faster growing erect algae (Carpenter, 1990; Glynn, 1990; McCook, 1996). Herbivores, such as fishes and invertebrates, influence species composition, productivity, nitrogen fixation, succession, and other ecosystem processes (e.g. Hatcher, 1988; Glynn, 1990; Roberts, 1995) and thereby play an important indirect role in generating ecological goods and services. For example the herbivorous territorial damselfishes enhance several reef processes such as primary production (Hixon and Brostoff, 1996), recovery of reef corals (Done et al., 1991) and nitrogen fixation since cyanobacteria are more common within their territories than outside (Hixon and Brostoff, 1996). Damselfishes may also, due to their aggressive territorial behaviour, exclude coral eating animals such as pufferfishes and parrotfishes, and possibly also crown-of-thorns starfishes (Hixon, 1997).

Other important keystone process species are the top predators in reef systems, such as triggerfishes and pufferfishes that regulate the herbivores (including sea urchins) (Hughes, 1994; McClanahan et al., 1994; Roberts, 1995). In Kenyan reefs, the overfishing of top predators resulted in population outbreaks of sea urchins which reduced coral accretion and at times led to a negative calcium carbonate balance (net erosion where the reef slowly disappears: McClanahan and Muthiga, 1988). The increased abundance of such boring sea urchins and their eroding activities not only impairs the reef growth but may also result in a loss of structural complexity, leading to decreased fish production (Jennings and Polunin, 1996) and other ecological services. The loss of fish predators might be partly responsible for the outbreaks of both the crown-of-thorns starfish and the coral eating mollusc *Drupella* (Glynn, 1990; Bell and Elmetri, 1995; Roberts, 1995). Further, predators feeding on corals may be important distributors of zooxanthellae (Parker, 1984; Muller-Parker and D'Elia, 1997), which are critical in the reef construction process as discussed above.

6.3. Biogeographic regions, reef types, and ecological services

There are four major biogeographic regions of the tropical oceans; the Indo-West Pacific (IWP); Eastern Pacific (EP); Western Atlantic (WA); and the Eastern Atlantic (EA) (Fig. 2). These regions display considerable variation in species composition and diversity (e.g. Sebens, 1994; Paulay, 1997), mainly resulting from differences in evolutionary history and oceanographic conditions (Veron, 1993; Birkeland, 1997a). The differences are expressed in, for example, that the IWP and WA have only one hermatypic coral species in common (Veron, 1993). The IWP has far higher diversity than the other regions and also highest endemism. Although the WA has the second highest reef community species diversity of the biogeographic regions, there are approximately ten times more scleractinian coral species (order Scleractinia, which includes almost all of the reef building coral species) in the IWP compared with the WA (Paulay, 1997). Fish diversity is approximately four to six times higher in the IWP than in WA reefs (Thresher, 1991; Lieske and Myers, 1994). In IWP reefs soft corals are often abundant and diverse, whereas Caribbean reefs have more gorgonians and sponges than the other regions (Paulay, 1997). In addition, mutualistic associations, e.g. giant clam zooxanthellae and anemone-anemone fishes, are more diverse in the IWP compared with reefs in the Eastern Pacific and Atlantic oceans (Birkeland, 1997a).

Despite the considerable variation in species diversity, many system parameters such as calcification, community productivity, and reef structure are often rather similar between regions (Kinsey, 1983, but see also Hatcher, 1997). However, reefs with maintained functions in spite of less diversity might have lower resilience, that is, lower capacity to absorb or buffer disturbance (Holling, 1973, 1986; Holling et al., 1995), as will be discussed below.

Hence, coral communities in different biogeographic regions may not be equally important in terms of supply of certain goods and services and sustaining their flow. Coral communities in the Eastern Atlantic that form no real reefs are of course less important providers of most of the services listed here compared with the other regions, e.g. no significant wave barriers, display lower diversity, less interesting for dive-tourism and play a minor relative role in the global calcium balance as well (e.g. Sebens, 1994; Paulay, 1997). This is not to say that these coral communities are of low value. Locally such less developed coral communities may be of great importance, e.g. for local fisheries (McManus, 1988) as fishery yields may be rather high even in low diversity reefs (Menasveta et al., 1986).

Furthermore, among different reef types (Table 1) there are functional differences. For example, as mentioned earlier (Section 4.3), nitrogen fixation appears to be more important in the functioning of isolated reefs than in coastal areas. Moreover, Hatcher (1997) concludes that fringing reefs most likely depart from the ‘sweeping gener-

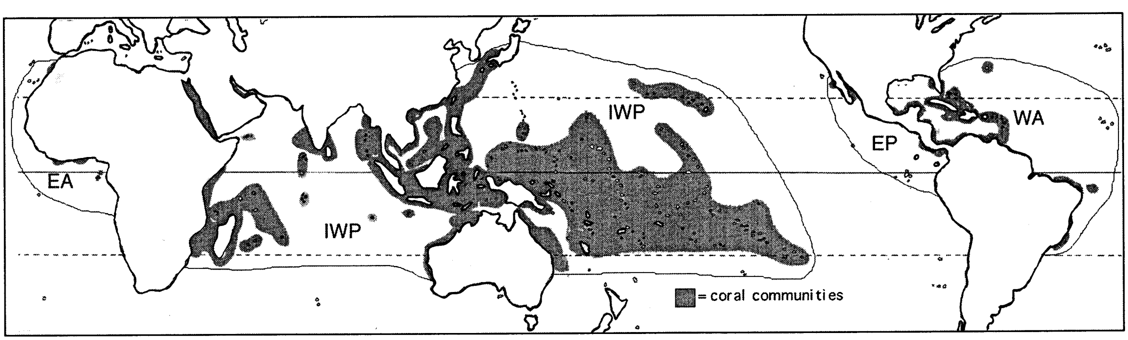


Fig. 2. The distribution of coral reefs in the four tropical biogeographic regions: the Indo-West Pacific (IWP); Eastern Pacific (EP); Western Atlantic (WA); and the Eastern Atlantic (EA).

alisation' that all reef ecosystems exist in crystal-clear nutrient poor waters and display similar metabolic performance. Thus, reefs close to human developments are poorly understood in studies at the system level and seem to have more of their primary production left for sustained reef growth, and export to adjacent ecosystems than was previously believed (e.g. Odum and Odum, 1955). The services listed in Table 2 that are associated with the seascape (mangroves, seagrass beds, coral reefs) are mainly of importance for fringing reefs and to some extent for barrier reefs.

7. Human impacts, loss of resilience and system flips

Many uses of coral reefs are unsustainable, and in this sense many of the assets of reefs are also the cause of their decline (Weber, 1993). On the list of destructive activities are coral mining for lime production, collection of reef organisms for the curio trade, destructive fishing methods like cyanide or dynamite fishing, fishing with small-sized seine nets, uncontrolled tourism activities and oil extraction (e.g. Hawkins and Roberts, 1994; Johannes and Riepen, 1995; Dulvy et al., 1995).

Furthermore, reefs are often affected by decisions taken in their drainage basins. For example, intensified land use and urbanization often increase run-off of pollutants, nutrients and sediment particles and cause major problems in the coral reefs (e.g. Kühlmann, 1988; Grigg and Dollar, 1990). Humans are thereby responsible for much of the change in the nature of disturbances in reef environments. Coral reefs seem to be resilient when facing natural disturbances with a periodicity occurring as pulses (e.g. hurricanes, predator outbreaks) (Connell, 1978; Grigg and Dollar, 1990; Connell, 1997). These disturbances seem to be a part of the dynamic development of coral reefs. However, chronic, persistent human induced disturbance (e.g. nutrient emissions and overfishing) appear to be more damaging to coral reefs (e.g. Richmond, 1993; Hughes, 1994; Connell et al., 1997). As a consequence, reef systems often show poor recovery when affected by natural disturbances if they have already been exposed to persistent human disturbances (Brown, 1997). This is presumably a consequence of loss of resilience (buffer capacity), making the coral reef ecosystem more susceptible to natural disturbance that otherwise could have been absorbed (c.f. Holling, 1973). Loss of resilience may cause unexpected and non-linear cascading effects as well as system 'flips', i.e. when the state of the ecosystem is so altered that it enters a new stability domain—a change that can be essentially irreversible (Holling et al., 1995).

7.1. System flips

Coral reef degradation may lead to invasion by populations of non-reef building organisms such as soft corals or zoanthids, but more often mass coral mortality is followed by an invasion of algae; this changes the community from a high diversity coral-based ecosystem to a macroalgae-dominated system, with diminished genetic, species and functional diversity (Done, 1992). Such 'flips' may be regarded as mere noise over evolutionary time scales, but within human life spans they certainly result in the loss of fish production (Bouchon et al., 1992), and a number of other ecological services (Done, 1992; Jennings and Polunin, 1996).

Although coral reefs are extremely complex dynamic systems with multiple stable states (e.g. Done, 1992; Knowlton, 1992), there seem to be a few main factors that trigger the shift from coral to macroalgae-dominance: (1) reduction or disappearance of grazers (Hughes, 1994); (2) increased nutrient and sediment loads (Rogers, 1990; Goreau et al., 1997); (3) reduced competition from corals by inhibiting their growth (Done, 1992); (4) rapid increase in substratum area available for colonisation by algae that exceeds the grazing ability of resident herbivores (Hatcher, 1984; Done, 1992).

The classic example of an ecosystem flip from coral to macroalgae-dominance is from Caribbean reefs in Jamaica and elsewhere (e.g. Hay, 1984; Lessios et al., 1984; Carpenter, 1990; Hughes, 1994). Overharvesting of fish that predate on sea urchins led to increased abundance of the keystone grazer, the sea urchin *Diadema antillarum*. After being damaged by Hurricane Allen in 1980 the corals did first recover, as the urchins could suppress algal growth which had been stimulated by increased amounts of nutrients from land use change. However, *Diadema* then suffered from a pathogen which caused mass mortality. Coupled with overfishing of herbivorous fishes, the mass mortality removed virtually all the grazers and the flip, or slide, to a community dominated by fleshy, unpalatable algae was a fact. In this stability domain, coral recruitment is inhibited by macro algae growth (Bell and Elmetri, 1995). However, there are other researchers who claim that the role of overfishing and *Diadema* die-off is overestimated (Jackson, 1997) and that eutrophication is a major reason (Goreau et al., 1997).

The sustained algal growth and lack of reef recovery in Jamaica is presumably also due to recruitment areas ('source reefs') having been degraded or lost, causing a lack of supply of larvae of corals, other invertebrates, and fish (Goreau, pers. comm.). In this context it is important to take metapopulations of reef organisms into consideration: that is, to include in management the location of upstream reefs for recruitment to reefs hit by disturbances in order to replenish damaged population on reefs downstream (Harrison and Wallace, 1990; Done, 1994, 1995a,b; Roberts, 1997).

These kinds of system flips, with large changes in ecology and poor recovery after disturbance, are less reported from more species diverse regions although disturbances are as common (Indo-West Pacific) (Eakin, 1993; Paulay, 1997; Connell, 1997). Therefore, it has been postulated that coral reefs in the Caribbean may in general be less resilient since they seem to have fewer species within each functional group compared with reefs in the Indo-West Pacific (McClanahan et al., in press). Such aspects may be of great importance for the provision of ecological goods and services of coral reefs in the long run.

7.2. Bleaching

There are a variety of natural and human induced disturbances affecting the delicate balance between the reef corals and their symbiotic microalgae (zooxanthellae). This often leads to loss of the zooxanthellae (or their pigment), a process called bleaching because corals lose their color (e.g. Brown, 1987; Goreau and Hayes, 1994). During 1997–98, coral bleaching was reported from all the major tropical oceans, implying that this is the most geographically widespread bleaching ever recorded. This mass bleaching is probably caused by elevated water temperatures, linked to one of the strongest El Niños of this century (ISRS, 1998). In addition, there are various other stresses that may lead to bleaching, including decreased salinity as a consequence of enhanced run-off due to clear-cuttings and urbanisation (Moberg et al., 1997), release of toxic substances such as heavy metals (Harland and Brown, 1989), and high UV radiation (Goreau and Hayes, 1994). Hence, impacts of human decisions taken elsewhere (e.g. in forestry or in cities) are impairing functions at the cellular level of reef corals. A disturbed symbiosis will affect coral nutrition, metabolism and the overall calcium balance in the reef system (e.g. Richmond, 1993). This will influence the resilience of the reef community at the ecosystem level and thereby the capacity of the reefs to generate essential ecological goods and services. Another thing that might affect reef calcification is the threat from human-induced increases in CO_2 in the air, resulting in decreased concentrations of carbonate in the water, and as a consequence, reduced growth of reef corals (Brown, 1997; Pennisi, 1997).

8. Concluding remarks

We have emphasized that to secure the capacity of coral reefs to supply humanity with ecological goods and services the resilience of reefs must be conserved. Loss of resilience is caused by unsustainable uses of the reef itself as well as unwise and inefficient fisheries management (Ludwig et al., 1993; Jackson, 1997). It is also caused by impacts on the marine environment from many uncoordinated human activities in the coastal zone and on land. Human impacts on coral reefs can have far reaching consequences on adjacent ecosystems such as mangroves, sea-grass beds and the open ocean, and vice versa. Therefore, coral reefs cannot be managed in isolation. To conserve the resilience of these complex systems we have to adopt an ecosystem approach (Christensen et al., 1996; Hatcher, 1997) that addresses management of coral reefs in the context of the seascape (Ogden, 1988; Done, 1994, 1995b). This approach has to recognise that the seascape in turn is affected by land use decisions in its drainage basin (e.g. Johannes, 1975; Done, 1995b; Birkeland, 1997a; Goreau et al., 1997; Done and Reichelt, 1998; Folke and Falkenmark, 1998).

The situation for coral reefs, in particular fringing reefs, is serious (e.g. Gomez, 1997). Humanity may choose consciously or unconsciously to continue to destroy coral reefs worldwide in the name of development. In our opinion it would be very sad for current and future generations to lose these unique ecosystems. To conserve the capacity of coral reefs to generate ecological goods and services requires innovative national and international policies, incentives, and effective institutional arrangements.

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