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THE EXPLOITATION AND CONSERVATION OF PRECIOUS CORALS*

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Abstract Precious corals have been commercially exploited for many centuries all over the world. Their skeletons have been used as amulets or jewellery since antiquity and are one of the most valuable living marine resources. Precious coral fisheries are generally characterized by the 'boom-and-bust' principle, quickly depleting a discovered stock and then moving on to the next one. Most known stocks are overexploited today, and populations are in decline. The unsustainable nature of most fisheries is clearly revealed by analyzing all available data. Precious corals belong to the functional group of deep corals and are important structure-forming organisms, so called ecosystem engineers, that provide shelter for other organisms, increasing biodiversity. Yet, their management is usually focused on single species rather than a holistic habitat management approach. This review compares the biology of precious corals as well as the historical ecology and the socioeconomy of their fisheries to improve precious coral management and conservation. The analysis demonstrates that a paradigm shift is necessary in precious coral exploitation, not only to conserve habitats of high biodiversity but also to achieve sustainable fisheries and stabilize a specialized jewellery industry.

Introduction

The exploitation of living marine resources for purposes other than for food and agricultural applications has a long tradition. Examples include coral, sponge and pearl fisheries, among others (Dall 1883, Russell-Bernard 1972, Pronzato 1999). Because they are in limited supply and coral jewellery can sell for high prices, precious corals are one of the most valuable marine resources. The use of precious corals as amulets or jewellery dates back millennia, and their industrial exploitation began many centuries ago (Tescione 1973). Their biology differs in many aspects from other commercially exploited marine organisms. Being sessile cnidarians, they are colonial organisms that depend on stable environmental conditions and are characterized by slow growth (Grigg 1984). The use

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of scuba-diving, remotely operated vehicles and manned submersibles improved our understanding of the population dynamics and ecological significance of these key species (Grigg 1976, Rogers 1999). However, in a similar way, advancing technology also permitted an overefficient exploitation (Food and Agriculture Organization [FAO] 1988, U.S. Department of Commerce 1989, Santangelo & Abbiati 2001, Grigg 2004, Tsounis et al. 2007). Apart from the slow renewal rate of this resource, the reason that all known stocks are overexploited are likely due to the same dynamics that can be observed in other fisheries (Pauly et al. 2002). The conflict between sustainable management and short-term economical interests, as well as the tragedy of the commons, are universal factors that have led to overexploitation of many commercial species. However, since precious coral populations provide shelter to other marine organisms and thus increase biodiversity or act as a fish nursery, managers realized the need for holistic management plans (Western Pacific Regional Management Council [WPCouncil] 2007, Magnuson-Stevens Fishery Conservation and Management Act).

There are currently sufficient data to create complete management models for only a few species, so simple models have to be used (Grigg 2001, Tsounis et al. 2007). In the future, density-dependent full-population models may help predict exploitation limits that allow harvested populations to maintain their ability to fulfil their ecological function (Caswell 2001, Santangelo et al. 2007).

While ecologists develop better models to sustainably manage the marine environment, it is wiser to apply conservative exploitation limits (Sutherland 2000). In the case of precious corals, errors in ecosystem management take especially long to rectify and may have permanent consequences that likely affect their entire ecosystem. This is therefore a critical moment for managers and decision makers wishing to preserve not only these habitats of high biodiversity, but also a traditional industry that unites the craft of fishing with the talent of jewellery artists, together enriching our culture.

To contribute to improving precious coral fishery management, this review analyses historical data on the exploitation of precious corals, summarizes the current knowledge of their ecology, identifies gaps of knowledge and discusses their management and conservation.

Ecology of precious corals

Taxonomic classification and functional definition

Precious corals belong primarily to three orders of the class Anthozoa (phylum Cnidaria), which are the Gorgonacea, Zoanthidea (subclass Hexacorallia; see Cairns et al. 2002), and Antipatharia (subclass Ceriantipatharia; see Cairns et al. 2002). The most valuable species are red and pink corals of the genus *Corallium* in the order Gorgonacea, such as the legendary Mediterranean red coral (*Corallium rubrum,* Figure 1), as well as the Pacific species *Paracorallium japonicum*, *Corallium elatius*, *C. konojoi* and *C. secundum*. Another important group of precious corals are black corals in the order Antipatharia. At least 10 species (mostly from the genus *Antipathes*) from the 150 species known worldwide are used in the jewellery industry. Other gorgonians used for jewellery are gold corals from the families Gerardiidae and Primnoidae (*Primnoa resedaeformis*, *P. willeyi, Narella* spp., *Callogorgia* sp.), as well as bamboo corals in the family Isididae (*Acanella* spp., *Keratoisis* spp., *Lepidisis olapa*). Semiprecious species, mainly stylasterine corals, *Allopora* in the class Hydrozoa, blue corals (*Heliopora*), *Tubipora* and several gorgonians in the family Melitodiidae, are used for jewellery to some extent but are of low value due to their skeleton quality and thus are not dealt with here in detail. Reef-building stony corals (Madreporaria or Scleractinia) are also of commercial value, but generally not within the jewellery industry (due to their pores) and are thus not considered as precious corals.

As a result of their bathymetric range, habitat preference and ecological role, precious corals belong to the functional group called “structure-forming deep corals” (Rogers 1999, Lumsden et al. 2007). By increasing 3-dimensional structural complexity, they provide habitat for commercially

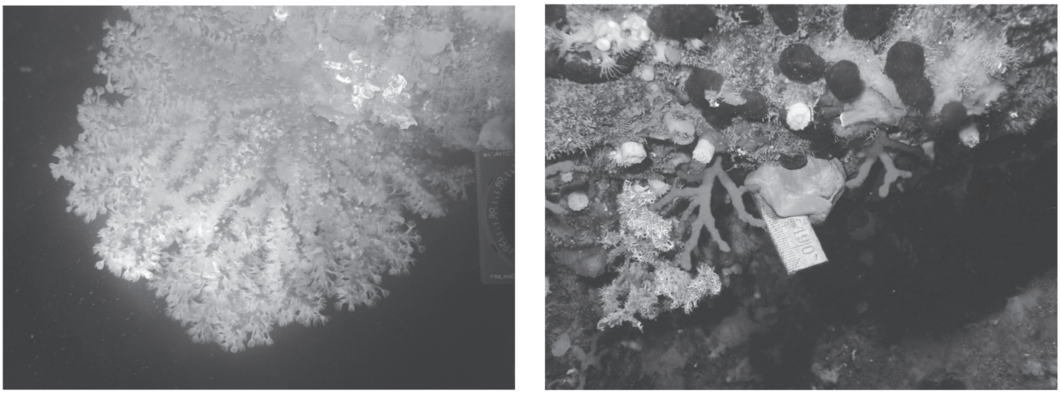

Figure 1 (See also Colour Figure 1 in the insert following page 212.) Unusually large red coral colony of nearly 20 cm (left) and an average sized colony of 3 cm height (right). (Courtesy of Georgios Tsounis (left) and Sergio Rossi (right).)

important fish species (Witherell & Coon 2000, Krieger & Wing 2002). Thus, the inclusion of precious corals in this group furthermore acknowledges their ecological significance. They have a complex branching morphology and sufficient size to act as refuge for other organisms. Some structure-forming deep corals are reef building, but precious corals are non-reef-building deep corals. Deep corals live mainly in continental shelves, slopes, canyons and seamounts, in depths of more than 50 m (although some species also extend into shallower water).

However, true deep-sea organisms are generally defined as those occurring deeper than the continental shelf (i.e., deeper than 200 m), whereas the term deep corals refers to corals that are neither shallow water corals nor true deep-sea organisms.

Deep corals are slow growing, long-lived organisms that are sensitive to disturbance such as dredging or extraction. Little is known about the gene flow between populations (Baco et al. 2006) and the need for their conservation results from the increasing anthropogenic impact on these organisms. Even though some deep precious corals have been exploited since antiquity, they have been known to science only since Carl von Linné (Linnaeus) published his *Systema Natura* in 1758. Today, they are the least-understood group of all corals (Rogers 1999, Roberts et al. 2006).

Deep coral communities are ‘hot spots’ of biodiversity and have been identified as a habitat for commercially important species of rockfishes, shrimp and crabs (Koenig 2001, Husebø et al. 2002, Krieger & Wing 2002, Freiwald et al. 2004, Martensen & Fosså 2006). Furthermore, their biodiversity may provide numerous targets for chemical and pharmaceutical research because several sponges and gorgonian species contain bioactive compounds that have medical potential (Ehrlich et al. 2006). Finally, due to their worldwide distribution and the fact that some gorgonian species can live for centuries, deep corals provide a source for geochemical and isotopic data that serve as a proxy for reconstructing past changes in ocean climate and oceanographic conditions (Smith et al. 1997, 2000, 2002, Adkins et al. 1998, Weinbauer et al. 2000, Risk et al. 2002, Frank et al. 2004, Thresher et al. 2004, Williams et al. 2007, 2009).

Primary threats to deep corals are damage by destructive fishing (i.e., bottom trawling; Witherell & Coon 2000, Krieger 2001, Hall-Spencer et al. 2002). Secondary threats include damage by entanglement in lost long lines and netting (Rogers 1999). The impact of pollution and siltation due to coastal development has not yet been studied. Secondary threats also include natural smothering by sediments, infection by parasites and invasion by alien species (Grigg 2004, Kahng & Grigg 2005, Kahng 2007). Global climate change and ocean acidification may alter the calcification of the skeleton of certain species and result in a weaker skeleton or lower rates (Hoegh-Guldberg et al.

2007). In the United States, the Magnus-Stevenson Act affirms the Regional Fishery Management Council's authority to protect deep-sea coral ecosystems as part of their fishery management plans without having to prove that corals constitute essential fish habitat.

A detailed review of deep corals can be found in the work of Rogers (1999), Roberts et al. (2006) and Lumsden et al. (2007). For the purpose of this review, the next section focuses on the biology of precious corals (Table 1).

General biological traits and ecological role of precious corals

All precious coral species are ahermatypic and non-reef building and occur in relatively deep water. Their skeletons consist of a complex of proteins or calcium carbonate. In general, they show a dendritic (arborescent) form, although some bamboo and black coral species grow in spiral or bushy form. Precious corals are long-lived organisms with low growth rates and low reproductive rates. Age at first reproduction is reached at a substantial age of more than a decade (except in *Corallium rubrum*, see p. 168). Many species can probably reach an age of more than a century (see Table 1).

Because precious corals lack zooxanthellae, they are benthic suspension-feeders, which means that they are sessile life forms on the seafloor that filter seston particles out of the water column (Cloern 1982, Officer et al. 1982). Their filtration rates are lower than those of sponges, bivalves and ascidians, but they do play an important role in pelago-benthic energy transfer processes (Fréchette et al. 1989, Kimmerer et al. 1994, Gili & Coma 1998, Riisgård et al. 1998, Arntz et al. 1999). They are usually gonochoric and brood their larvae, and some species synchronize their spawning (see next section). Fragmentation and reattachment (asexual reproduction; see Fautin 2002) appears to occur rarely in precious corals (Grigg 1994).

As in other corals, precious corals are important keystone species in various ecosystems because they provide 3-dimensional complexity to habitats, structuring and stabilizing the ecosystem (Hiscock & Mitchell 1980, Mitchell et al. 1993) and thus significantly increasing biodiversity (True 1970, Dayton et al. 1974, Jones et al. 1994, Jones & Lawton 1994, Gutiérrez et al., in press). An overview on the biology of the major precious coral groups is provided next.

*Tropical pink and red corals (*Corallium *and* Paracorallium *sp.)*

The genus *Corallium* (Cuvier 1798) along with the genus *Paracorallium* (Bayer & Cairns 2003) belong to the family Corallidae (Lamouroux 1812) and contain the most valuable precious corals due to their hard calcium-carbonate skeleton. Thirty-one *Corallium* species are known, of which seven species are currently used for jewellery (Cairns 2007): *Corallium secundum, C. regale, C. elatius, C. konojoi, C.* sp. nov., *C. rubrum*, and *Paracorallium japonicum*. Because it has been particularly well studied and is geographically separated from the other *Corallium* species, the Mediterranean *Corallium rubrum* is discussed separately (see next section).

Corallium species are found throughout the world in tropical, subtropical and temperate oceans (Grigg 1976, Bayer & Cairns 2003), including five species in the Atlantic, two from the Indian Ocean, three from the eastern Pacific Ocean, and 15 from the western Pacific Ocean (Grigg 1976, Cairns 2007). They have also been found on seamounts in the Gulf of Alaska (Baco & Shank 2005, Heifetz et al. 2005), the Davidson Seamount off the California coast (DeVogeleare et al. 2005) and the New England Seamounts in the Atlantic (Morgan et al. 2006). The depth range of this genus extends from about 100 to 2400 m (Bayer 1956), which is a broader range than found in *C. rubrum*. Dense tropical *Corallium* populations of commercial interest have been exploited at 200–500 and 1000–1500 m off Japan, the Island of Taiwan, Midway Island and the Emperor Seamounts. Near Japan, *Paracorallium japonicum* can be found at depths of 76 to 280 m on rocky bottoms in Sagami Bay on Japan's Pacific coast, as well as between the Ogasawara Islands and Taiwan, and near the Goto Islands. Pink coral (*Corallium elatius*) is found between 100 and 276 m at Wakayama at the

Table 1 Biology of precious coral species

Species	Common name	Zoogeographic distribution	Depth range (m)	Maximum height (cm)	Growth rate (height)	Growth rate (diameter) mm yr^{-1}	Maximum age (yr)	Reference
Corallium rubrum	Red coral	Mediterranean and neighbouring Atlantic shores	7–300	50	1.78 + 0.7 mm yr^{-1}	0.24 ± 0.05	ca. 100	Marchetti 1965, Tescione 1973, Zibrowius et al. 1984, Garrabou & Harmelin 2002
						0.34 ± 0.15		Marschal et al. 2004
						0.62 ± 0.15		Bramanti et al. 2007
Corallium secundum	Pink coral, angel skin, boké	Hawaiian Archipelago	340–475	75	0.9 cm yr^{-1}		45	Grigg 1974, 2002
						0.17	>90	Roark et al. 2005
Corallium sp. nov.	Midway deep-sea coral	Midway Island to Emperor Seamounts (W. Pacific)	700–1500	—	—			Grigg 1984
Corallium konojoi	Shiro sango (white coral)	Japan to northern Philippine Islands	50–382	~80	—	0.58		Kithara 1902, Kishinouye 1903, Grigg 1984, N. Iwasaki & Suzuki in press
Corallium elatius	Momoiro sango (red coral)	Northern Philippines to Japan	150–330	110		0.19 ± 0.15		Kithara 1902, Grigg 1984, N. Iwasaki & Suzuki in press
						0.15		Hasegawa & Yamada in press
Corallium regale	Pink coral	Hawaii	390–500	—	0.58			Bayer 1956
Paracorallium japonicum	Aka sango (red coral)	Japan, Okinawa and Bonin Islands	100–300	~100		0.3 ± 0.14		Kithara 1902, Grigg 1984, N. Iwasaki personal communication
Antipathes griggi	Black coral	Major Hawaiian islands	30–100	250	6.4 cm yr^{-1}			Grigg 1976, 1984
						0.18–1.149		Roark et al. 2005
Antipathes grandis	Black coral	Major Hawaiian islands	45–100	300	6.1 cm yr^{-1}		50	Grigg 1976, 1984
Antipathes salix	Black coral	Caribbean	190–330	250	4.5 cm yr^{-1}			Olsen & Wood 1980, Brook 1889

(continued on next page)

Table 1 (continued) Biology of precious coral species

Species	Common name	Zoogeographic distribution	Depth range (m)	Maximum height (cm)	Growth rate (height)	Growth rate (diameter) mm yr^{-1}	Maximum age (yr)	Reference
Gerardia	Gold coral	Hawaii, Caribbean	300–600	250	6.6 cm yr^{-1}		250 ± 70	Grigg 1984, Messing et al. 1990
							1800 ± 300	Druffel et al. 1995, Goodfriend 1997
						0.014–0.045	450 ± 2742	Roark et al. 2005
Primnoa resedaeformis	Gold coral	South-east Alaska to Amchitka, Aleutian Islands	50–80	—	4–5 m			Cimberg et al. 1981
			65–3200					Sherwood et al. 2005
		(NE Atlantic)	64–457		1.5–2.5 mm		320	Risk et al. 2002
Primnoa willeyi	Gold coral	South-east Alaska to Amchitka, Aleutian islands	50–80	—	—			Cimberg et al. 1981

Pacific coast, from the Ogasawara islands to the northern China Sea, and off the Goto Islands. One of the largest *C. elatius* specimens was harvested off Okinawa in 2006. It measured 1.1 m in height and 1.7 m in width and weighed 67 kg (Iwasaki & Suzuki in press). *Corallium konojoi* is distributed at all of these locations at a similar depth range. (N. Iwasaki personal communication, Kishinouye 1903, 1904, Eguchi 1968, Seki 1991, Nonaka et al. 2006, Nonaka 2010).

In the Hawaiian Islands, *C. secundum* has been found to grow on flat exposed substrata, whereas *C. regale* prefers encrusted uneven rocky bottom habitat (Grigg 1975). Both species are absent from shelf areas (<400 m depth), off populated islands, and substrata periodically covered with sand and silt (Grigg 1994). Similar to red coral (Tsounis et al. 2006c), other *Corallium* species exposed to the Kuroshio current have been found to dwell in shallower water than usual, which may be attributed to the high productivity of this turbid zone (Kuroshio means black current in Japanese). Because Mediterranean red coral thrives better under turbid conditions and has a varied diet, it may be that the diet spectrum among *Corallium* species is similarly broad, also including particulate organic matter (see p. 168).

Corallium species have a hard intense red or pink calcium carbonate skeleton, and Pacific species can grow to over 1 m in height (Iwasaki & Suzuki in press). The lifespan of most species has been estimated at about 45–100 yr. Growth rates are low (see Table 1). In *C. secundum*, studies using growth ring analysis resulted in an estimate of 9 mm height increase yr^{-1} (Grigg 1976), but radiometric studies indicated that growth rings in other species may not be annual and growth rates might be slower (Roark et al. 2006). However, even among modern radiometric techniques there are contradictions between the data (see p. 172).

Other species have been found to grow considerably slower: 0.3 ± 0.14 mm yr^{-1} (*Paracorallium japonicum*), 0.19 ± 0.04 mm yr^{-1} (*Corallium elatius*), and 0.58 mm yr^{-1} (*C. konojoi*) (N. Iwasaki personal communication). *Corallium konojoi* has been recorded to reach 30 cm, while *Paracorallium japonicum* and *C. elatius* reach a height of 1 m (Iwasaki & Suzuki in press). Few data on the reproductive biology are available at present for species other than *C. rubrum* and *C. secundum* (Kishinouye 1903, 1904). The latter reaches sexual maturity at 12 yr.

Corallium secundum has been found to coexist in the same depth zone and habitat with bamboo coral (*Lepidisis olapa*) and the parasitic gold coral (*Gerardia* spp.) at nearly 400 m depth off Makapu'u, Oahu (Grigg 1984). Populations of *Corallium secundum* in Hawaii (Makapu'u bed) were dominated by 15- to 20-yr-old colonies, and the oldest colonies found were 80 yr old (corresponding to a height of 80 cm). Natural mortality in the absence of fishing was estimated at 6% (Grigg 1984, 1994), three times higher than Mediterranean *C. rubrum* (Tsounis et al. 2007). Studies that used population trends to analyse fishing pressure found that coral abundance remained similar after a period of harvesting pressure that reduced the biomass by extracting older, larger corals (Grigg 2002). However, DNA microsatellite research suggested that the harvesting pressure on Hawaiian seamounts might have led to inbreeding suppression (Baco & Shank 2005).

Mediterranean red coral (Corallium rubrum)

The Mediterranean red coral (*Corallium rubrum* L. 1758, Gorgonacea, Octocorallia) is an arborescent gorgonian whose colonies can reach a height of 50 cm (Garrabou & Harmelin 2002). One of its main habitats is the hard substratum in the so-called coralligéne (Laubier 1966), where it is a characteristic species of high importance (Ballesteros 2006). The coralligenous zone extends from the lower photophilic algae to more than 100 m depth. Calcareous algae growing on coarse gravelly substrata coalesce the calcareous sediments to form a continuous, organogenic substratum on which a community develops that is comparable with tropical coral reefs in its diversity and complexity (Margalef 1985). The name 'coralligenous' may originate from findings of red coral branches and calcareous organisms in trawling hauls of semidark sublittoral bottoms with coarse gravel, which were thought to be "generators of coral" (Ros et al. 1984). According to other authors, the term coralligenous originated from the coralline algae (calcareous algae), which form the secondary substratum on which the whole coralligenous community settles (Sarà 1969).

Red coral is one of the most long-lived inhabitants of the coralligenous, possibly living for more than 100 yr (Riedl 1983, García-Rodríguez & Massó 1986a). It is a sciaphilous species that can be found in depths of 5–800 m, although more commonly at 30–200 m (Carpine & Grasshoff 1975, Rossi et al. 2008, Costantini et al. 2009), and is distributed throughout the Mediterranean and the neighbouring Atlantic coasts (Marchetti 1965, Tescione 1973, Zibrowius et al. 1984, Chintiroglou & Dounas-Koukouras 1989). Its commercial beds, however, are found in Sardinia, Corsica, Elba, southern Italy, Croatia, the Greek islands, Turkey, Mallorca, Alboran Sea, Costa Brava, southern France and the northern African coast (Liverino 1983). Other precious corals occur exclusively in deeper water, mainly below the euphotic zone (Grigg 1984).

Red coral is one of the most thoroughly studied gorgonians because it has been of interest to science since the controversies over whether it should be included in the plant or animal kingdom (Marsili 1707). Lacaze-Duthiers's pioneering (1864) study on the biology of red coral started a series of studies on its reproduction, growth and population dynamics.

Gorgonians usually have a protein (gorgonin) skeleton, but red coral grows a calcium carbonate skeleton that owes its red colour to a carotenoid pigment of unknown function (Cvejic et al. 2007). Furthermore, it is calcitic instead of aragonitic, as scleractinian skeletons usually are (Dauphin 2006). Long-term experimental data showed that it took 22 yr for red coral colonies growing within a cave to grow to colonies of 4- to 8-mm thick and 1.3–7 cm in height, with corresponding growth rates of 0.24 ± 0.05 mm yr^{-1} in base diameter and 1.78 ± 0.7 mm yr^{-1} in height (Garrabou & Harmelin 2002). The 22-yr-old corals developed only one to eight branches, further stressing how long it takes for these organisms to provide habitat structure. However, these corals grew in particular conditions (a cave) with relatively little water movement, and because suspension-feeders depend not only on seston concentration but also water movement to feed (Gili & Coma 1998), their energy input, and consequently growth rates, vary according to the habitat. Other *in situ* experimental observations therefore determined a diametric growth rate of red coral of 0.62 ± 19 mm yr^{-1} during its early life phase (Bramanti et al. 2005). Furthermore, a new sclerochronological method, which stains the organic skeleton matrix, found an average diametric growth rate of 0.35 ± 0.15 mm yr^{-1} in colonies from a variety of environments (Marschal et al. 2004).

Studies of the natural feeding of red coral have in fact found some variability between habitats, which may partly explain some of these findings. Red coral feeds mainly on organic matter and zooplankton (Tsounis et al. 2006c), although pico- and nanoplankton are also part of their diet (Picciano & Ferrier-Pages 2007). Due mainly to hydrodynamics, red coral colonies on the Costa Brava at 45 m depth captured more particles than shallower ones, and the seasonal fluctuation of capture rates was dampened by the constant availability of particulate organic matter (Tsounis et al. 2006c).

Probably the best-understood aspect of red coral biology is its reproductive cycle, thanks to a long series of studies that were motivated by its commercial importance. Most gorgonians seem to reproduce primarily sexually (Gili & Coma 1998), and because this method is more efficient in dispersing the population than asexual reproduction, most research has focused on sexual reproduction. *Corallium rubrum* is a gonochoric brooder with internal fertilization that releases lecitotrophic larvae during late summer (Vighi 1972). Female oocytes develop for more than a year, so that two generations can be found within the polyps, of which only the larger, mature ones are released (Santangelo et al. 2003, Tsounis et al. 2006a). Under certain environmental conditions, the polyps can reabsorb their oocytes and use the material to produce fewer, larger ones or not spawn at all (Santangelo et al. 2003, Pablo Lopez, University of Seville, personal communication). The male gonads develop in less than 12 months.

Red coral is characterized by a higher recruitment rate than most other octocoral species, which are generally considered organisms with relatively slow colonization and recovery rates (Grigg

1989, 2004, Garrabou & Harmelin 2002, Bramanti et al. 2007). *Corallium rubrum* reaches sexual maturity at an age of 3–10 yr (Santangelo et al. 2003, Torrents et al. 2005, Tsounis et al. 2006a), whereas even the relatively fast-growing black coral *Antipathes griggi* reproduces only after reaching 12–13 yr (Grigg 1976). Data showed that selective harvest in fish has lead to 'undesirable evolution' that results in commercial stocks growing to a smaller size (Conover et al. 2009). Similarly, it is possible that early reproduction and small size in *Corallium rubrum* is a response to the millennia of fishing pressure it has experienced.

Larvae are reported to show no pronounced phototaxis but do exhibit negative geotaxis and gregariousness (Weinberg 1979). They develop their negative geotaxis only after an initial period of positive geotaxis, and their free-swimming phase lasts only hours or days (Weinberg 1979, FAO 1983), which results in a limited dispersal distance of red coral larvae. It is therefore very likely that most populations are genetically isolated. In fact, recent studies demonstrated the occurrence of genetic differences among populations even over short distances of less than 3 km (del Gaudio et al. 2004, Calderon et al. 2006, Costantini et al. 2007a,b, 2009). As a result of slow growth and short larval dispersal distance, populations in some overharvested locations have been quickly reduced to few young populations that may not be connected with each other (Weinberg 1978, Plujà 1999, Rossi et al. 2008). This vulnerability to isolation has implications for the management of this species because it is often assumed that deep populations act as a refuge by providing larvae to the shallower ones. Furthermore, since red coral shows a uniquely broad depth range and remarkable morphological variation, the question whether these populations actually belong to the same species has been raised (Y. Benayahu personal communication). Future research may confirm whether deep populations are able to contribute larvae to shallow-water habitats.

Further implications of the reproductive biology of the species for the management of the fishery become apparent when taking population structure into account. To our knowledge, the only extensive study on the abundance of *C. rubrum* has been conducted on the Costa Brava and indicated an extreme patchiness, with a total colony abundance on coralligenous hard substratum (20–50 m depth) of 3.42 ± 4.39 colonies m^{-2} (Tsounis et al. 2006b). Due to geographic variation, this study is certainly not representative for the whole Mediterranean. The only comparable data available are on the abundance within patches, which varies considerably among geographic locations as well as between depths and habitats and is not indicative of total abundance. Values recorded range among 1300 colonies m^{-2} in Calafuria, Italy, 130 colonies m^{-2} at the Costa Brava (Spain), and 400–600 colonies m^{-2} in France (Santangelo et al. 1993a, 1999, Garrabou et al. 2001, Tsounis et al. 2006b, Rossi et al. 2008). For other regions, presence or absence may be recorded, but in general there is a lack of data on abundance.

Red coral abundance on the Costa Brava is inversely proportional to depth; deep habitats are characterized by a more scattered distribution, in contrast to the dense patches observed in shallow water (Tsounis et al. 2006b, Rossi et al. 2008). This distribution pattern can have implications for the harvest of deep populations because a low abundance may make exploitation unfeasible. In general, the extreme patchiness results in such a high standard deviation that abundance data are of no particular use for abundance comparisons and identification of population decline. In the case of *C. rubrum*, size and age structures give a better indication of population decline because the fishery is size selective, and a decline in numbers will inevitably coincide with a decline of large colonies. Data on population structure are also more useful in identifying a trend in proportion of mature and immature colonies, which is more useful as a basis for management decisions that need to ensure recruitment is sufficient for the population to survive.

The presently observed size–frequency distribution in shallow water shows that unprotected populations consist mainly of small corals under 8 cm height, with an average height of 3.1 ± 0.16 cm, and an average basal diameter of 5.1 ± 2.0 mm yr^{-1} (Tsounis et al. 2006b), which corresponds to an age of 8–15 yr (Marschal et al. 2004, Bramanti et al. 2007). In comparison, a population protected for 15 yr had an average height of 4.2 ± 2.5 cm, and an average basal diameter of 6.9–2.4 mm (Tsounis et al. 2006b), that corresponds to an age of 11–20 yr (Marschal et al. 2004, Bramanti et al. 2007). In the same area, palm-sized colonies could be found in the 1960s at 35 m depth (J.G. Harmelin personal communication).

Results from two biological studies on the stocks off Morocco revealed a similar situation and confirmed the observed pattern; average height of colonies in two harvested stocks was 7.25 cm (Topo–Cala Iris) and 6.4 cm (Sidi Hsein), with an overall size range of 3–13 cm (Abdelmajid 2009, Zoubi 2009). These data originate from subsampling the harvesters' catches, so the actual average size may be even lower.

The only two published demographic studies on red coral populations below 50 m show that harvesting pressure is proportional to the degree of accessibility of the sites to divers (Rossi et al. 2008, Angiolillo et al. 2009). These populations were heavily dredged until 1994 and appear to consist of 10- to 16-cm tall colonies that show a well-developed branching pattern but an average basal diameter of only 9 mm (Rossi et al. 2008, Angiolillo et al. 2009).

Causes of the young population structure other than fishing impact can be excluded, or at least regarded as insignificant compared with fishing mortality, as natural disturbances are likely to affect young colonies more than older ones. Therefore, a dense, young population structure may indicate an early recovery stage after a disturbance. The study of natural *C. rubrum* populations certainly has to deal with the lack of a baseline; however, video observations by coral divers harvesting at 90–110 m in Sardinia confirmed the frequent occurrence of 50- to 60-cm tall colonies in these populations (M. Scarpati personal communication). Natural mortality in red coral is relatively low, a trait shared with other precious corals (Harmelin 1984). Natural mortality may be increased by the parasitic boring sponges *Spiroxya heteroclite* and *Cliona sarai,* which affect the corals by perforating their bases until they are perfused with holes and lose structural stability. Except on granite, it appears that the sponges enter the corals via the substratum (G. Bavestrello personal communication). Older corals are affected at a higher rate, with a noticeable increase after 4 yr (Corriero et al. 1997). Interestingly, the apical parts are never infected by the sponges, so it can be deduced that they cannot penetrate the live coenosarcs. Apart from the fact that colonies above a certain size may no longer be supported by the perforated stem, these corals are also of less value for the jewellery industry (Bavestrello et al. 1992, Corriero et al. 1997). Other parasites may potentially increase mortality (Abbiati & Santangelo 1989), and interspecific competition may further influence the population structure of red coral (FAO 1983, Giannini et al. 2003). However, both have an insignificant effect compared with harvesting.

Another cause for increased mortality in *Corallium rubrum* is mass mortalities (Cerrano et al. 2000, Garrabou et al. 2001, Bramanti et al. 2005, 2007), which have been reported as early as or earlier than 1983 in the French maritime province (FAO 1983), but very little is still known about the cause of these episodes. The fact that they manifest themselves during abnormally warm summers suggests that temperature tolerance may be a contributing factor, as may pathogenic agents or pollutants (Garrabou et al. 2001). *Corallium rubrum* is reported to be tolerant of high temperatures and even sudden temperature peaks (FAO 1983). However, because Mediterranean suspension-feeders suffer a trophic crisis due to low plankton abundance and water movement in summer (Coma et al. 2000, Rossi & Tsounis 2007), physiological stress (starvation) could be a further contributing factor. Not surprisingly, the affected red coral populations seem to be the shallower ones because the partial or total mortality decreases with depth and is insignificant below 40 m (Linares et al. 2005). In general, though, natural mortality appears to be low, a conclusion based on a single experiment on growth and survival in a cave (Garrabou & Harmelin 2002).

Consequently, the extremely young population structure is a direct result of overharvesting (Santangelo et al. 1993b, Santangelo & Abbiati 2001, Tsounis et al. 2007). The history of intensive fishing (see p. 176) also has its impact on scientific studies because even the oldest marine protected areas are too young to serve as a baseline for the study of the red coral population structure. Specimens in museums and private collections demonstrate that this species can reach a size of more than 50 cm (Bauer 1909, Barletta et al. 1968, Cicogna & Cattaneo-Vietti 1993, Garrabou & Harmelin 2002), but the percentage of these large colonies in a natural population is not known.

*Black coral (*Antipatharia*)*

Seven families and about 150 black coral species are known today, most of which are antipatharians (hexacorals with branched or unbranched skeletons). Their protein skeleton is dark brown to black and of a consistency resembling hardwood, but their tissue and polyps make them appear rust, yellow, green or white. The genus can be found in all oceans, from New Zealand fjords in the temperate Pacific (Grange 1997), through the tropical Pacific (Grigg 1965), the Caribbean (Olsen & Wood 1980), to the Canary Islands and Mediterranean submarine canyons (Davidoff 1908). They mainly prefer deep-water habitats of tropical and subtropical oceans (Lumsden et al. 2007). Only a few species are of commercial interest. Many species, even harvested ones, are little known, thus the following information relates especially to the main commercial species.

The best-studied black coral species are the two most important commercial species, *Antipathes grandis* and *A. griggi* (a redescription of *A. dichotoma*, Opresko 2009), which are distributed over the tropical Pacific between 30 and 100 m depth (Grigg 1976). Together with red coral and the semi-precious bamboo coral, these black corals are the only precious corals that dwell at depths shallow enough to be harvested by scuba divers.

Populations in the Hawaiian Islands show the highest densities on hard, sloping substratum in areas exposed to 0.5- to 2-knot currents (Grigg 1965). *Antipathes* spp. preferably settle in depressions, cracks or other rugged features along steep ledges, with few colonies found on smooth basaltic substratum (Grigg 1965). The lower depth limit of the distribution coincides with the top of the thermocline in the Hawaiian Islands (ca. 100 m; Lumsden et al. 2007). Some other black coral species occur in shallow water, underneath ledges and in caves (*Cirrhipathes anguina* can occur at 4 m depth). Depth appears to influence the distribution of various coral taxa, whereas substratum and environmental conditions (flow, sedimentation) seem to influence patchiness of precious corals (Grigg 1976).

Several black coral species, especially *A. grandis* and *A. griggi*, are large branching species and therefore important structure-forming corals (Parrish et al. 2002). Their erect branching structure creates substratum for attachment of sponges, tubeworms, barnacles, molluscs, anemones and echinoderms and provides shelter from predators for small fishes, as well as a sleeping perch for large fishes and rock lobsters (Warner 1981, Grange 1985). A study in the Hawaiian Islands revealed that populations of the endemic and highly endangered Hawaiian monk seal (*Monachus schauinslandi)* forage on fish species thriving among black coral communities (Goodman-Lowe 1998, Parrish et al. 2002, Boland & Parrish 2005, Longenecker et al. 2006). Species that associate with *Antipathes* include 17 different pontoniine shrimp from the Indo-Pacific (Australia, Madagascar, Kenya, Maldives, Indonesia, Zansibar, New Caledonia, Borneo and Hawaii) and the Caribbean (Spotte et al. 1994). Many invertebrate species have been found only among antipatharians (Love et al. 2007).

Black coral is known to grow to heights exceeding 4 m. Growth rates are low, as *in situ* observations and growth ring analysis demonstrated (Brook 1889, Grigg 1976, Olsen & Wood 1980; see Table 1)—6.12 cm yr^{-1} (*A. grandis*) and 6.42 cm yr^{-1} (*A. griggi*)—although not as low as temperate water black corals (1.6–3 cm yr^{-1}, *A. fjordensis*; Grange 1997) or *Corallium* species. The oldest specimens of *Antipathes grandis* and *A. griggi* observed in Hawaii are reported to be 75 yr old (WPCouncil 2007), which was supported by radiometric data (Roark et al. 2005).

Other black coral species have been estimated to live longer than a century (Love et al. 2007, Williams et al. 2007), while Roark et al. (2005) estimated a lifespan of 2377 yr for *Leiopathes glaberrima*. The diet of *Antipathes grandis* and *A. griggi* is largely unknown (Grigg 1965, Lewis 1978, Warner 1981).

Sexual maturity in *A. grandis* and *A. griggi* is reached at a size of 64–80 cm, corresponding to an age of 10–12.5 yr (Grigg 1976). This is typical for the K-selection generally observed in deep corals. Observations of natural recruitment seem to be scarce, however, indicating recruitment limitation in Hawaiian *Antipathes* populations. The temperate species *A. fjordensis,* a gonochoric broadcast spawner with a seasonal reproductive pattern (Parker et al. 1997), reaches maturity at a similar size range (70–105 cm) but at a notably higher age of 31 yr (Parker et al. 1997).

In *A. grandis* and *A. griggi,* fertilization takes place externally in the water column (broadcast spawning), and their larvae are negatively phototactic. Data on deep-water genera of black corals are still scarce. Their morphology can be branched, feathered (*Myriopathes*, *Bathypathes* spp., *Stauropathes* and *Leiopathes*) or whip-like (*Stichopathes* spp.).

The age structure of an unfished *Antipathes griggi* population showed that juvenile corals under 20 yr old dominated the populations, and that 40-yr-old corals made up 2% of the population (Grigg 1976).

The invasive octocoral *Carijoa riisei* (snowflake coral) was first observed in Pearl Harbour in 1972 and has spread to the eight main Hawaiian Islands (Kahng & Grigg 2005). It overgrew large areas of substratum and adult colonies of black coral in 70- to 100-m depth in the Au'Au channel off Maui. The invasion may have contributed to a decrease in recruitment, diminishing a deep-water refuge that was assumed to contribute to recruitment of the intensively harvested shallower stocks. Results suggest that the invasion may have slightly abated (Grigg 2004, Kahng 2007), although further data are needed for confirmation (WPCouncil 2006, 2007). Therefore, the observed decline in biomass appears to be mainly due to harvesting of the stocks shallower than 70 m (Grigg 2004) rather than the invasion of *C. riisei*.

Little is known about black coral populations outside Hawaii.

Gold corals (mainly Gerardia *spp.)*

The Gerardiidae is a family about which very little is known, and its taxonomy is not well defined (Lumsden et al. 2007). Gold corals of the family Gerardiidae are found on hard substrata such as basalt and carbonate hard grounds on seamounts in the north and equatorial Pacific and Atlantic Oceans. In Hawaii, their depth range is 350–600 m and in the Straights of Florida at around 600 m (Messing et al. 1990). Gold corals are found in commercial quantities in the Hawaiian Islands (Grigg 1984, 2002). A *Gerardia* sp. fishery in Turkey was abandoned after learning that it served as substratum for several shark species to lay their eggs (B. Öztürk personal communication).

Gold corals in the order Zoanthidae are known to broadcast spawn during mass spawning events, but nothing is known about the reproductive strategies of *Gerardia* species except that their larval stages settle out on other coral species (particularly bamboo corals) and eventually overgrow those colonies (Lumsden et al. 2007). Gold corals of the genus *Primnoa* have skeletons of protein that are abundantly infused with calcite ($CaCO_3$) spicules (Grigg 1984).

Gold corals undoubtedly are quite long lived. However, there is considerable variation between data on the lifespan of *Gerardia* species among the various studies, probably resulting from different methods. Estimates by Grigg (2002) using growth ring counts indicated a maximum longevity of less than 100 yr for Hawaiian *Gerardia* species. A study using radiocarbon dating on *Primnoa resedaeformis* confirmed a similar maximum age of 78 yr in the north-western Atlantic Channel off Nova Scotia and confirmed that growth rings are annual for this species (Sherwood et al. 2005). Sherwood & Edinger (2009) found a slightly older age of 200 ± 30 yr for the same species and area. Risk et al. (2002) reported a lifespan of more than 300 yr for another *P. resedaeformis* colony collected off Nova Scotia. Goodfriend (1997) calculated an amino acid racemization age of 250 ± 70 yr on an Atlantic *Gerardia* specimen.

In contrast to these studies, Druffel et al. (1995) dated the same specimen to 1800 ± 300 yr. Slower growth rates and older lifespan were also reported by Roark et al. (2006), who used ^{14}C dating to measure growth rates that corresponded to ages of 450–2742 yr. The differences were explained by arguing that radiocarbon dating revealed that growth rings were not annual in these species (Roark et al. 2006). On the other hand, carbon dating accuracy can be affected by corals feeding on ^{14}C sources that have a different origin (and thus age) than assumed (Druffel & Williams 1990, Druffel et al. 1992). While this type of error is usually accounted for (Roark et al. 2006, Sherwood & Edinger 2009), there remain differences in growth rate measurements, even between radiocarbon studies. For example, Roark et al. (2006) reported a lifespan of 2377 yr for the black coral *Leiopathes glaberrima,* whereas Williams et al. (2009) found this and other black corals to have shorter lifespans of a few decades or several centuries.

Clearly, further research is necessary to resolve and understand these contradicting data (Parrish & Roark 2010). Therefore, the WPCouncil has issued a 5-yr moratorium on the fishing of gold coral until the lifespan is confirmed (WPCouncil 2006). However, the consensus of all studies at this point is that precious corals, including gold corals, are particularly long-lived species and are therefore vulnerable to overexploitation.

Other precious corals

Other important although less-valuable precious corals are the gold corals *Primnoa resedaeformis* and *P. willeyi* within the family Primnoidae. Primnoidae is a large family containing more than 200 species that are among the most common of the large gorgonians (Etnoyer & Morgan 2003, 2005). The family exhibits a particularly broad depth range of 25–2600 m, while most species occur shallower than 400 m. The commercially important *P. resedaeformis* dwells between 91 and 548 m (Cairns & Bayer 2005).

They grow branching colonies with a skeleton of a horn-like protein called gorgonin and can reach 4–5 m in height (Krieger 2001). Linear growth rates in the Gulf of Alaska have been found to be low, with just 1.6–2.32 cm yr^{-1}, and diametrical growth was estimated at 0.36 mm yr^{-1} (Andrews et al. 2002). Linear growth in *P. resedaeformis* is higher in the first 30 yr of its life (1.8–2.2 cm yr^{-1}) than after that (0.3–0.7 cm yr^{-1}). The oldest corals sampled in the Canadian Atlantic were 60 yr old (Buhl-Mortensen & Mortensen 2005), but large colonies in Nova Scotia were found to be hundreds of years old (Risk et al. 1998, 2002). Very little is known about their reproduction, but it is likely that they are gonochoric broadcast spawners similar to other octocorals (Fabricius & Alderslade 2001).

Another group of precious corals that deserves mention is bamboo corals in the family Isisidae (*Acanella* spp., *Lepidisis, Olapa*). This family consists of over 150 species that are primarily deep-water species. The most common deep-water genera are *Isidella*, *Keratoisis* and *Acanella*. Bamboo corals consist of skeletons with alternating sections of calcium carbonate and proteins (Lumsden et al. 2007). They are important structure-forming species in the Gulf of Mexico, Hawaii, south-eastern U.S. waters, the north-eastern Pacific and Indopacific (Fabricius and Alderslade 2001, Etnoyer & Morgan 2003). Although some genera have been reported from 10 to 120 m (Fabricius and Alderslade 2001), most species occur below 800 m (Etnoyer & Morgan 2005), with the deepest recorded at 4851 m (Bayer & Stefani 1987). Some species are bioluminescent (Etnoyer 2008).

Their morphology can be whip-like but is usually branched, bushy or fan-like, with sizes ranging from tens of centimetres to over 1 m (Verrill 1883). Their skeleton consists of heavily calcified internodes and gorgonin nodes, giving it a bamboo-like appearance. Diametric growth of *Lepidisis* sp. in New Zealand waters ranges between 0.05 and 0.117 mm yr^{-1}, with maximum ages between 43 and 150 yr (Tracey et al. 2007).

Culture and history of precious coral exploitation

Cultural significance of precious corals

Few other natural resources have fascinated humankind more than precious corals. The findings of perforated red coral beads with Paleolithic human remains demonstrates that corals have been treasured by humans for at least 25,000 yr (Tescione 1965, Skeates 1993). The history of precious corals starts with the Mediterranean red coral, the precious coral *par excellence*. In addition to its ornamental use in the Neolithic (3000–5000 yr ago), red coral also developed a tremendous cultural importance, as its appearance in decorative arts of the Minoan and Mycenean civilization documents (Tescione 1965).

Greek mythology originally elevated red coral to magical status (see Ovid's *Metamorphoses*). The ancient myth of Perseus killing the Gorgon monster Medusa, feared for her petrifying stare, states that on laying down Medusa's severed head, her blood seeped into seaweeds that were subsequently petrified and stained red. Red coral was born, and coral is therefore a symbol of rebirth. The legend of Medusa further states that Perseus gave Medusa's head to the goddess Athena, who used it as a shield against her enemies, which may explain why coral talismans are used for protection. It is also said that in petrifying the algae, some of Medusa's magic was conferred to the corals. The Romans ingested and applied coral powder as an antidote to poison, a cure against stings, comfort for fainting spirits, to counteract fascinations, to protect humans against sorcery, to purify the blood and to cure imbecility of the soul, melancholy, mania and other maladies. Protection against the shade of Satan is attributed to red coral in Christian cultures; in various other religions, it is a protector against the evil eye and any misfortune (Tescione 1973, Wells 1983). In Iranian beliefs, red coral protects against lightning and storms. In Buddhism, precious corals are revered as treasure from paradise and are used to decorate statues of Buddha (Kosuge 1993). The attractive blood red colour made it a symbol for the blood of Christ. Its hardness and the tree-like shape of its skeleton made it a symbol for immortality (hence the name 'tree of life'). Coral necklaces or coral branches are an element in many works of spiritual or religious art, such as the works of the fifteenth century Renaissance artists Piero della Francesca and Andrea Mantegna. Entire churches have been built thanks to economic wealth that coral fishing created, such as the church of San Giorgio built in 1154 in Portofino (Italy), which contains a chapel dedicated to coral fishermen (Mazzarelli 1915), the church of San Giovanni at Cervo, Italy (Liverino 1983), and the Sant Esteve in Begur (Spain).

As Marco Polo reported, red coral has been found as far away from the Mediterranean as ancient Tibetan temples. It has also been used as a decoration in Chinese clothes dating back several millennia (Knuth 1999). In the 1950s, coral beads were still widely used as ornaments on kimono belts in Japan (Liverino 1983). Similar protective powers were also attributed to black coral. According to Indonesian folklore, a black coral bracelet worn on the right arm increases virility, whereas on the left it cures rheumatism (Wells 1983). The name *Antipathes* translated from Latin means 'against disease', and Albertus Magnus mentioned corals used as cures. In addition to its ornamental use and its importance in religious rituals, precious corals were one of the most sought after exchange products on the oriental markets of the Phoenicians and Egyptians about 15 centuries before Christ. Pliny mentioned trade of red coral with India. Today, its use as an aphrodisiac or a cure is limited compared with its use as a raw material in the manufacture of jewellery and artistic sculptures (see p. 183). The high cultural importance of precious coral still lives; black coral is the official state gem of Hawaii, and red coral art has never lost its sacred fascination. When considering various management options (listed in that section), the cultural importance of the fishery and art should be taken into account.

History of coral exploitation

The origin of the name 'coral' is generally attributed to the Greek word for pebble ('korallion'), but Hebrew ('goral', meaning small pebble) and Arabic ('garal', small stone) origins are also possible, maybe due to the names given to them by early traders travelling between Europe and the Middle East (Hickson 1924). In ancient times, Mediterranean red coral was collected when washed up on beaches after heavy storms had broken off branches in shallow water. During these times, traders listed it as spice (S.J. Torntore personal communication).

Intentional precious coral exploitation, however, did not start until about 5000 yr ago in the Mediterranean, when iron hooks were used to harvest red coral (Grigg 1984). Greek islanders called these tools 'kouralió' (Tescione 1973). It can be assumed that this was done while free diving. At a later stage, the free divers were equipped with Japanese goggles that must have made the harvesting quite efficient, considering the warm summer water in the Mediterranean and the fact that red coral can still be found as shallow as 7 m in shadowed overhangs and crevices (G. Tsounis personal observation). Ancient artworks show swimmers emerging with large coral branches, indicating an abundance of large specimens. The efficiency of free diving should not be underestimated, as other examples of free-diving fisheries show. Greek sponge divers descended to considerable depths, even down to 80 m, using a marble stone as a weight (Mayol 2000), and the legendary Japanese Ama pearl divers made, and still make, a living by diving for pearls and shellfish in the Okinawa Islands and the Izu Peninsula (Hong et al. 1991, Hlebica 2000). The last example furthermore suggests that the early coral free divers might have harvested the sea for food at the same time as looking for red coral. Regarding the efficiency of early coral diving, it is significant to note that a recent study found that children of sea nomads in Thailand, who play and fish in the sea without goggles, possess better underwater vision than other children (an improvement that can be achieved by training; Gislén et al. 2003, 2006). We can therefore assume that harvesting pressure on precious corals in shallow water was considerable. Fishing by free diving was probably practiced in various Mediterranean Islands. The first coral-harvesting tools that could be employed from boats are dated to the fourth to third centuries BC, that is, during the Hellenistic, Roman-Carthaginian and late Etruscan ages (Galili & Rosen 2008).

Precious coral 'fishing' became more efficient during the fourth century BC when the Greeks or Arabs developed a dredging device known as 'ingegno' or 'Saint Andrews cross' (Galasso 1998, 2001). It consisted of a wooden cross with nets attached that was dragged along the bottom, entangling red coral in the Mediterranean Sea. Political struggles over existing coral beds, and the discovery of new ones, dictated the production at this early phase. Industrial-scale exploitation for red coral began during the early 1800s when the Kingdom of Naples probably employed more than 1000 boats dredging for coral. By 1870, this number had decreased to 612 (Tescione 1973).

Throughout history, there were various centres of coral jewellery manufacture. In the tenth and eleventh centuries, Marsa'el Karez on the northern African coast was the largest coral port and trade centre. In the fourteenth century, Barcelona was famous for its coral art (Lleonart & Camarassa 1987); later, the main activity shifted to Lisbon and in the seventeenth century to Marseille. Parallels between these shifts have been attributed to Jewish migrations (G. De Simone personal communication). From 1100 to 1600, Genoa was already one of the important centres, and in that century nearby Torre del Greco finally established a firm position in the coral-fishing business and remains the main centre of *Corallium rubrum* jewellery manufacture today (Tescione 1973, FAO 1988).

Many coral fisheries in the world are characterised by depleted stocks (Grigg 1989, Santangelo et al. 1993b, Santangelo & Abbiati 2001). This boom-and-bust exploitation, more similar to coal mining than to a fishery, made for unstable yields, with various peaks and troughs. As early as the 1800s, the coral-fishing fleets made substantial trips to foreign shores in search of new stocks (Tescione 1973). The following figures from G. Tescione's extensive compilation of historic data demonstrate the size of the industry. In 1862, there were 347 boats fishing for corals, which in 1864 rose to 1200 vessels fishing, with 24 factories in Torre del Greco (Italy) and 17,000 persons employed in total (Tescione 1973, FAO 1983). Political regime changes and wars were also responsible for unstable fishing, and coral fishing stopped completely during the WWI in 1914–1918. At about the same time, imports of Japanese coral started to reduce demand, and thus fishing, dramatically. The Italian coral industry adapted to market demand and crafted large coral pieces of the popular pale pink coral, but it struggled to survive. Demand for Mediterranean coral increased again, and apart from another pause during WWII (in 1941, there were only 5 boats active, which increased to 31 in 1947), larger-scale coral fishing was resumed. In 1982, there were 200 boats, 50 divers, and 150 factories, employing 4000 workers and 1600 fishermen.

A discovery of large beds of dead, subfossil red coral between Sicily and Tunis in the 1880s led to a 'coral rush' of 2000 vessels into the small area and quickly depleted those grounds, while lowering prices and reducing fishing in other areas (Tescione 1973). The area where the so-called Sciacca coral was found is subject to subsidence, volcanic activities and earthquakes, making it likely that undetermined geological processes had a fatal impact on the populations (Cicogna & Cattaneo-Vietti 1993). The coral trade therefore depended not only on the state of the resource but also on market forces and the political situation. Ironically, the Sciacca coral that drove prices down in 1880 is the most valuable *C. rubrum* variety today.

During the Industrial Age, the Saint Andrews cross was abandoned in favour of a modified metal version called 'barra italiana'. It was made of a heavy iron bar with nets attached along its length. Even with the most efficient coral dredges, it is estimated that only about 40% of the corals broken off the substratum are entangled and retrieved (FAO 1983). In 1876, dredging was forbidden temporarily by royal decree in Italy, allowing only diving in helmeted suits. In the light of the immense ecological damage that dredging inflicts on coral habitats (Thrush & Dayton 2002), coral dredging in European Union waters was banned in 1994, and scuba-diving using advanced technology remains the dominant exploitation method today. After the invention of the Cousteau/Gagnan Aqualung in 1943, scuba-diving quickly found its application in coral harvesting because it allowed divers to selectively pick large corals in protected crevices that were inaccessible to dredging. The first 5 kg of red coral harvested by scuba were brought to Torre del Greco in 1954 by the sport diver Leonardo Fusco, who became a professional scuba coral harvester after discovering coral while free diving in Palinuro near Naples (Liverino 1983). In his first season, he harvested 250 kg, which he sold for 15,000 Italian lire kg^{-1}. Quickly, the small circle of scuba pioneers in Italy (Guido Garibaldi, Alberto Novelli and Ennio Falco) became coral fishermen and discovered further banks in Sardinia, Elba and Corsica (Roghi 1966). Accidents also started to occur that same year. One of the most spectacular and valuable source of *C. rubrum* was discovered at that time in the legendary Capo Caccia Cavern in Sardinia at a depth of 37 m (Liverino 1983). Liverino reported that in 1956 divers worked at 30–35 m, but in 1958 at 40–45 m. By 1964, an ever-growing group of divers was working at depths of 72 m, and inevitably a long list of accidents was the result of the spreading 'coral fever' among the young divers (Liverino 1983). Leonardo Fusco reported that in 1955 he harvested at 60 m in the Gulf of Naples, but in 1964 he had to descend to 90 m. Similarly, the pioneer Fausto Zoboli is reported to have said that he worked as one of the first at 60 m in 1964 (near Rome), while in 1971 he was forced to work at 100 m in Alghero, Sardinia (Liverino 1983). Others similarly documented that by the late 1950s divers in France and Italy already had to descend to depths of 80 m, and at times to even more than 100 m, to find coral (Galasso 2000). In 1974, helium-based mixed-gas diving techniques developed by the French ocean engineering company COMEX started to spread among coral divers, permitting them to work at 120 m for 20 min without the dangers of nitrogen narcosis (Liverino 1983).

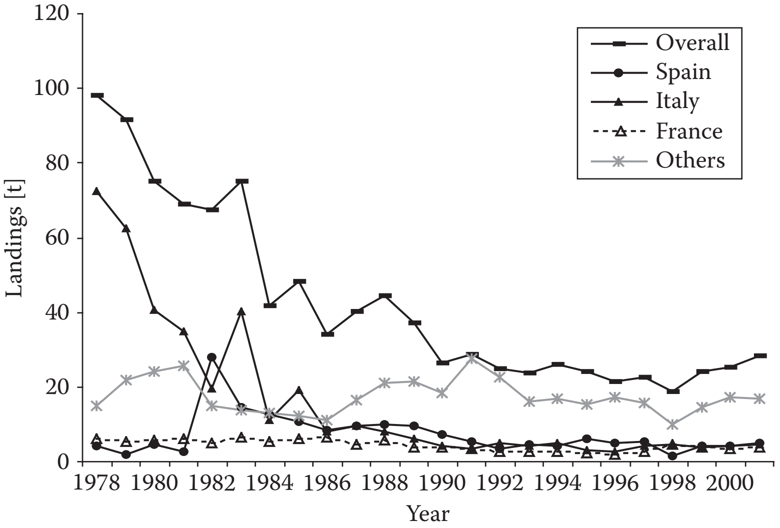

Figure 2 Red coral harvest in the Mediterranean. Note that dredging was phased out from the early 1990s until it was banned EU wide in 1994. (Data from FAO 1984, http://www.fao.org)

The 14-mile long Scherchi Channel from Sicily to Tunisia was regarded as a coral 'el Dorado', with 80 divers from Italy, France and Spain harvesting 70–120 t in 1978, starting at 60 m and gradually working their way down to 130 m. This submarine canyon was described as an oasis for marine fauna and flora, uncontaminated and exceptionally rich in rare species. In 1979, there were 366 boats at work (283 of them were registered in Italy) and 150 divers (Liverino 1983). Algeria and Morocco developed a local management programme with the aid of Italian coral divers (Liverino 1983). Then, in 1977, following Jacques Cousteau's recommendations, Algeria placed a temporary ban on coral fishing. Tunisia allowed fishing by Italian dredging boats ('corallinas') and French divers until it developed its own fishery in 1974. The last major peak recorded lists 100 t of *C. rubrum* in 1978, but from then on, the reported landings remained below 30 t (Figure 2). In the 1980s, France reported a production of about 5 t yr^{-1} by 40 licensed divers and 1 t by dredging.

In contrast to the development in the Mediterranean, the Hawaiian black coral fishery relied early on scuba diving since the 1960s. In the United States, selective harvesting methods (manned submersibles, remotely operated vehicles [ROVs]) have been required since 1980 (J. Demello, WPCouncil, personal communication). However, dredges are not completely banned in other parts of the world.

Unlike Mediterranean red coral and Hawaiian black coral, Japanese coral inhabits depths beyond 100 m and was not washed up on beaches. *Corallium rubrum* was imported into Japan, was regarded as one of the most valuable presents to state officials, and is still highly revered (Kosuge 1993, S. Kosuge personal communication). In the early 1800s, other *Corallium* precious coral species were discovered in the Pacific Ocean. Off Japan, coral dredging started soon after (1804) but was initially prohibited. The shoganates did not, however, enforce this law strictly and published a document in 1838 that stated that harvesters were prohibited from selling freely and should offer the corals to the government (Kosuge 1993). Thus, coral fishing in Japan flourished only after the Meiji Reform abolished the feudal system in 1968. Konojoi Ebisuya is credited with developing the Japanese fisheries, including the invention of a more efficient coral-gathering net (Kosuge 1993).

Coral was exported directly or through the Japanese bank Mitsui (especially to the Netherlands). The Pacific coral export increased steadily because its pale pink colour and large size enjoyed great popularity (Tescione 1973). *Corallium* species have been harvested in the western Pacific islands,

Table 2 Changes in the fishing grounds of the Japanese precious coral (*Corallium* and *Paracorallium*) fishery illustrating ever more extensive fishing trips

Year	Species	Location
1950/51	*P. japonicum* (Aka), *C. elatius* (Momo)	Hachijo (150 miles off Tokyo)
1952/53	*P. japonicum, C. elatius*	Amani Island
1952/53	*C. elatius*, *C. konojoi* (White)	Amani and Goto islands
1960	*C. elatius*	Okinawa
1961/63	*P. japonicum, C. elatius*	Sumizu off Okinawa and Hachijo
1965	*C. elatius, C. secundum* (Boké)	South China Sea
1965	*C.* sp. nov. (Midway coral)	Midway

Source: Data from Liverino 1983.

Note: Japanese common name in parentheses.

including Japan, Taiwan and the Philippines, for 200 yr (Grigg 1994). The dredging devices used in the Pacific were coral mops (tangle nets, weighed down with natural stones) that were pulled along the bottom at 100–330 m (Grigg 1984). The 'rascle' is a similar device, consisting of a V-shaped metal frame supporting a net (FAO 1983).

The Pacific fishery extracted *Corallium* species off Japan, around Okinawa, off the Bonin Islands and off Taiwan, at either 200–500 m depth or 1000–1500 m. The golden era is said to have been from 1954 to 1970 (Liverino 1983). In 1950 to 1955, the harvest concentrated on the islands of Shikoku and Kyushu. Tosa Bay and the islands off Goto were noted as particularly rich in *C. elatius* and *Paracorallium japonicum* (Liverino 1983). Subsequently, after discovering banks at the Ryu-Kiu Islands south of Kagoshima (Okinawa, Amani, Miyado) and those south-east of Osaka and Yokohama (Ogosawara, Hachijo, Sumisu), the fleet started making ever-more-distant fishing trips (Table 2). Inshore vessels of more than 5-t displacement were used, while long-range boats displaced 150–180 t and were manned by a 25- to 30-man crew, which did 2- to 5-mo trips. The boats could employ up to 18 minidredges simultaneously. The dredges consisted of a round 10-kg stone that had five nets attached to it (Liverino 1983). Working this way, a boat could harvest up to 80 kg day^{-1}. The fishery and trade were locally managed by the three fishery associations: the All Japan Sango Fishing Association, the Sukomo Kyodo Kumiai and the Goto Sango Kogei Kyodo Kumiai.

Eventually, the fishing trips by the Japanese fishermen were so far reaching that in 1965 they discovered a very large bed of pink coral (*C. secundum*) in 400 m at the Milwaukee Banks, Mellish Bank and surrounding seamounts in the Emperor Seamount chain north of Midway Island, near the Hawaiian Archipelago. Subsequently, most of the world's tropical *Corallium* landings came from that bed (Grigg 1994). About 200 vessels from Taiwan and Japan made up to 7 trips yr^{-1} (Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES] 2007). The fishery reached a peak of 150 t in 1969 but had finally depleted the stocks, and yield remained low for the next 5 yr until a previously undescribed deep-water species (Midway coral, *Corallium* sp. nov.) was discovered at a depth of 900–1500 m. The colour of this species is spotty (sometimes called 'scotch'), varying between pink and white, and it was extremely abundant (Grigg 1994). This discovery led to another coral rush, with over 100 boats from Japan and Taiwan involved in the harvesting. In 1973, four boats from Suao were guided by the research vessel Jungmei 6 and harvested coral worth 90,000 Italian lire in just 1 wk (Liverino 1983). In total, the 100 boats working the entire season made over 3 billion Italian lire. Production peaked at 300 t in 1981 (Liverino 1983, Grigg 1994). Over the whole Pacific, the production totalled about 400 t at that time (FAO 1983). The principal extraction method was dredging, but manned submersibles and ROVs were also employed to a small extent in the 1980s for exploration purposes (Grigg 1989, CITES 2007).

In 1981–82, the market was flooded with Midway coral, and prices fell so low that many fishermen suffered losses or even went out of business (only 21 vessels in 1981). Buyers in Italy paid

2000 lire kg^{-1} instead of the initial 80,000 (Liverino 1983). Yield consequently sank (84 t), but demand rose again, and the fishing continued for many years, until the stocks were depleted and yield dropped a few years later to about 10% (20–30 t) of the maximum and ceased with less than 3 t in 1988 (FAO 1983). In 1991, an all-time low of less than 3 t of precious coral production was recorded throughout the Pacific (Grigg 1994), with prices for raw material at unprecedented heights (Grigg 1994), indicating the depletion of all known stocks. Coral fishing has not been resumed in those areas; one reason cited is that the corals found in by-catch of fishing trawlers is of low quality. Precious coral yields worldwide (all species) reached a peak of 450 t yr^{-1} in 1984 but fell to about 28–54 t during the last 18 yr (http://www.fao.org).

In 1923, coral banks were discovered in Taiwan, and in 1934 the Penghu government sent the research vessel Kai Peng Maru to study the stocks and set up a limitation of 20–40 vessels, which contributed to the longevity of the fishery (Liverino 1983). In 1962, coral was harvested by the same fishermen off Hong Kong at a depth of 70–100 m. In 1968, new banks off the Pratas Islands were discovered (Liverino 1983).

In 1958, large black coral populations consisting primarily of *Antipathes griggi* and *A. grandis* were discovered in the Hawaiian Islands between 30 and 90 m deep (the presence of the species was first reported during the Challenger Expedition; Brook 1889). Traditionally, these stocks were harvested by scuba divers. The black coral jewellery industry grew steadily between 1960 and 1970. In 1966, pink coral was discovered in the Makapu'u bed off Oahu, and a small group of fishermen dredged the bed using tangle nets (Grigg 1994). Prior to 1974, harvest was low, and the sales generated only around US$70,000, but the industry doubled within 6 mo during that year. In the 1980s, technological advances in coral processing led to a dramatic decrease of the amount of coral needed to produce the same value of finished product. Furthermore, import of cut and polished black coral from Taiwan affected the demand for coral by the Hawaiian industry, which consumed less than 2 t yr^{-1} on average (Oishi 1990). At that time, about 70 t of raw material were processed in Taiwan, most of which originated in the Philippine Islands, primarily *Cirrhipathes anguina* (whip coral) (Carleton 1987). About 90% of black coral sold in Hawaii are beads, rings, bracelets and necklaces made of *C. anguina* that has been worked in Taiwan. *Antipathes* species maintained their popularity due to their denser and higher-quality skeleton and their designation as the official state gem of Hawaii. However, import of inexpensive black coral from the Philippines and Tonga (Harper 1988) and more efficient manufacturing combined to keep the demand within sustainable limits. The Hawaiian black coral fishery was the first fishery that was managed on the basis of an extensive fishery research programme, which was conducted at the University of Hawaii in the early 1970s (Grigg 1976, Grigg 2001).

The same programme also discovered a small bed of pink coral (*Corallium secundum*) at 400 m off Makapu'u, Oahu, and developed a selective harvesting system employing a manned submersible. Maui Divers of Hawaii incorporated this system and harvested 0.5–2 t pink coral, gold coral (*Gerardia* sp.) and bamboo coral (*Lepidisis olapa*) per year from the same area. Non-selective fishing gear was banned in favour of non-destructive harvest. However, the operation was discontinued in 1978 because of high operating costs (a diving accident resulting in two deaths during the launch of the submersible increased insurance costs). It is estimated that the fishery extracted 32% of the standing stock in the time from 1966 to 1978 (Grigg 1994). Since then, the industry in Hawaii has relied on stockpiles of gold corals and imports of pink and red corals, mostly from Taiwan and Japan (Grigg 1994). An attempt to harvest pink corals domestically within the Exclusive Economic Zone (EEZ) used tangle nets at Hancock Seamount (Emperor Seamounts chain) but was cancelled after 450 kg of dead, low-quality *Corallium secundum* were brought to the surface (Grigg 1994). The Hawaiian pink and gold coral fishery was revived by American Deepwater Engineering (ADE), which used two 1-person submersibles to exploit an established bed and an exploratory area in 1999–2000. In 2000, the company harvested 1.2 t of *C. secundum*, 150 kg of *Gerardia* sp. and 61 kg of *Corallium regale* (Grigg 2002). However, the declaration of the north-western

Hawaiian Islands as a U.S. Coral Reef Ecosystem Reserve per Executive Order 13196 in the year 2000 excluded two-thirds of the precious coral deep-water habitats from exploitation. Given this reduction of potential supply, combined with marginal investment returns due to high operational costs, ADE suspended operations in 2001 (Grigg 2002). Foreign poaching has been a problem in the past because during the 1980s Japanese and Taiwanese coral vessels continuously violated the EEZ near the Hancock Seamounts. In 1980, about 20 Taiwanese coral draggers reportedly poached about 100 t of *Corallium* from seamounts within the EEZ north of Gardner Pinnacles and Laysan Island (Grigg 1994). However, it appears that since the 1980s poaching within the EEZ by foreign coral fishing has been negligible, in part due to the general fishing activity in the area. Fishing has now been terminated with the declaration of the area as a national monument, so it is not clear if current enforcement will prevent the reoccurrence of poaching (J. DeMello, WPCouncil, personal communication).

Socioeconomy

Modern exploitation methods

Harvesting methods

There is a variety of methods used to harvest precious corals today. At depths that can be accessed by scuba-diving, it is used as the exclusive harvesting method. Traditional compressed air scuba-diving is used to harvest populations between about 30 and 80 m deep, while mixed-gas scuba (see p. 181), is used between 80 and 150 m deep. Traditional air diving gear is cheap and readily available, whereas only a small number of divers invest in more expensive mixed-gas diving.

In contrast to dredging, scuba harvesting inflicts little direct damage to non-target species in the same habitat. However, coral exploitation by diving allows absolute selectivity only in theory. In practice, it has been reported that divers sometimes make a ‘clean sweep’ of an entire precious coral population at one site (FAO 1988). Since the market value of small coral branches has risen to US$240 kg^{-1}, the alternative of doing business with immature coral taken in shallow water appeals even to licensed fishermen and poachers, although this practice appears to affect only shallow-water populations in certain regions (e.g., Costa Brava, Spain). Poachers using air scuba have been convicted of harvesting up to 30 kg of young coral from one shallow dive site in 1 day (Fisheries Department, Government of Catalonia, personal communication). The increased amount of raw material that poaching makes available to the market may reduce the price, thereby causing further damage to licensed divers. In some cases, poachers reportedly sell to licensed divers, who resell the corals, or sell directly to Taiwanese buyers. In Spain, fishing licenses are issued without requiring special fees, but the selection of the few licensees is based on a consideration of personal and family history in coral fishing.

Towards the eastern Mediterranean, coralligenous habitats occur in deeper water, and coral fishermen rely on mixed-gas diving for harvesting, sometimes aided by ROVs for prior surveying of the target sites (personal observation). These divers selectively harvest large colonies once they have located them using the ROV. No data on poaching of these deep populations are available, so it is difficult to estimate poaching intensity. Another consideration is unconfirmed information that license holders may occasionally harvest areas outside the designated stocks, as opportunist amateurs do.

The method of removing coral is assumed to influence its recovery potential. Ideally, responsible divers cut the red coral base instead of extracting the whole colony. Leaving the base in place leaves a chance that this colony might regrow. This regrowth has been observed on a few occasions (Rossi et al. 2008) but is not well studied. Furthermore, the considerable time pressure and the difficulty of working underwater and at depth is quite incapacitating, so that red coral divers may not be able to consistently perform a precise size selection or partial harvest of corals. In fact, some studies demonstrated that up to 60–70% of confiscated poachers' catches were entire corals with the substratum still attached to their base (Hereu et al. 2002, Linares et al. 2003).

In the Mediterranean, harvesting concentrates on the warmer summer months (May–October), removing most of the corals at a time they produce their larvae. This practice should be of little impact (Kwit et al. 2004) but is an important fact to take into consideration in a socioeconomic analysis because it means that most of the divers are effectively working part time and have often invested into other businesses as well (e.g., hotels, aquaculture). On the Costa Brava, all divers are natives and older than 45 yr. In Hawaii and Spain, teams of three or more divers often work from one vessel. In Sardinia, 80% were said to be non-natives. Divers usually dive alone using mixed gas and from boats that are crewed by one coxswain and one diver (Andaloro & Cicogna 1993). In Hawaii and the Costa Brava (Spain), current coral fishermen are in their 50s and will leave the fishery in the near future due to the hazards of the occupation (WPCouncil 2007). The youngest licensed diver on the Costa Brava is 45 yr old.

In Morocco, 50-t boats with an onboard dry decompression chamber are mandatory. Two divers work from this boat and complete their decompression onboard instead of underwater. In Hawaii, the water temperature and visibility make for better diving conditions, and coral can be harvested year round, although currents, swell and sharks do present a challenge for Hawaiian black coral divers. In both cases, ocean conditions allow access only on relatively calm days, even though the Mediterranean fishery often operates close to shore.

The tools used to detach the coral and containers to store them vary between divers because they have traditionally been individual solutions. Some sort of pick is frequently used in the Mediterranean, perhaps with modifications such as a chisel incorporated into its shaft. The detached coral is usually put into a basket made of netting. These nets are often clipped to a rope during decompression and lifted to the boat (lift bags seem to be rarely used to lift a dive's red coral catch because the dimensions and weight are manageable). Also noteworthy are modern dive lights that consist of powerful rechargeable batteries that are attached to the diving tanks, and the small but bright light head itself is fixed to the forearm or head. This allows the diver to quickly find corals in crevices and work with two hands. Fishermen remark that diving safety issues are rarely considered in management plans and that divers are not invited to scientific consultation meetings (M. Scarpati, personal communication).

The Hawaiian black coral grows on exposed substrata and is harvested when at least 1.2 m tall and more than 2.54-cm thick. It is therefore harvested differently from Mediterranean red coral because the divers need to cut or break the thick keratinous coral stem with an axe or sledge. Selecting corals that exceed the minimum size is far easier in the case of Hawaiian black coral than it is with Mediterranean red coral (where millimetres of base diameter need to be distinguished). The coral harvest used to be tied to the boat anchor and buoyed to the surface using an inflating lift bag after the dive. Today, it is more common for the divers to use lift bags to transport coral to the surface, while the boat follows the buoys. Mixed gas, rebreather diving and ROVs are not yet used in Hawaii (Bruckner et al. 2008).

Modern scuba technology

Modern technology has made scuba-diving, and thus coral fishing, much more efficient. This includes better thermal protection suits that reduce the risks of hypothermia. Hypothermia affects cognitive capacity and vital aspects of diving physiology and can reduce the efficiency of decompression, which is mandatory after the deep and long dives that coral diving requires.

In the late 1990s, the so-called technical diving industry brought mixed-gas diving techniques from offshore commercial diving and rebreather technology from the military to recreational diving, making these techniques widely available and giving divers greater access to deeper water (Pyle 2000). Few coral divers use rebreathers at the moment, but this can be expected to change. It can be assumed that especially younger divers will use modern techniques to access corals in excess of 100 m. On the Costa Brava, divers are reported to mainly dive to 30–50 m deep using air because red coral grows as shallow as 20 m in this area. In any case, the recommended maximum depth for air diving of 40 m (Bove & Davis 1997) has always been, and still is, routinely exceeded. The preference for traditional scuba is due to decades of experience with the simple and rugged equipment as well as lower cost of operations. This also implies that divers will only take the risk to dive deeper than 50 m if no corals can be found in shallower water. In other Mediterranean areas, such as Italy, coral fishermen dive much deeper because of depletion of the shallower stocks (FAO 1988).

ROVs and manned submersibles

Because robotic extraction is not practical and not permitted in many fisheries, ROVs are increasingly being employed to scout a potential coral bed, improving the yield per dive. Basic ROVs are available today for as little as US$5000 and consist of a motorized real-time video camera that is controlled from the boat via a cable that also transmits the video signal to a topside monitor and recorder. ROVs can also be equipped with a robotic arm that permits remote-controlled harvesting, although this option raises the acquisition cost considerably. ROVs allow harvesting at greater depths and with fewer time restraints than scuba-diving but at lower cost than using manned submersibles.

ROVs have been used for the exploration of new beds since 1983 in Japan (Grigg 1994, CITES 2007). In general, however, remote harvesting is considered impractical compared with direct methods (scuba, manned submersibles): Currents, nets and the topography of coral habitats make it difficult to manoeuvre the tethered machines, and without dedicated technicians, a minor malfunction may easily render an ROV unusable for an entire expedition. Also, the ROV tether may damage precious corals if not carefully used (WPCouncil 2007).

The methodology for harvesting with manned submersibles originates from the commercial application of an exploration and sampling protocol that was developed in the course of a long-term Sea Grant research programme at the University of Hawaii in the early 1970s. It was used in Hawaii in 1972–1978 and experienced a short-lived renaissance in 1999–2001 (see p. 179). Apart from Hawaii, submersibles have been used in the Mediterranean, Japan and Taiwan to support exploration efforts of the fishery (Grigg 1989). In the state of today's market, the operational costs are so high that the profit margins do not justify their use. An exception is their current use in Japan to access deeper precious coral beds (N. Iwasaki personal communication).

Operational costs using manned submersibles are high due to the necessity of a large mother ship equipped with a heavy-duty crane. The aforementioned protocol applied in the 1970s in Hawaii reduced these costs considerably by designing a launch-and-recovery system operating from a platform that could be submerged to 20 m to release the submarine and be made buoyant again for towing the sub back into port.

Progress on the marine technological front during the 1990s allowed the construction of small, lightweight, low-cost submersibles, such as the Deepworker 2000 made by the Canadian company Nuytco Research. This class of submersibles represents one-person vehicles that weigh less than 2 t and can operate at a depth of 610 m. Their low cost and small size make it possible to use them in tandem (Grigg 2001), which increases safety. However, the overall operating costs in relation to precious coral prices are presently still too high, considering furthermore that only about 20% of the time each year are there adequate weather conditions (especially wind and swell) to launch a submersible.

Use of precious corals

The raw material for the precious coral jewellery industry is the skeleton of the corals. In general, it is easier to work with the species with harder skeletons. In some species, such as *P. japonicum,* there is considerable waste of material due to imperfections in the skeleton structure (S.J. Torntore personal communication).

Precious corals are used primarily for jewellery pieces like rings, pendants, amulets, necklaces, earrings and carved art objects such as statues. The market can be divided into the ethnic market that sells mainly rough coral beads, the tourist market and the high-end luxury fashion market that is the realm of jewellers' shops (Torntore 2002).

Despite extensive legends, present medical uses of precious corals appear to be negligible. Red coral powder is still being sold as a cure against various maladies or as an aphrodisiac. However, similar to the fraud with worked coral pieces that are made of plastic or low-quality species, it is often powder made from sponge coral (*Melithea* sp.) that is sold as *Corallium* powder (S.J. Torntore personal communication). In general, it is reef-building coral species that are frequently used as bone prostheses because their pores are quickly filled with capillaries (Pechenik 2005). Both stony corals and precious corals are sold as curios or decorations and for aquaria.

The genus *Corallium* is the most coveted group of precious corals. Their skeletons are appreciated for their hardness, purity and colour, and the lower abundance of these corals further increases their value. Depending on colour, striations (colour patterns also called 'anima') and consistency, whether collected alive or as fossils and whether they are infected by boring sponges, the material is divided into quality categories when priced. Colour varies according to species and locality, and popularity of colours on the market follows fashion. The dark red colour of *C. rubrum* has become the gold standard for the industry. Thin branches are of lower quality, and red coral skeletons from colonies infected by boring sponges are mainly of interest to the ethnic market because their skeleton is not solid but contains holes, which do not allow the piece to be given a polished surface (FAO 1983).

Coral branches of less than 7 mm in diameter used to be of negligible use, but this changed with the introduction of composite coral manufacture, a hardened mix of coral powder and a plastic such as epoxy (FAO 1988). This allows small branches and fragments to be ground to powder and formed into larger blocks, such as beads. Chemical analysis or inspection of growth rings under the microscope can identify coral pieces made from reconstituted coral (Smith et al. 2007). There are no data about the species that are used preferably to manufacture this type of jewellery, although some wholesalers state that they can sell coral powder only as a medical potion to Asian markets. It is unlikely that high-quality manufacturers in the fashion market produce reconstituted coral, and although FAO reports confirmed its existence, some industry insiders consider it a myth (G. Tsounis personal observation). In any case, reconstituted coral and small coral fragments are more likely to be sold in the tourism and ethnic marketplaces.

Precious corals are supplied to jewellery manufacturers as whole dried colonies, unworked branches or polished beads. In the last state, it is not straightforward to identify the species. Bamboo coral is often dyed red or black and sold as *Corallium* or *Antipathes*, whereas sponge coral (*Melithea* sp.) is often impregnated with acrylic polymers and sold as *Corallium*. Another inexpensive species that is sold as precious coral is rose coral (Scleractinia). Finally, there are bracelets from Bakelite or celluloid on the market that are also sold as precious coral jewellery.

Economy and trade

Prices for unworked precious corals have varied throughout time, depending on demand. The trade of precious coral has been increasing in recent years, judging from *Corallium* spp. import data into the United States (the largest importer of precious corals; CITES 2007) and a recent 50% increase in sales volume recorded in Hawaii (Grigg 2004).

Prices of *C. rubrum* have risen steadily over the last decades because demand always exceeds the diminishing supply (FAO 1983, 1988). *Corallium rubrum* is sold for relatively high prices; high-quality raw colonies are sold for US\$1500 kg^{-1}, worked beads sell for US\$30–50 g^{-1}, and necklaces cost up to US\$25,000 (Torntore 2002). Manufacturing 1 kg of beads takes 115.5 h or 10.5–14.5 days. Prices for *C. rubrum* have risen from US\$100–900 kg^{-1} to US\$230–2900 kg^{-1} (FAO 1983, Moberg & Folke 1999). Today, even thin juvenile branches are bought for US\$230–300 kg^{-1}, whereas they were practically worthless some decades ago (FAO 1988, Tsounis et al. 2007). Single, large *C. rubrum* colonies with a base diameter greater than 4 cm are reportedly sold for as much as EUR 45,000 per colony.

In Europe, the specialized red coral jewellery industry situated in Torre del Greco, near Naples (Italy), is estimated to generate more than US\$230 million yr^{-1} (Assocoral personal communication). Around 270 companies participate in the labour-intensive manual manufacture of jewellery. The majority are small family businesses consisting typically of a father and sons. A substantial number of those specialize in outsourced processes for the larger companies (Ciro Condito, Assocoral, personal communication). The three oldest companies (Liverino, Antonio De Simone and Ascione) deserve special mention because they are significantly larger than the rest. More than 90% of all *C. rubrum* extracted has been processed in Torre del Greco since the 1800s (see p. 175). However, only 30% of the processed corals are *C. rubrum* now because 70–80% are imported from Japan and Taipei (Castiligliano & Liverino 2004). In fact, Italy has become a major importer of precious corals (CITES 2007). Industry insiders say that the black market is significant, maybe totalling 50% of the trade.

Tropical *Corallium* species are also of high value. In 2001, *C. secundum* was priced at US\$187 kg^{-1}, *C. regale* was worth US\$880 kg^{-1}, and *Gerardia* was sold for US\$400 kg^{-1} (Grigg 1984). Recently, a large *Corallium elatius* colony 1.1 m high and weighing 67 kg was reported to have been sold for about US\$100,000–300,000 (N. Iwasaki personal communication). It is not clear, however, if colonies of this size occur in sufficient quantities to make fishing trips commercially worthwhile. Large jewellery pieces of *C. elatius* that were sold to tribal groups in Nigeria during the 1960s are now being bought back by the industry to be resold to the luxury market, indicating a shortage of large tropical *Corallium* colonies.

Black coral sold for a relatively low price of about US\$15 kg^{-1} (Grigg 2001) during the 1980s when Taiwan and the Philippines started to export large numbers (70 t to Hawaii alone in 1987; Carleton 1987) but rose to about \$70 kg^{-1} today. The Hawaiian precious coral industry imports pink coral from Taiwan and is estimated to have generated US\$30 million in 2004 with over 100 retailers (Grigg 2004) and in recent years US\$70 million yr^{-1} (WPCouncil 2006). Recent sales volume has risen 50% because in 2001 the value was US\$15 million (Grigg 2001), already much higher than the US\$2 million reported in 1969 (Grigg 1994).

The United States is the largest importer of precious corals, including unworked coral from China and Italy. While the United States does not export coral or coral products, a large part is sold to tourists (especially in Hawaii). Taiwan exported 90% of the worked black coral on the market, previously importing much of the raw material from the Philippines (CITES 2007). Japan and China are also important manufacturing centres, with an annual value in 1982 of US\$50 million (CITES 2007), although a large proportion of the exports are semifinished products (such as beads; S. J. Torntore personal communication).

In 2002, the data show a massive export of *Corallium* sp. from Italy into the United States that was about five times higher than the previous and following years. This situation may reflect the discharge of stockpiling rather than the discovery of a new bed. Italy and China contributed about 90% of all precious coral imports into the United States, while Italy's contribution decreased from 50% in 2002 to less than 4% in 2006. Thailand's contribution to the overall import volume rose from 0.2% in 2001 to 5% in 2006. China and Taipei (pooled here to reveal their impact on the South Pacific) were responsible for 84% of 1,807,357 precious coral products imported into the United States in 2006.

Recent yield data

The overall landings of red coral from the Mediterranean have been relatively stable at 25–30 t over the last 15–20 yr. The annual harvest is about 25% (25 t) of what it was in the early 1980s (Figure 2). However, as the more detailed discussion that follows will show, a stable yield should not be mistaken for a sustainable fishery because coast guard controls indicate that fishermen have been forced to harvest ever-smaller colonies in recent decades (Linares et al. 2003, Fisheries Department–Government of Catalonia personal communication), and a progression towards deeper beds and more remote stocks may maintain the yield. Today's main stocks are located on the Costa Brava (Spain), Corsica, Sardinia, and the northern African coast, although harvesting also occurs in Sicily, Mallorca and some other locations.

In addition to the general FAO landings data, which are pooled per country, there are a few detailed case studies. In Morocco, harvesting was done by foreign fleets and divers until the 1980s. Two boats with two divers each have been active since 1984 (10 boats in 2004) and are issued 500-kg individual annual quotas for specific areas that are managed using 10-yr rotation systems (Zoubi 2009). Al Hoceima was the most prosperous zone, with 8.6 t landings in 1985, but yield decreased after 3 yr and continued to fall during the 1990s. After closing the region for 12 yr (the fleet diverted to other areas and towards the Atlantic), the region was opened, only to be depleted within a year, and the fishery shifted to Tofino, where 145 kg were harvested in 2004 and 510 kg in 2005. Exploration for new stocks began in 2007 and identified Sidi Hsein as a stock with potential for continuing the fishery. In Sardinia there are 20–30 licenses (16–17 boats) harvesting ca. 1.1–1.4 t per year in 2008–2009 (Cannas et al. 2009, Doneddu 2009).

Thirteen of the total of 16 licensed divers in Spain are authorized to participate in the Costa Brava fishery (as a comparison, there are 25 active licenses on the island of Sardinia). One of those licenses is restricted to so-called interior waters (i.e., areas within transects connecting capes), whereas three licenses are issued only for the area outside. Nine licenses are for all of the Costa Brava, and any license is in general valid for more than one region of Spain (Fisheries Department, Government of Catalonia, personal communication).

The Costa Brava fishery concentrates on the Cap de Creus area, a 190-km^2 sparsely inhabited peninsula that is exposed to frequent northern gales. The length of the coastline measures about 42 km. In contrast to the easily definable coral beds in Hawaii, red coral habitat is very heterogeneously scattered, forming small patches in microhabitats (Tsounis et al. 2006b). Recruitment and habitat preference are not yet well understood, but competition with other benthic species and a short dispersal distance seem to be influential factors. A bionomic study in a nearby area (Ros et al. 1984) showed that 1 km of shoreline corresponds to about 0.01 km^2 of coral habitat. The annual yield for inshore waters on the Costa Brava ranges from 0.8 to 1.7 t, whereas the overall yield of inshore and offshore waters in Spain was about 4–5 t (Fisheries Department of Catalonia, personal communication). These numbers do not, however, take into account the severe problem of intensive poaching in the Mediterranean (see p. 180). An additional problem is that current management does not record the size of the harvested corals.

In the Pacific, a similar stabilization of yield following a dramatic decline can be observed (Figure 3). Current production in the Pacific is about 5% (20 t) of the yield in 1982 (400 t; FAO 1983). After a peak of 400 t in the mid-1980s, the yield of *Paracorallium japonicum*, *Corallium regale, C.* sp. nov. and *C. konojoi* remained at around 10 t after the 1990s (data from FAO).

Pink and gold coral were not harvested in Hawaii after 1979 because the cost of selective harvesting of deep beds was too high, and apart from a brief operation in 1999–2000 (1.2 t), these species are not currently harvested in the EEZ.

Black coral landings in Hawaii have increased considerably in recent years (WPCouncil 2006). Landings in the last 7 yr make up 58% of the total catch since 1985. From 900 kg yr^{-1} between

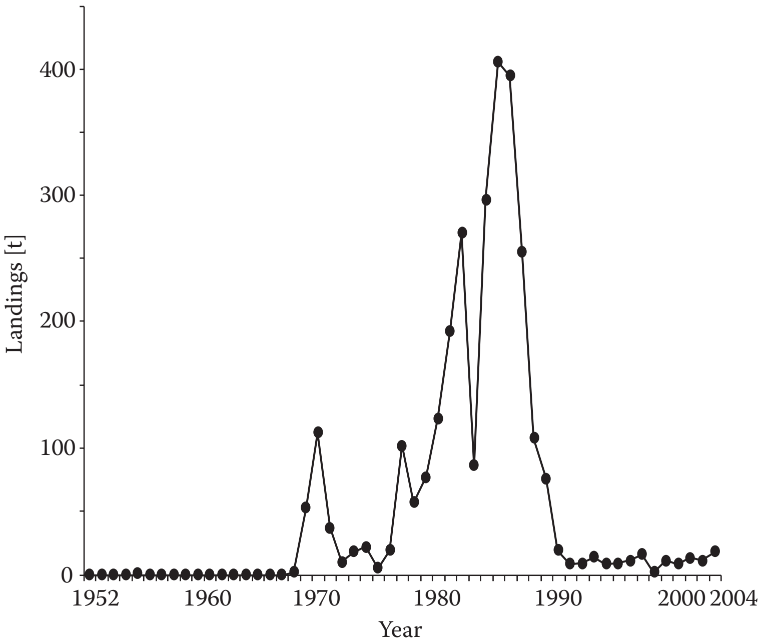

Figure 3 *Corallium* spp. harvest in the Pacific. The graph shows peaks that mark the discovery-exploitation-depletion cycle of several stocks located in seamounts (except the decline due to overproduction in 1982), and after 1991 a more constant yield from harvesting coastal stocks. (Data from FAO Fisheries Statistics Programme, http://www.fao.org.)

1985 and 1991, the yield rose to about 3.5 t yr^{-1} in 1999–2005 in the same coral bed (the Au'Au channel), and the maximum sustainable yield (MSY) of 5 t (Grigg 1976) was exceeded in at least 1 yr (WPCouncil 2006). New beds were not discovered for this diving-based fishery. Since 1980, virtually all black coral harvested in the Hawaiian Islands has been taken from the Au'Au Channel bed (with an areal coverage of 1.7 km^2). The Kauai Bed with an area of 0.4 km^2 has also been harvested, but to a lesser extent. Currently, only about five coral divers are active in this region, which is a surprisingly low number considering the amount of biomass removed and the impact on the population structure.

In the past, the hope of any precious coral fishery has depended on the discovery of new beds. Nearly two decades ago, southern oceans had been identified as the most promising areas for the future of precious coral exploitation, and in fact this is where most precious corals are harvested today. Potential new areas include channel waters around Madagascar (Grigg & Brown 1991). The Committee for Coordination of Joint Prospecting for Mineral Resources in South Pacific Offshore Areas (CCOP-SOPAC) reported *Corallium* sp. in Tasmania, the Cook Islands, Fiji, Kiribati, Solomon Islands, Tonga, Vanuatu and Western Samoa but not in commercial quality or abundance (Harper 1988). Within the U.S. EEZ, the following areas are still open for exploration: around the Hawaiian Islands, Guam and the Commonwealth of the Northern Marianas, American Samoa and all EEZs of the U.S. Pacific Island possessions. Commercial harvesting of precious corals has not been reported in the United States outside the Hawaiian Archipelago except for potions (Lumsden et al. 2007).

Bamboo coral harvest in Bone Bay, Sulawesi (Indonesia), appears to have increased significantly in recent years (S. Ferse, Centre for Tropical Ecology, Bremen, personal communication) because exports of more than 100 t were reported in 2005 (Department of Fishery and Marine Affairs [Dinas Perikanan dan Kelautan Bone sudah tercatat]). This development may represent the phenomenon called ‘fishing down the price list’, that is, shifting to the next-available resource after depleting the most valuable ones.

Management and conservation

This section attempts to give an overview of the management and conservation of precious coral fisheries in various countries. Gold and pink corals are no longer fished in the U.S. EEZ for economic reasons (see p. 179), and because the Asian fisheries are only now being thoroughly studied, it is necessary to focus on a comparison of the two best-documented case studies: the Mediterranean red coral fishery and the Hawaiian black coral fishery. The differences in socioeconomy and in the ecology of the species help to highlight causes and effects and to better understand precious coral exploitation in general.

Coral harvesting in territorial waters is controlled by a licensing system permitting a controlled number of divers to harvest coral. Harvest quota are used to further control the yield, and usually minimum size limits are used as well. However, management based only on harvest quota is not effective in preventing overharvesting (WPCouncil 2007) because immature corals cannot be protected in this way.

Management

Precious coral fisheries in Asia

Most fisheries in Asia have not yet been studied in detail, and there are no published data on some species. Some countries, such as Thailand and the Philippines, have banned coral fishing. The majority of black coral landings in the past were reported to have been harvested in the Philippines (Ross 2008). However, coral trade in the Philippines was banned in 1977, and any stockpiles had to be sold 3 yr after the closing date. In July 2008, China listed the four *Corallium* species *C. elatius, C. konojoi, C. japonicum* and *C. secundum* in Appendix III of CITES, thereby controlling their export (CITES 2008).

Coral fisheries in Japan are authorized by prefectural governors and therefore differ from each other. Red, pink and white corals are harvested by traditional stone-weighted non-selective tangle nets in Kochi. Since 1983, in waters extending from Kagoshima to Okinawa, harvesters have used manned and unmanned underwater vehicles and follow self-imposed size limits (Iwasaki & Suzuki in press). There is no official quota for these fisheries because the research needed to manage the stocks has only recently been initiated (N. Iwasaki personal communication). According to unpublished information by Sadao Kosuge (Institute of Malacology, Tokyo), yields have been stable over the last decade.

Of 24 areas, only three are open to fishing. One area is fished by submersible, while strong currents in the other two allow only tangle nets to be used. Each boat deploys one dredge for 4 h per day, and is active for about two weeks per year. Yield per boat and year is about 12 kg, and 120–230 vessels are active. One of these areas (Kochi prefecture) consists of soft bottoms with deposits of dead coral, which is targeted using dedicated gear (resulting in 80% of the Kochi area’s catch). Total catch in Japan is 3.6–4.8 t in 2003–2008 (S. Kosuge unpublished data).

The Taiwanese precious coral fishery began in 1929 and in 1983 was limited to 150 vessels. Currently, there are 53 vessels harvesting *Corallium* sp. in five regions, each vessel with an annual quota of 200 kg vessel^{-1} over a 220-day activity limit for each year (Chih-Shin Chen, Institute of Marine Affairs and Resource Management, National Taiwan Ocean University, personal communication). The fishermen employ traditional non-selective gear consisting of the tangle nets typical for Asia deployed at a slow speed of 1.5 knots. Only 2% of the harvested coral in Taiwan is live coral; 83% is dead coral, and a further 15% is dead coral that has been on the seafloor long enough to decay. Penalties for poaching are severe in Taiwan because they include a 3-yr imprisonment and a fine of US$20,000 (C.-S. Chen personal communication).

Hawaiian black coral

In Hawaii, commercial black coral beds are located in state *and* federal waters. State waters include areas within 3 mi of islands as well as interisland waters, where black coral is predominantly found, and harvest is regulated by the Department of Land and Natural Resources (DLNR), Division of Aquatic Resources (DAR). The area outside the state of Hawaii falls under federal jurisdiction and is referred to as the U.S. EEZ (Grigg 1994, National Oceanic and Atmospheric Administration [NOAA] 2006). Precious coral exploitation in this zone has been managed since 1983 by the National Marine Fisheries Service of the NOAA through the Precious Coral Fisheries Management Plan of the WPCouncil.

The Federal Fishery Management Plan by the WPCouncil classifies precious coral beds as established beds, conditional beds, refugia beds and exploratory permit areas (Grigg 1994). Selective harvesting gear is mandatory, although until 1999 conditional and exploratory beds could be harvested with non-selective gear (Bruckner et al. 2008). The Makapu'u bed (the densest and most productive bed, measuring 1.7 m^2) and Au'Au channel bed (0.4 m^2) are currently the only established beds. Conditional beds, for which yield has been estimated relative to their size assuming identical conditions to known beds, are Kea-hole Point, Kaena Point, Brooks Banks and 180 Fathom Bank (Grigg 1994). The WP Council bed between Nihoa and Necker Island is the only designated refugium (Bruckner et al. 2008).

The need for *sustainable* management of precious coral fishery was first recognized when the precious coral jewellery industry in Hawaii began to grow steadily. In response, the University of Hawaii set up a research programme to study the ecology and fisheries management of precious corals in 1970 (Grigg 1976). The state of Hawaii management programme is thus the first precious coral fishery management based on the ecological characteristics of the species.

The study revealed that the minimum size limit at which divers were harvesting black coral voluntarily was above the age at first reproduction. The fishermen voluntarily refrained from harvesting black coral colonies smaller than 1.22 m in height and 2.54 cm in base diameter (reproductive maturity in *Antipathes griggi* is reached at about 64–80 cm; Grigg 1976). Smaller colonies were of little value to the curio industry, and it made economic sense to spend the dive time harvesting larger coral. Small black coral trees were already of some value to the curio or display market, which bought them at US$50 kg^{-1} instead of US$10 kg^{-1}, but apparently as long as large coral trees can be harvested and sold for more to the jewellery industry, the small corals are not harvested intensively by these fishermen.

The UH-Seagrant study applied the Beverton-Holt model to estimate an MSY of about 5 t for the Au'Au Channel stock (Makapu'u bed) and 1.25 t for the Kauai bed (Grigg 1976). This model defines maximum production in a fishery as the point at which natural mortality losses are balanced by population growth (Beverton & Holt 1957). Despite being a simple model that has been surpassed by more advanced models in various fisheries, it has been used successfully to assess various coral populations (Grigg 1976, García-Rodríguez & Massò 1986b, Tsounis et al. 2007, Goffredo & Lasker 2008, Knittweis et al. 2009).

The age at maximum yield per recruit for *A. griggi* was estimated to be 22–40 yr, corresponding to corals that measure 1.7 and 3.2 m in height (the oldest black corals can reach 3.5 m across and more than 4 m in height). However, corals continued to be harvested when they had reached 1.22 m, instead of 1.7 m. The reason for the discrepancy is shown by an analysis of *optimum* yield. Harvesting all corals exceeding the height limit of MSY would, in theory, provide a 100% efficiency of the fishery. Lower efficiency than that, however, may result in more profit if catch per unit effort and optimum yield are considered. Therefore, the most economic and yet sustainable strategy often is to fish at low intensity and catch the coral at an earlier age than at MSY (Grigg 1976). As

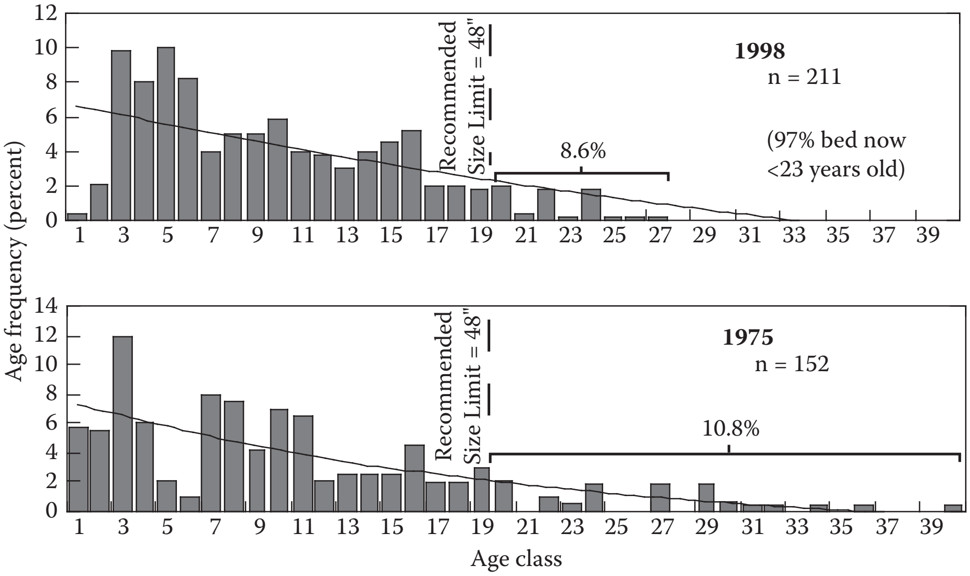

Figure 4 Age frequency distribution of black coral off Maui, Hawaii, in 1975 and 1998. (Data from Grigg 2001, with kind permission from *Pacific Science*, University of Hawai'i Press.)

long as the harvested corals are significantly older than the age at first reproduction, a reproductive cushion is ensured (i.e., the colonies are allowed to contribute to recruitment for several generations before they are harvested, ensuring sufficient recruitment and thus survival of the population). On the other hand, this policy means that care must be taken to control fishing intensity by using monitoring programmes. This practice does not produce maximum yield but allows for maximum profit (thus called *optimum yield*) because yield per fishing effort is maximized (achieving maximum yield may in some cases result in less profit if it requires disproportionally higher fishing effort).

The new management rules did not conflict with the fishermen's interest of harvesting large colonies and were voluntarily accepted. The Hawaiian black coral fishery may therefore be the only sustainable precious coral fishery in history (Grigg 2001). The comparison of the population structure between 1975 and 1998 showed that the oldest and largest colonies were no longer present, but that the structure of the population at the younger spectrum remained unchanged (Figure 4).

However, in 1998 demand in black coral started to increase (sales increased by 50%; see 'Economy and Trade' section), and the state of Hawaii lowered the size limit, introducing a grandfathering scheme that allowed veteran divers (those who had reported black coral harvest in the preceding 5 yr) to collect corals of 0.9 m in height to meet the rising demand. Another reason that the fishery has become more efficient is the availability of detailed bathymetric maps and the adoption of GPS (global positioning system) navigation (Bruckner et al. 2008). Use of this equipment has led to a decline in black coral biomass of 25% (Grigg 2004), possibly posing a threat to the population. In 1998, after 23 yr of harvesting, no colonies older than 27 yr remained (Grigg 2001), but enough mature colonies still remained in the population (maturity is reached at 10–12.5 yr; see p. 172). Three yr later, no colonies older than 24 yr were left (Grigg 2004), illustrating a biomass loss due to increased intensity of fishing. A further negative impact on the black coral populations is the aforementioned invasion by the octocoral *Carijoa riisei*. The affected populations are beyond the depth range and were previously thought to be important contributors to larval recruitment of the overharvested populations but were found to be non-reproductive (R. Grigg unpublished data).

Responding to this situation, the state of Hawaii has returned to the minimum size limit of 1.2 m. Recent surveys furthermore suggest that MSY be adjusted downward by approximately 25% (Grigg

2004, Parrish 2006). Also, the state of Hawaii is in the process of setting up an inventory-tracking system using bar codes to gather data on the harvest and trade of black coral (T. Montgomery, DAR, personal communication). Adaptive management (Walters 1986) is likely to improve this fishery because two factors favouring the recovery of the stocks are (1) the ecology of the species is fairly well understood and (2) the conclusions have been successfully applied for more than 20 yr and a steady state has been achieved. The reasons that lead to biomass decrease are known, and the precious coral management system can be described as better organized than other precious coral fisheries. Furthermore, demand is not excessively high because the industry does not depend solely on production from the Hawaiian Islands, and there is a low number of fishermen (5 licenses), with no indications of poaching. For these reasons, and due to relatively fast growth, Hawaiian black coral beds have the best potential for recovery and sustainable harvesting among precious coral fisheries.

Mediterranean red coral

The management of the Mediterranean red coral fishery was traditionally based on social, market and political considerations, but ecology was taken into account as early as 1882, when Professor C. Parona from the University of Cagliari was asked to help improve the efficiency of the fishery. In the 1870s, the naturalists Cavolini, Milne-Edwards, Marsili, Lacaze-Duthiers, Issel and Canestrini, as well as the fishermen themselves, studied the distribution and reproduction of red coral to create a basis for management decisions (although their recommendations did not have much influence; see Tescione 1973). The growth rate was only studied for the first time half a century later (Dantan 1928). Fishery statistics before the 1980s were documented by noblemen and various governmental organizations and were summarized by Tescione (1973). In Italy, the fishery was for a long time essentially unregulated, giving absolute freedom to dredging and divers (Arena et al. 1965, Liverino 1983).

Responding to the dramatic decrease of yields in the late 1970s and early 1980s (Chouba & Tritar 1988, Cattaneo-Vietti et al. 1998, Santangelo & Abbiati 2001), the FAO (1983, 1988) hosted technical consultation meetings; however, these resulted in few management changes other than banning coral dredging. Intrusions of foreign poachers into national waters off the island of Alboran in the 1980s initiated efforts to ban dredging as well as to list *C. rubrum* in CITES Appendix II.

With the advent of selective scuba harvesting, the voluntary minimum harvesting size of 7 mm was eventually established as a rule, and for a long time smaller corals continued to be of little value to the industry (FAO 1983). Similar to the Hawaiian fishery, later studies found red coral to reproduce at an earlier age, so that the protection of immature juveniles was ensured. Determining MSY was not possible at that time. Although the biometry of red coral had been studied (Marín & Reynald 1981), the population structure of red coral was first studied in 1986 (García-Rodríguez & Massó 1986c). A subsequent study was then able to determine the MSY at 80 yr (García-Rodríguez & Massó 1986b), which has since been confirmed by Tsounis et al. (2007), who obtained a very similar value (although slightly higher due to using lower growth rates) of 98 yr. In contrast, the corals that are legally fished are about 14 yr old. García-Rodríguez and Massó (1986a) recommended a minimum size of 8.6 mm, but to date this has not been adopted, and 7 mm remains a widespread minimum size of harvest. Exceptions are Algeria, where 8 mm is applied (CITES 2007), and Sardinia, where a minimum size of 10 mm does not interfere with the intent of the divers to harvest only large colonies in very deep water. Morocco has not set up any size limit and manages its stocks through quotas (Abdelmajid 2009, Zoubi 2009).

Although red coral becomes sexually mature at an age of 3–4 yr, fertility does not reach 100% before 6–9 yr (Santangelo et al. 2003, Tsounis et al. 2006a). The legal minimum of 7 mm in diameter corresponds to about 11-yr-old colonies, depending on the growth rate, which varies according to habitat and geographic region (see p. 168). Thus, fishing does not allow the majority of the population to reach its full reproductive potential (Figure 5). Three yr of reproductive buffer may not

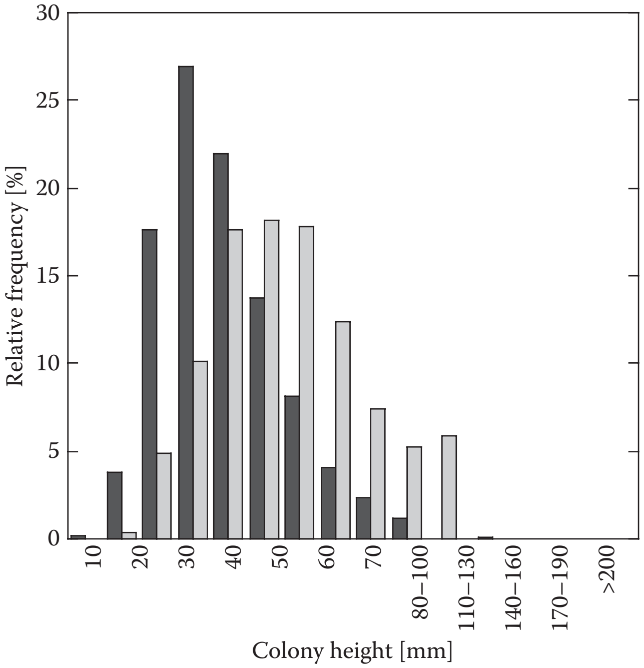

Figure 5 *Corallium rubrum* colony height distribution on the Costa Brava (black) and the Medas Islands Marine Park (grey) (both in Spain). The slight but significant size difference is the result of about 14 years of protection. (Data from Tsounis et al. 2006b, with kind permission of Reports for Polar and Marine Research.)

be long enough to ensure high recruitment if compared with black coral in Hawaii, which reaches maturity at 10–12.5 yr but is not fished until it is 20 yr old. This is significant in modular, highly branched organisms such as corals because only a small fraction of the older colonies contributes the majority of the recruits (Miller 1996). In some species, up to 98% of the recruits are produced by the older half of the population (Babcock 1991, Sakai 1998, Beiring & Lasker 2000).

Again, similar to the Hawaiian fishery, red coral harvesting below the age limit corresponding to MSY was continued, increasing the catch per unit effort. In both fisheries, the main factor that has led to overharvesting and decreasing biomass and yields is the problem of balancing fishing effort against age at first capture. When harvesting at an age below MSY to achieve optimum/economic yield, fishing effort needs to be sufficiently low. If the fishery is too efficient for the assumed effort or the effort misjudged (e.g., due to poaching or forged statistics), the stocks can be harvested down to the targeted age at first capture. In fact, this appears to be the cause for the documented overharvesting.

Harvesting down a stock to the minimum size limit is not desirable because it is unsustainable and depletes the stocks. More sophisticated models are likely to allow better predictions of harvesting effects based on a certain fishing effort. Leslie-Lewis transition matrices, for example, are age-structured, nonlinear models based on demographic data (Caswell 2001) and can take density dependence into account as well. The advantage lies in linking reproduction, growth, mortality and demographic structure into one model. These models have been used to simulate the trends of a red coral population over time (Santangelo et al. 2007).

The results of the transition matrix modelling show that the present, extremely young red coral populations may not be able to recover from the combination of overfishing and frequent mass mortalities (Santangelo et al. 2007). If natural catastrophes of any kind occur with an elevated frequency, the affected population can only survive if it has a strong recruitment. Recruitment potential is directly linked to the number of polyps; thus, heavily fished populations with only young colonies are driven to local extinction. Strategies to avoid this so-called Allee effect of populations decreasing below critical size (Allee et al. 1949, Stephens et al. 1999, Dulvy et al. 2000) are setting adequate quotas, controlling poaching and the introduction of a minimum size limit higher than 7 mm. Conservative management plans such as this one usually conflict with short-term socioeconomic interests, and decision makers therefore hesitate to implement them (Bearzi 2007). However, in case of the red coral fishery, the additional dilemma lies in the fact that the fishery has left only a small fraction of the populations with colonies that surpass this limit. The fishery in Sardinia, however, decided to ban coral harvest in waters shallower than 80 m. The management was strong enough to allow it to shut down the fishery completely in 2007 to study the stocks and revise management (Cannas et al. 2009, Doneddu 2009). Furthermore, considerable no-take areas are in place, although their size may not reach 80% of the total stock, as in Hawaii. These measures represent a favourable development, and when the data are analysed and published, the Sardinia situation may well turn out to be a case study of sustainable management of *C. rubrum*.

In general, however, all known *C. rubrum* stocks have been recognized as overexploited since 1989 (FAO 1988, Cognetti 1989, Santangelo & Abbiati 2001, Tsounis et al. 2007), but the full extent of the situation in the Mediterranean is only now being understood through a recent accumulation of data. No discoveries of new coral beds have followed the overexploitation of known stocks. The fishery progressed towards deeper depths and smaller colonies and, as the data showed, is approaching limits in both aspects. The fishery has not extended its reach into depths beyond 130 m because dredges are prohibited, and submersibles are not economic. ROVs are occasionally used for scouting, but remotely controlled extraction does not appear to be feasible. Ironically, there is hope within the industry of exploiting deeper strata, but they were depleted in the 1980s, and scuba-diving has been able to access coral in crevices and cave entrances only because this species is cryptic in shallow water. It appears that a vast part of the deep populations is presently not of high commercial viability because red coral grows at low densities at these depths and at more exposed positions, so that crevices in deep habitats contain fewer large corals than shallow water crevices. The most important aspect is that these populations have not yet recovered from centuries of heavy dredging, and part of their habitat may be irreversibly occupied by fast-growing *Lophelia pertusa* deep corals (Rossi et al. 2008, Orejas et al. 2008). Exploiting the deeper populations of Mediterranean red coral can be problematic because they may more vulnerable to harvesting than shallow-water colonies. Consequently, the future of Mediterranean red coral fishery is likely to see a further reduction of yield in one way or another.

The only way to meet demand is to import Pacific species, whose stocks are not yet studied, and the sustainability of their fisheries therefore remains questionable. The question of how to achieve sustainability of the Mediterranean fishery is an enormous socioeconomical challenge. Optimum yield for an overharvested stock is focused on rebuilding its full capacity (Magnuson-Stevens Fishery Conservation and Management Act, U.S. Department of Commerce 2007), but this requires a reduction of yield.

Conservation

Habitat conservation considerations

The importance of non-reef-building deep-water coral species for ocean biodiversity creates a conflict between habitat conservation and traditional precious coral fishery management. Whereas fishery management allows an intensive exploitation of a population, accepting a significant modification of its age structure, habitat conservation intends to maintain a population structure that guarantees a minimum functionality. Overfishing is in some cases defined as a biomass reduction of the target species population to 20–30% of the baseline (CITES 2007, WPCouncil 2007). Today, however, precious coral fishery managers realize the need for an ecosystem approach in fishery management rather than single-species-oriented management (WPCouncil 2007), and recent management research has expanded into connectivity of coral taxa in the Hawaiian Archipelago (Baco & Shank 2005, Baco et al. 2006) and associations with other species. This ecosystem-based fishery management (EBFM) represents a holistic approach that considers the connectedness of different species and links between species and environment, rather than managing species as if they were in isolation (Bruckner et al. 2008).

In the case of deep corals, studies highlight with increasing tendency the importance of deep-water corals as ecosystem engineer species for improving biodiversity and productivity and stability of their ecosystem (see p. 171). An intensively exploited population, even if sustainably managed, is surely less efficient in providing these 'ecological services' (Moberg & Folke 1999) than a population with a balanced age structure (containing both recruits and very old individuals). Future precious coral management is therefore challenged with determining, and maintaining, the level of modification of population structure by fishing pressure that still allows an acceptable ecosystem engineering effect.

The implementation of marine protected areas may be an important measure to ensure the biodiversity of nearby commercial areas if refugia are large enough and interconnected. In contrast, traditional rotation systems (in use since the Middle Ages) that harvest one stock and then work on others while the exhausted one is left to recover are problematic. The severe depletion of one stock is not in line with habitat management because it does not account for the ecological services of the corals. If the spatial scale chosen is too broad, overharvesting of one area may interrupt the gene flow between coral populations, as well as of invertebrate and fish populations seeking shelter in their branches. Therefore, management should instead monitor the fishery ensuring that no age class is eliminated completely. The present precious coral fisheries are far from this ideal, but lessons could be learned by examining the plenter principle that is applied to terrestrial forestry (O'Hara et al. 2007). As a starting point, given the lack of models, the maximum size of colonies in a population could be determined by ROV transects and a percentage of them prohibited from being harvested to maintain habitat structure. In a way, this approach would add maximum size limits (protecting habitat structure and thus biodiversity) to the already common minimum size limits and protect the reproductive potential.

International conventions versus local management

As illustrated, local precious coral fishery management has in many cases proven inadequate, so there is no doubt that management strategies need to be revised. One reason is the 'tragedy of the commons' that is typical for most fisheries, that is, the overexploitation of common resources by competing fishermen who exceed quotas for fear their competitors will soon exhaust the commonly exploited resource anyway. However, the fact that precious corals are sessile, non-migrating species may offer a possibility of avoiding this problem by granting indigenous exploitation rights or forms of comanagement and stewardship. Overfishing is, however, in part due to poaching and the location of several precious coral stocks in international waters. Therefore, the question arises regarding whether international conventions might help to improve precious coral management as it does with other fisheries.

At present, it is up to each country to manage their stocks because, unlike many migratory fish species, precious corals have not been included in regional fisheries management organizations as is the case in other fisheries, such as the International Commission for the Conservation of Atlantic Tunas (ICCAT), the Western and Central Pacific Fisheries Commission (WCPFC), the Indian Ocean Tuna Commission (IOTC) or the General Fisheries Commission of the Mediterranean (GFCM). The approach taken by the last organisation has been suggested as a means of managing *C. rubrum* fisheries, but it is unclear if the GFCM recommendations would be enforced. The European Union placed *C. rubrum* in Annex V of the European Union Habitat Directive (2007), and it is also listed in Appendix III of the 1979 Bern Convention on the Conservation of European Wildlife and Natural

Habitat Protection (Council of Europe 1979). Consequently, the currently observed overexploitation is in large part due to lack of enforcement.

The management and conservation of precious coral populations in international waters has not been addressed by international treaties, although fishermen operating out of ports in the United States do need a permit for high-seas fishing. In other countries, seamounts in international waters can currently be harvested without licenses. It is likely that these unstudied habitats contain the last natural populations, treasuring a significant biodiversity so that they should be protected by declaring them, for example, as UNESCO (United Nations Educational, Scientific and Cultural Organisation) World Heritage Sites in Danger. Some organizations, such as the Northwest Atlantic Fisheries Organization (NAFO) are designing international protection treaties for the UN, vulnerable marine ecosystems (VMEs), which might serve as role models for other precious coral habitats. The declaration of the north-western Hawaiian Islands as a marine national monument served a similar purpose. However, in all cases of declaring precious coral communities in international areas as protected, there is the problem of enforcement. Trade control may thus be an important further measure (see next section). International trade control can be an efficient tool in discouraging poaching and illegal trade as well as fostering research into better management, but strong local management and enforcement will certainly remain the basis of precious coral management.

Control of the precious coral trade through CITES

The ecological importance and vulnerability of precious corals has led to several proposals to include these species in Appendix II of CITES. CITES is an agreement between 175 governments that was created in 1975 to ensure that international trade of wild animals does not threaten their survival. Unlike the Red List of the International Union for Conservation of Nature (IUCN), which identifies and documents species in danger of extinction, CITES actively controls trade. Both organisations distinguish various levels of threat, but the most relevant category of protection for precious corals is presently Appendix II (which contains the bulk of CITES listed species). It includes species not necessarily threatened with extinction but in which trade must be regulated to protect declining populations and ensure sustainable exploitation. More drastic measures include the entire prevention of precious coral import into the United States via the Lacey Act, closing down the largest segment of the precious coral market. CITES Appendix II, however, does not ban exploitation but instead regulates trade.

Several orders and families containing precious coral species have been included in Appendix II, such as Antipatharia (black corals), Coenothecalia (blue corals), Tubiporidae (organ-pipe corals) and Stylasteridae (lace coral). Some of them, like blue corals, are not traded at all, and little is known about their biology.

Since 1986, proposals to include *Corallium* species were rejected because of lack of data that could confirm whether these species were threatened. The existence of refuge populations in deep water were assumed, and as species with a broad depth range and scattered distribution, they are less likely to suffer from extinction. On the other hand, their high value, the slow recovery of overexploited stocks and the short larval dispersal do increase the risk of genetic isolation and extinction, as recent data indicate. In general, it is thought that commercial species go *economically* extinct before the species is threatened by *ecological* extinction. But, multispecies exploitation sustains the industry, while part-time poaching may lead to local extinction of some isolated populations. Furthermore, factors such as manufacture of reconstituted coral from small branches and mass mortality epidemics make the risk of extinction difficult to predict.

What is beyond doubt, however, is the unsustainable nature of most precious coral fisheries outside Hawaii. For this reason, and because errors regarding precious coral management may take decades to rectify, the United States proposed the inclusion of the genus *Corallium* in Appendix II of CITES in 2007.

Several issues arose that led to some controversy regarding this proposal. First, identification was seen as a hindrance to enforcing the implied trade control because *Corallium* species are not easily identified. In fact, once worked and polished, it becomes unfeasible for an enforcement officer to distinguish *Corallium* species (even fake coral can be hard to identify, and DNA identification is not economical). However, the need to identify *Corallium* species already exists because China listed four *Corallium* species in Appendix III in 2008. Also, identification of *Corallium* species is easier than *Antipathes* species, which is already listed (E. Cooper, WWF Canada, personal communication). An effective solution would be to list the family Corallidae instead of the genus. This solution is certainly desirable because of the family's ecological significance and vulnerability and it would reduce administrative effort. However, it is not clear whether it is necessary to identify *Corallium* shipments to species level. On the one hand, if the whole family is listed, identification to that level is feasible (E. Cooper personal communication). On the other hand, conservation efforts are local and on the species level, so that an accurate identification may help identify the origin of harvested coral.

Other concerns are that international trade control might be seen as a substitute for local management. In the case of black coral, effective local management was in place before the listing, and the CITES listing affects the industry because each permit requires 2 h of employee time and a $129 processing fee, increasing the costs of the business (R. Grigg unpublished manuscript). Processing time per permit takes 1 month. Problems occur when jewellery under warranty is sent back to the manufacturer for repair and is held in customs due to missing permits (T. Montgomery, DAR, personal communication). In response to these administrative burdens, some companies no longer sell outside the United States. Overall, less black coral is sold, and in this sense, black coral resources are conserved because less raw material is purchased (R. Grigg unpublished manuscript). Regarding the significance of a Corallidae listing for the Italian coral jewellery industry, this type of burden would be especially severe on small family businesses that are typical in Torre del Greco (C. Condito, Assocoral, personal communication). The industry is also concerned about losing sales due to the resulting stigma of a CITES listing (G. De Simone personal communication).

Perhaps the most difficult subject of discussion is the question of how to deal with stockpiles of coral that were harvested before the convention. These are, by definition, exempt from the treaty, but existing standard procedures such as delayed implementation may not deal effectively with the potentially large quantities. However, all these considerations are also of a general nature and not coral specific.

Further discussion during the initial evaluation of the 2007 proposal (including a preparatory FAO consultation) arose over uncertainties whether the criterion of biomass decline was met for all species. A lack of data was identified for several species, but further species can be proposed for listing based on 'lookalike criteria' in comparison with similar species. Landings do exist for several species but were criticised as not reflecting biomass trends, as when fishing intensity decreases independently (e.g., if market forces render fishing economically infeasible), catch declines may erroneously indicate a biomass decline. However, the change of prices does easily identify if the reason for the declining yields (Figures 2 and 5) is dependent on the availability of corals. Two cases are known when an overabundance of corals drove prices down and forced the industry to stop fishing (other than during the world wars): (1) the 1880 crisis that was caused by the discovery of large beds of fossilised Sciacca coral (see p. 176) and (2) in 1982 the consequences of harvesting large amounts of Midway coral. In other known cases of reduced fishing activity, prices increased and have continued to do so in recent years.

Recent catch declines do therefore reflect biomass declines, if changes in harvesting methods and fishing effort are accounted for. Furthermore, the only two case studies that evaluated population structure/biomass, or standing stock, are of the precious corals in Hawaiian waters and a few populations in the Mediterranean. Identifying population biomass decline requires a time series comparison or comparison with unfished populations. In any case, population decline in colonial animals must be identified by analyzing polyp numbers, not colony numbers, because the polyps are the reproductive modules (Bruckner 2009). Population structure data serve well for that purpose, in contrast to abundance data, which are associated with high standard deviations due to patchy distribution (see p. 169).

In any case, with the exception of black coral in Hawaii, there is no baseline because no other species has been studied before intensive harvesting began. Considering that today's populations lack the very old colonies that contained a number of polyps several magnitudes higher than today's small/young colonies, it is certain that populations of most species in question did decline dramatically, bringing with it a reduction of recruitment.

While local management remains the basis of conservation (Pani & Berney 2007, Pani 2009), supporters of the CITES listing argue that a listing in Appendix II would stimulate this kind of research and management because CITES obliges each member country to assess its fishery to be able to issue non-detrimental findings to harvesters who apply for an export permit. (However, the listings of black coral in Appendix II have not resulted in further local management programmes.) CITES is not meant to be a substitute or a replacement for local or regional management but rather a means of ensuring that harvest and trade are legal. It is difficult to assess and foresee management options in all countries. In Spain, for example, a CITES listing may lead to more severe penalties, including jail terms rather than fines, and might therefore strengthen local management.

These complexities are reflected in the initial adoption of the 2007 proposal in CITES Committee One and its subsequent overturning during deliberations in Plenary on the final day of the listing due to concerns regarding its implementation (Morell 2007). Between the CITES Conference of Parties 14 in 2007 and the time of publication of this review, two *ad hoc* workshops were held to clarify these issues and discuss whether and how the listing can be implemented.

The consensus was that the FAO GFCM (General Fisheries Commission of the Mediterranean) may be the appropriate organisation to effectively manage *Corallium rubrum*, and that shallow water populations should be protected (University Parthenope, in press). The United States and European Union submitted an updated proposal to be evaluated at the Conference of Parties 15 in 2010. In a consulting function to CITES Conference of Parties (CoP), the FAO found that the data do not meet the decline criteria and recommends strong local management to prevent unsustainable harvesting, while highlighting implementation issues and the administrative burden of a CITES listing (FAO 2007; FAO 2009). The IUCN (International Union for Conservation of Nature) and TRAFFIC (the Wildlife Trade Monitoring Network) also advise the CoP and came to the conclusion that the data do not meet the CITES criteria (IUCN & TRAFFIC. 2007).

Active restoration

Rearing red coral to provide the jewellery industry with unlimited resources has been tested with no notable success (Cicogna & Cattaneo-Vietti 1993). The slow growth rates imply that the risks of the operation are high and the investment return low. However, due to the long recovery time of devastated precious coral populations, it is feasible to design programmes that combine *ex situ* or *in situ* rearing with transplantation techniques. This procedure could enable ecosystem managers to actively restore habitats that have suffered local extinction and create a network of stepping stones that can ensure sufficient gene flow and recruitment. The recovery of complex coral ecosystems, which takes decades or more (Dayton 2003), might be accelerated in this way. Active restoration is seen as the future of conservation and has evolved notably during the last decade (Young 2000, Rinkevich 2005). Restoration methods such as transplantation of coral fragments, branches and whole colonies have been pioneered since the 1970s through pilot studies, yet restoration of coral reefs is still in its infancy (Edwards & Clarke 1998) and has until recently not been a widely applied management option (Lindahl 1998).

The most significant advance in coral reef restoration over the last decade has probably been the introduction of the concept of 'coral gardening', which is a two-step protocol for the mariculture of coral recruits (spats, nubbins, coral fragments and small coral colonies) in nurseries (Rinkevich 1995). *In situ* pools, installed in sheltered coastal zones (Epstein et al. 2001), and *ex situ* tanks (Becker & Mueller 2001) are used to mariculture coral recruits to an adequate size, thus providing ecosystem managers with an unlimited source of colonies for transplantation (Rinkevich 2005). This concept represents the most efficient and advanced approach to ecosystem restoration.

However, efforts have focused on tropical reef-building corals, and there are few data on temperate and cold-water coral restoration (Grigg 1984, Cicogna & Cattaneo-Vietti 1993, Montgomery 2002). The settlement and early-life-phase biology of *Corallium rubrum* have been studied *in situ* using marble tiles (Bramanti et al. 2005, 2007), providing the basis for the subsequent transplantation of the tiles. Future research may further refine transplantation protocols, including the evaluation of measures that increase growth rate (Rinkevich 2005).

Nevertheless, considerable deep coral and temperate coral restoration research will be necessary to prepare conservation scientists and managers to actively support the natural recovery of these habitats. This research needs to include precious coral communities devastated by harvesting as well as other deep coral communities that were destroyed as a result of dredging or natural events.

Of course, prevention is to be preferred for many reasons (including financial considerations) over active restoration. It should be the last resort because the only feasible outcome that can realistically be expected is an increase in the natural recovery rate (Edwards & Clarke 1998). Future research may test appropriate methods and estimate the rate of increase of recovery. In some cases, recovery would not occur without active restoration (habitats geographically isolated from the gene pool), but it would still be a slow process and assumes the concept would prove feasible in deep corals.

Summary and conclusions

The analysis of historical data revealed that today's precious coral populations are heavily modified by commercial extraction. These are the slowest-growing organisms of any fishery known, past or present. In some cases, such as the *Corallium* sp. harvest at the Emperor Seamounts, the populations have been devastated, and later sampling found only dead and broken coral; in the case of *Antipathes* sp., there are few exploitable populations left in diving range. *Corallium rubrum* populations in the Mediterranean Sea resisted exploitation due to their uniquely high reproductive capacity, but their population structure in shallow water has changed from providing a forest-like habitat to one resembling a grass plain. The Mediterranean red coral was dredged for centuries until the populations declined, then divers harvested corals inaccessible to dredges until depths reachable with traditional air scuba became largely depleted. Since the industrial exploitation of *C. rubrum* began centuries before marine science was born, the baseline of the population structure under undisturbed conditions is not known. Recent research indicates that, despite the hopes of the industry, populations below scuba limits have not yet recovered from dredging significantly enough to expose them to the pressure of a deep coral fishery. Poaching appears to be a severe problem for the shallow-water populations, and some areas need urgently improved protection.

The single example in Hawaii of a fishery where local management plans have been based on a prior study of growth rate, population structure and other ecological parameters shows that sustainable management is possible, at least for faster-growing species. The analysis of all available data showed that any exploited precious coral populations that have been studied have been harvested down to the target age or size.

Nevertheless, the U.S. and European jewellery industries have been able to grow despite limited or declining stocks because they have shifted to imports from Asian stocks and species. This shift is worrying because 80% of the coral harvested in Taiwan is dead coral, which means that these beds will not renew themselves significantly. The size of landed coral may already be decreasing in tropical corals because jewellers have started buying back large coral pieces that can be cut to high-fashion jewellery. Furthermore, there are first signs that even economically less-valuable species such as bamboo coral have become exposed to heavy harvesting pressure.

Thus, although there remain controversies about the age of some species, about the existence of undiscovered stocks and a lack of biological data for many species, there is little doubt that most all known precious coral stocks have been overexploited. In fact, given the nature of the exploitation, the terms ‘harvesting’ and ‘fishery’ inaccurately imply a renewal of the resource, which in reality rarely occurs. In management terms, the majority of fisheries can more precisely be characterized as ‘coral mining’.

The recent studies and the proposal to list the genus *Corallium* in CITES Appendix II mark 2007 as a watershed year for the precious coral fishery. There remains little doubt that deep and precious coral habitats are in urgent need of better protection, even though management and conservation are made more difficult by the lack of scientific data on the population structure and basic biology of many species.

Precious corals stand out from many other known fished species due to their significance as structure-forming organisms. However, the discussion about sustainable fisheries and species preservation is only starting to acknowledge the need to ensure complex and diverse precious coral habitats. Recent management plans have emerged that have the goal of considering habitat in a holistic approach, but until now, the specific measures of how to achieve this goal in precious coral stocks have yet to be pioneered. At present, there are only few refugia, and not all of them had been put in place before harvesting began, so effectively few virgin populations are known. In the case of shallow populations, there are probably none left.

The need for a paradigm shift in precious coral resource management is therefore apparent. Implementing sustainable management based on best-available knowledge and maintaining high habitat complexity will not only provide a high biodiversity and productivity of deep coral habitats but will also ensure the survival of the coral jewellery industry. These unique traditional industries have survived political and market force-induced hardships, but they depend on the fishery and ecosystem managers to advance the state of the art of precious coral management and ensure a future for this craft.

Recommendations

In the light of the data presented in this review, we make the following recommendations for the future protection, management and conservation of precious corals:

1. Legally binding transnational management, as typical in many other fisheries. This recommendation is more likely to unite expertise and resources in an effort to adapt local management plans and enforce them. At present, however, CITES is the only international organisation with legal authority that has been proposed. Because it controls trade, rather than management, further support is necessary.
2. Identification of potential unfished virgin populations. If such populations exist, a fraction of them should be protected, for example, as UNESCO World Heritage Sites. Overharvested sites, which most likely means all shallow-water populations in air-diving range (about 0–70 m depth), should be exempt from fishing. All other sites that show a moderate impact, or new sites, may be continued to be harvested under new guidelines and a reduced number of licenses. This will require further research, and care must be taken that once new

populations are identified, they are protected before a coral rush begins. Further models for international precious coral habitat protection treaties may be the example of UN VMEs, which are designed by NAFO.

3. Improved monitoring, as is common in other fisheries. Usually, the only published landings data list the weight and location of coral harvested. Some other data are available from authorities, but to our knowledge there is usually no information on harvested colony size. Authorities need to collect data on the size of the landed coral, possibly through observers on fishing boats or at harbours. Data on the minimum and, more important, the maximum size of the harvested coral will give an additional indication of when the stocks are overharvested. Should fishermen consistently fail to harvest large corals, it is a reliable indication that a stock is depleted.

   In any case, regular fishery-independent monitoring of the stocks is advisable. In the absence of landings data, price increase (e.g., for previously little harvested species such as bamboo corals) could provide indications for further investigation. In populations for which recruitment is thought to be limited, this variable should also be monitored. Early warning programmes for invasive species could be designed by educating coral divers and providing contacts to whom observations could be reported. In cases where doubts about severe overharvesting exist, moratoria might be put in place until the data mentioned are obtained and analysed. This proposed procedure should not be confused with rotation harvesting, which appears to have more disadvantages than advantages.
4. Improved local enforcement against poaching where necessary. In Hawaii, Japan and the Mediterranean, it is reported that licensed fishermen long ago developed voluntary guidelines for harvesting to sustain their livelihood. The failure to stop poaching is hurting these wise practitioners. In countries where only fines are given, penalties for poaching need to be increased. Penalties for unlicensed fishing are lighter than those for poaching wildlife on land in some countries. Protection of red coral through CITES would lead to stricter penalty measures, at least in Spain, and would therefore strengthen local management.
5. Revision of yield quotas and revision of minimum size limits. In the Mediterranean, the minimum allowable base diameter limit should be at least 10 mm (following the example of Sardinia), and the colonies must be branched to a certain degree to preserve a minimum number of polyps that provide larvae. This minimum size is far smaller than size at MSY, so the fishery must operate at considerably lower efficiency than 100%. If fishing effort cannot be controlled, then the minimum size should be much higher. Morphology is subject to geographic variation, so the minimum branching allowed for harvesting must be determined locally. In Hawaii, experience shows that the grandfathering scheme is detrimental, so adherence to the traditional 1.22-m size limit is recommended.
6. Ban the trade of precious corals for display purposes in the curio and aquarium trade as well as jewellery made of composite coral powder because both practices provide incentive for the harvest of immature colonies.
7. In traditional fisheries using tangle nets, government incentives should be given to develop a selective fishery (e.g., using ROVs). The ROV footage will furthermore provide fishery-dependent data for better management.
8. Research on how cold-water, deep and precious corals act as ecosystem engineers and increase biodiversity and productivity of their habitat. Furthermore, the causes of mass mortality, including the recovery of populations from mortality and the growth of partially harvested colonies should be studied.
9. Research on the population structure and distribution of little-known species (or deep populations in the case of *C. rubrum*) and study of the larval biology and dispersion limits

between shallow and deep populations. In many species, there are no data on growth rate and population structure. Species for which growth rate estimates span a wide range would benefit from further research (i.e., *Gerardia* sp.).

Ecological research should be accompanied by a socioeconomic component that looks at how to implement the newfound knowledge. In the Mediterranean, for example, implementation issues rather than lack of knowledge need to be addressed.

10. Creating a network of microreserves. The main objective would be to ensure gene flow between deep and shallow populations and between populations along the coast. Microreserves would have the secondary function of protecting all those organisms associated with the corals. It is important that commercial stocks also contain microreserves, which should be monitored. The goal is to maintain a minimum proportion of large colonies within the stocks, at a distance at which they can provide larvae to the habitat, and provide shelter to associated organisms. For the same reason, rotation harvesting should be abandoned in favour of truly sustainable harvesting of each population.

    The slower the growth rate of a species, the more conservative the yield quotas should be and the smaller should the fraction of the harvestable stock be in relation to the total population.
11. Humane reduction of licenses where necessary. The number of licenses is often adequate if poaching is reduced and there is adherence to quotas. However, where necessary, license numbers should be reduced by not transferring licenses of retiring divers.

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