Ecosystems
DOI: 10.1007/s10021-010-9404-8

ECOSYSTEMS

Historical Changes in Marine Resources, Food-web Structure and Ecosystem Functioning in the Adriatic Sea, Mediterranean

Heike K. Lotze,[1]* Marta Coll,[1,2] and Jennifer A. Dunne[3,4]

[1]*Biology Department, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4J1, Canada;* [2]*Institut de Ciencies del Mar (ICM-CSIC), Passeig maritim de la Barceloneta 37-49, 08003 Barcelona, Spain;* [3]*Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501, USA;* [4]*Pacific Ecoinformatics and Computational Ecology Lab, 1604 McGee Avenue, Berkeley, California 94703, USA*

Abstract

The Mediterranean Sea has been strongly influenced by human activities for millennia. Although the environmental history of its surrounding terrestrial ecosystems has received considerable study, historical changes in its marine realm are less known. We used a multidisciplinary approach combining paleontological, archeological, historical, fisheries, and ecological data to reconstruct past changes in marine populations, habitats, and water quality in the Adriatic Sea. Then, we constructed binary food webs for different historical periods to analyze possible changes in food-web structure and functioning over time. Our results indicate that human activities have influenced marine resource abundance since at least Roman times and accelerated in the nineteenth and twentieth centuries. Today, 98% of traditional marine resources are depleted to less than 50% of former abundance, with large (>1 m) predators and consumers being most affected. With 37% of investigated species rare and 11% extirpated, diversity has shifted towards smaller, lower trophic-level species, further aggravated by more than 40 species invasions. Species providing habitat and filter functions have been reduced by 75%, contributing to the degradation of water quality and increased eutrophication. Increased exploitation and functional extinctions have altered and simplified food-web structure over time, especially by changing the proportions of top predators, intermediate consumers, and basal species. Moreover, simulations of species losses indicate that today's ecosystems may be less robust to species extinctions than in the past. Our results illustrate the long-term and far-reaching consequences human activities can have on marine food webs and ecosystems.

Key words: ecological history; marine populations; exploitation; habitat loss; eutrophication; extinction; invasion; food-web structure; ecosystem modelling.

Introduction

Throughout history, people around the world have settled along coastlines to make use of living marine resources. Yet only recently have marine ecologists started to reconstruct the history of human-induced changes in marine populations and ocean ecosystems (Jackson and others 2001;

Received 10 June 2010; accepted 15 November 2010

Electronic supplementary material: The online version of this article (doi:10.1007/s10021-010-9404-8) contains supplementary material, which is available to authorized users.

Author Contributions: HKL and MC designed the study, performed the research, analyzed the data, contributed new methods or models, HKL, MC and JAD wrote the paper.

**Corresponding author; e-mail:* hlotze@dal.ca

Published online: 14 December 2010

Rick and Erlandson 2008; Lotze and Worm 2009). Knowing the magnitude of past changes is essential to judge the current state of marine ecosystems, and understanding past drivers and consequences of change is needed to mitigate current and future human impacts. Also, historical reference points are needed to develop sound management and conservation goals (Pauly 1995).

Most studies in marine historical ecology have focused on single species, often large and charismatic animals, and a single human impact, exploitation (Lotze and Worm 2009). Only a few studies have analyzed historical changes across several taxonomic or functional groups due to multiple human impacts, revealing strong historical declines in coral reef and estuarine ecosystems (Jackson and others 2001; Pandolfi and others 2003; Lotze and others 2006). Yet the consequences for food-web structure and ecosystem functioning remained unclear.

Other studies have used ecosystem modelling to evaluate past food-web changes. For example, Dunne and others (2008) constructed ancient Cambrian food webs from fossil records, and used stochastic niche models (Williams and Martinez 2000) to show that they have similar network structure to modern food webs, with some interesting differences. Network models including analyses of cascading extinctions were used to explain the instability of Early Triassic terrestrial communities (Roopnarine and others 2007). Detailed food-web data were compiled to characterize the trophic roles of Aleut hunter-gatherers over the past 6000 years in the northeast Pacific (Maschner and others 2009). Mass-balanced trophic models were used to reconstruct past food webs revealing strong declines in predatory fishes since 1900 in the North Atlantic (Christensen and others 2003) and changes in trophic structure in the Benguela upwelling system after the onset of industrial fishing (Watermeyer and others 2008). Sala (2004) described possible past and present changes in a Mediterranean rocky-shore food web and suggested that historical removal of top consumers may have significantly changed past food webs. Recently, Coll and others (2008) modeled Catalan and Adriatic Sea food webs for the 1970s and 1990s revealing higher degradation and less robustness to species loss compared to non-Mediterranean ecosystems. They showed that binary network models and more complex biomass and trophic-flow models delivered comparable results suggesting both approaches capture fundamental information about how food webs are structured and change under human pressures.

Here, we combined historical data analysis and ecosystem modelling to reconstruct past changes in marine resources and food-web structure in the Northern Adriatic Sea, Mediterranean. The Adriatic has a long history of human influence and several previous studies have analyzed past changes in marine species, fisheries, and environmental conditions (for example, Barmawidjaja and others 1995; Lotze and others 2006; Fortibuoni and others 2008; Gertwagen and others 2008). We synthesized this information to derive the history and consequences of ecological changes from pre-human to modern times. Our aim was to (1) reconstruct the magnitude of historical changes in marine populations, habitats, and water quality; and (2) evaluate their consequences for food-web structure and ecosystem functioning. Because empirical data of species abundance in the deeper past are generally scarce, we used binary network models which use presence/absence of species and their trophic linkages. Such models are simple, require few assumptions, and have low data requirements for parameterization (Dunne and others 2008). This approach is conservative as it covers only basic changes in food-web structure, yet delivers comparable results to trophic-flow models in terms of food-web degradation (Coll and others 2008).

Materials and Methods

Study Area

The Northern Adriatic (Figure 1A) constitutes the largest continental shelf in the Mediterranean Sea with a depth range of 10–200 m and high biological productivity (Ott 1992; Pinardi and others 2006). The Adriatic basin was inundated around 8,500–6,000 BC, and the northern deltas and lagoons were formed about 6,000 years ago (Brambati 1992). Due to river runoff and oceanographic conditions, the region exhibits decreasing nutrient concentration and primary production from north to south and west to east (Zavatarelli and others 1998).

Historical Data Sources

We compiled available ecological, fisheries, historical, archeological, and paleontological records on major marine ecosystem components. First, we briefly outline the human history around the Adriatic Sea to derive a timeline of cultural periods and associated activities. Trends in human population size were compiled from population data in the surrounding countries of Italy, former Yugoslavia, Albania, and Greece for 200 BC to 1800 AD

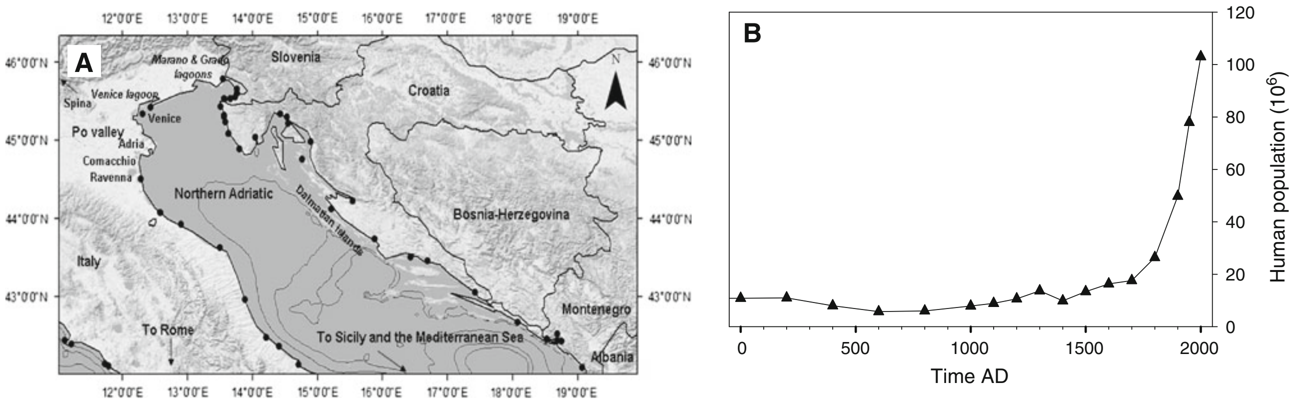

Figure 1. **A** Map of the Adriatic Sea depicting major regions and cities mentioned in the text (dots represent today's cities and ports) and **B** human population size in the surrounding countries from 0 to 2000 AD (McEvedy and Jones 1978; Lahmeyer 2006).

(McEvedy and Jones 1978) and 1800–2000 AD (Lahmeyer 2006). We then review detailed qualitative and quantitative records on the abundance, distribution, size, and exploitation of marine resources over time across six taxonomic groups: marine mammals, birds, reptiles, fish, invertebrates, and plants. This included species that have been of economic or ecological importance and thus, for which records were available. The history of water quality changes was reconstructed based on long-term sediment core and more recent hydrographic data. This included records of plankton abundance, eutrophication-associated species, harmful algal blooms, nutrient loading, oxygen depletion, and the abundance of heterotrophic bacteria. Records on invasive species were collected for different taxonomic groups and over time. A summary of these historical data has been published in Lotze and others (2006) in comparison with 11 other estuarine and coastal ecosystems worldwide.

Synthesis of Historical Changes

To summarize historical trajectories of change across different species groups, we used available qualitative and quantitative records of abundance to derive a standardized index of relative abundance (Table 1) for each of 90 species or species groups (Appendix 1 in Supplemental Materials) at the end of each cultural period. These estimates are denoted throughout the text [in brackets]. This often required some judging in terms of magnitude and timing of overall depletion, especially for the earlier time periods, and we generally choose the more conservative estimate until signs of depletion were clearly evident. This is not perfect but provides a general idea of possible historical changes based on the available information. We then calculated the average relative abundance for 24 functional and 6 taxonomic groups (Appendix 1 in Supplemental Materials). Although it is not possible to provide every record collected for each species, we aimed at describing major changes in each taxonomic, functional, and species group that provided the basis for estimating a relative abundance index.

To assess changes in species diversity, we calculated the percentages of species that were estimated as depleted, rare, and extirpated (Table 1) at the end of each cultural period. To evaluate ecosystem changes, we calculated the relative abundance of all megafauna (large carnivores and herbivores >1 m body size), macrofauna (small carnivores and herbivores), and species providing habitat and filter functions including benthic suspension feeders and vegetation (Appendix 1 in Supplemental Materials). To derive an overall estimate of water quality degradation we calculated the average relative change across all variables.

Construction of Food Webs

Binary networks were constructed to represent ''who-eats-whom'' food webs for each of the ten historical periods (Dunne and others 2008; Coll and others 2008). We adopted a common trophic structure for each food web through time to avoid biased results due to model construction. Historical records were complemented with recent information to fully represent all food-web components in the Adriatic Sea (Appendix 2 in Supplemental Materials). We added eight functional groups: hydrozoans, polychaetes, zooplankton, phytoplankton, natural

Table 1. Relative Abundance Estimates Based on Quantitative and Qualitative Records of Abundance and Exploitation

Estimate	Quantitative (%)	Qualitative records
Pristine = 100%	100-91	High abundance, no signs of human exploitation
Abundant = 90%	90-51	Medium to high abundance, regular human exploitation without signs of depletion, species common
Depleted = 50%	50-11	Low to medium abundance, strong exploitation with signs of overfishing and depletion (that is, at least 50% decline in abundance, catch, CPUE, size, or distribution), species depleted
Rare = 10%	10-1	Low to very low abundance, at least 90% decline in abundance, catch, CPUE, size, or distribution, collapse of stocks or exploitation, listed on endangered species list, species rare
Extirpated = 0%	0	Locally, regionally, or globally extinct, species absent

detritus, fishing discards, imports (organic matter from outside the system), and humans representing exploitation. We further split seven functional groups into two or three to account for different feeding types (carnivore, herbivore, and omnivore) and habitats (demersal, pelagic), excluded wetlands, and reached a total of 39 possible trophic groups (Appendix 2 in Supplemental Materials). Information on foraging behavior and diet for all species was obtained from the literature and previously published Adriatic models (Appendix 2 in Supplemental Materials, Coll and others 2008) to create predator–prey relationships. Because historical foraging data are not available, we used records from 1950 to 2000. When species-specific information was not available, taxa were assigned to functional groups composed of similar species. We did not include invasive species as their trophic position and diet is often less clear.

Based on these functional groups and predator–prey matrices we then compiled food webs for each cultural period and four possible scenarios: (i) all functional groups and humans if present (FW_All); (ii) all functional groups without humans (FW_WoH); (iii) same as (i), but excluding functional groups with relative abundance below 10% assuming they were functionally extinct (FW_E); and (iv) same as (iii), but without humans (FW_WoH&E). These scenarios allowed us to separate the effects of human exploitation and species extirpations on food-web structure.

Analysis of Food-Web Structure

We used 14 properties to characterize food-web structure (Williams and Martinez 2000; Dunne and others 2002a) and evaluated their expected trend of degradation in terms of overexploitation of high trophic levels and simplification of food-web structure (Coll and others 2008). Multi-variate statistical analyses including non-parametric Cluster analysis and ANOSIM (PRIMER software, Plymouth Marine Laboratory), based on the Euclidean distances dissimilarity index, were used to analyze differences among food webs of 10 historical periods and 4 scenarios. For each test, we first assessed individual correlations between food-web properties by constructing a draftsman plot and examining Spearman rank correlations. We removed one of each pair of properties that were significantly correlated ($\rho \geq 0.95$) to reduce redundancy and dimensionality of the data. Data were log transformed ($\log(x + 1)$) prior to analysis to correct for skewedness. Because properties represented different measures (%, counts, and so on), they were also normalized (subtracting their mean and dividing by their standard deviation) prior to the construction of a Euclidean distance matrix (Clarke and Gorley 2006).

Extinction Analysis

Finally, we explored the robustness of different food webs to simulated species loss by measuring the amount of resulting secondary extinctions (Dunne and others 2002b). A secondary extinction is defined when a non-basal species loses all of its prey or a cannibalistic species loses all of its prey except itself. Species losses were simulated sequentially by removing the most connected species until the food web collapsed, that is, all the species were lost.

Results

Human History

The Mediterranean was occupied more than 100,000 years ago, with modern humans having a sustained influence for around 50,000 years (Haywood 1997; Blondel and Aronson 1999) (Table 2).

Table 2. Description of Human History across Chronological Time and Cultural Periods

Time (BC-AD)	Cultural period	Abbr.	Description
Before ~ 100,000 BC	Prehuman	Pre	No human presence
100,000–6000 BC	Hunter–gatherer	HG	Paleolithic and Mesolithic sites around Adriatic Sea, human remains since ~ 8,000-10,000 BC, subsistence
6000–900 BC	Agricultural	Agr	Neolithic period with farming spreading from the east, agriculture and subsistence
900–500 BC	Local Market	Loc	Iron Age culture, Greek colonization and trading
500 BC–600 AD	Classical	Class	Etruscan and Roman periods, first cities, expansion of regional trade and market
600–1500 AD	Medieval	Med	Growth and expansion of economy, market, trade
1500–1800 AD	Early Modern	EM	Rise commercialization of resource use, development of luxury and fashion markets
1800–1900 AD	Late Modern	LM	Industrialization and urbanization
1900–1950 AD	Early Global	EGl	Global economy and market develops, industrialization and technological progress
1950–2000 AD	Late Global	LGl	Global economy and market established, industrial fishing increases after World War II and spreads from inshore to offshore

Remains of earliest hunter–fisher–gatherer communities were found along the Adriatic coasts more than 10,000 years ago, when shores took their present shape after the last glaciation (Kovačević 2002). Farming appeared about 6200 BC in Southern Italy (Kovačević 2002), and the first cities and states developed in the early Iron Age, including the Villanova culture in Tuscany, which spread to the Po valley, and the Etruscans in Northern Italy around 800 BC. The Greeks colonized the Mediterranean around 800–500 BC and established a trading post in Spina, Italy in the sixth century BC (Haywood 1997).

From 500 BC–600 AD the Classical period dominated around the Mediterranean (Haywood 1997). The Etruscans gained control of the Po valley and established two cities at the Adriatic coast: Adria and Spina. The Celts settled northern Italy in 400 BC and the Etruscan civilization declined. In 300 BC, the Romans expanded their empire around the Mediterranean, reaching its greatest extent in 100 AD. Major cities and industries were concentrated along the Adriatic coast. Increasing human population growth and associated activities since the Neolithic, but especially since Roman times (Figure 1B), strongly influenced the natural environment (Marchetti 2002).

The Medieval period began with the spread of the Carolingian empire about 600 AD, when Venice and Comacchio became trade centers and ports (Haywood 1997), while the eastern Adriatic belonged to the Byzantine Empire. In 1000 AD, northern Italy became part of the Holy Roman Empire. Around 1300 AD, Italy and France had the highest population density in Europe with more than 30 people/km^2 (Haywood 1997), yet the Black Plague and famine caused great losses in human population in the fourteenth century (Figure 1B, Blondel and Aronson 1999). During the fifteenth century, the Venetian territory expanded, Venice had a population of greater than 40,000 people, and was a center of trade, finance, and manufacturing until the late eighteenth century (Haywood 1997).

1500–1800 AD was a period of rising commercialization of resource use and development of luxury and fashion markets. In the nineteenth century, industrialization and urbanization increased, but most markets and trade remained in a regional context. The global economy and trade developed in the twentieth century and there was great technological progress and industrialization of resource use. After World War II industrial fishing spread from inshore to offshore waters (Tudela 2004). The Adriatic Sea also became a major tourist destination with its Italian coast covered with buildings, roads, seawalls, recreational facilities and jetties (Cencini 1998) greatly transforming coastal and shallow water habitats (Airoldi and Beck 2007). The general sequence and description of human cultural periods is outlined in Table 2.

Historical Changes in Marine Mammals

Whaling has not been very important in the Mediterranean Sea (Marini 1998), yet in Roman times whale meat was sold on markets, used for medicinal purposes, and whale bones were used. An active whale hunt occurred in the western Mediterranean, but stranded whales were used throughout [abundant] (Bode 2002). Sperm whales (*Physeter macrocephalus*) were heavily hunted for their oil throughout the North Atlantic since the 1700s, particularly from 1820 to 1850, but rapidly declined afterwards [depleted] (Evans 1987). Global estimates of sperm whale numbers suggest more than 1 million in 1700, of which 71% were left in 1880 and 32% in the 1990s (Whitehead 2002). In the Adriatic, strandings, sightings, and captures of sperm whales have been reported between 1713 and 1885, but rarely in the twentieth century [rare] (Bearzi and others 2004). Occurrences of fin whales (*Balaenoptera physalus*) have been reported since the early eighteenth century, but only occasionally in recent decades (Bearzi and others 2004). Fin whales were targeted throughout the North Atlantic since 1860, with more than 48,000 whales taken until the mid twentieth century (Evans 1987; Perry and others 1999). A fin whale fishery off Spain and Portugal began in 1921, but it took only 7 years for the local stocks to be depleted to the point of being economically unsuitable for further exploitation [rare] (Perry and others 1999). Today, great whales are rare, listed as endangered in the Mediterranean (Table 3) and only occasionally enter the Adriatic Sea [rare] (Marini 1998; Bearzi and others 2004).

Ancient people respected dolphins (Hughes 1994), yet recipes and medicine involved dolphins, and Aristotle mentioned dolphins drowning in fishing nets (Bode 2002). The common dolphin (*Delphinus delphis*) may have been one of the most abundant cetaceans in the Mediterranean until the early twentieth century, but museum collections from 1851 to 1993 indicated steep declines with today's population listed as endangered (Table 3; Bearzi and others 2003). In the northern Adriatic, common dolphins have progressively declined during the twentieth century [depleted] and are largely absent today [rare], due to systematic culling campaigns, direct and by-catch in fisheries from the 1850s to 1960s, and habitat degradation in recent decades (Bearzi and others 2004). Bottlenose dolphins (*Tursiops truncates*) have been abundantly reported in the northern Adriatic in historical times, but today's numbers are also low [rare] due to the difficult environment for the survival of any marine mammal species (Bearzi and others 2003).

The monk seal (*Monachus monachus*) once occurred throughout the Mediterranean Sea and was used for its meat, oil, and hides for millennia (Johnson and others 2009). Seal bones were identified in archeological middens on Croatian islands from 4800 BC (Della Casa and Bass 2001), and monk seals were hunted in classical Greek (Blondel and Aronson 1999), Roman and Medieval times (Sergeant and others 1979; Johnson and others 2009). They were still fairly common in the mid-nineteenth century (Blondel and Aronson 1999), before substantial numbers were killed and breeding locations directly destroyed [depleted]. Ongoing population decline in the twentieth century has been attributed to persecution by fishermen, limited protected breeding caves and by-catch [rare] (Johnson and others 2009). In the Adriatic, only 20 seals were left in Yugoslavia in 1971–1976 (Sergeant and others 1979) and the species is likely

Table 3. Species Reviewed in our Study that are Listed as Endangered or Threatened in the Mediterranean Sea (EEA 1999) and Bird Species Listed as Critically Endangered, Endangered, Vulnerable, Rare, Localized, Depleted, or Declining in Europe (BLI (BirdLife International) 2004)

Marine species	Birds
Marine mammals	Raptors
Balaenoptera physalus	*Haliaeetus albicilla*
Physeter macrocephalus	*Aquila clanga*
Tursiops truncatus	*Aquila chrysaetos*
Delphinus delphis	Seabirds
Monachus monachus	*Pelecanus onocrotalus*
Sea turtles	*Pelecanus crispus*
Caretta caretta	*Larus genei*
Chelonia mydas	*chthyaetus (Larus) audouinii*
Dermochelys coriacea	*Phalacrocorax pygmeus*
Lepidochelys kempii	*Sterna albifrons*
Fishes	*Sterna sandvicensis*
Acipenser naccarii	*Gelochelidon (Sterna) nilotica*
Acipenser sturio	*Puffinus mauretanicus*
Huso huso	Shorebirds
Carcharodon carcharias	*Tringa glareola*
*Anguilla anguilla**	*Charadrius alexandrinus*
Bivalves	Waterfowl and Waders
Patella ferruginea	*Phoenicopterus ruber*
Patella nigra	*Grus grus*
Gibbula nivosa	*Ardeola ralloides*
Seagrasses	*Ardea purpurea*
Posidonia oceanica	*Plegadis falcinellus*
Zostera marina	*Tadorna ferruginea*
Zostera noltii	*Anas angustirostris*
Rockweeds	*Anas clypeata*
Cystoseira amentacea	*Aythia ferina*
Cystoseira mediterranea	*Anas acuta*
Cystoseira sedoides	*Anas querquedula*
Cystoseira spinosa	
Cystoseira zosteroides	

** Species has been recently added to the IUCN Red List of threatened species (IUCN 2010).*

extinct today [extinct], whereas the Mediterranean population is critically endangered with fewer than 600 seals (Table 3; Johnson and others 2009).

Historical Changes in Coastal Birds

Seabirds, shorebirds, waterfowl, waders, and raptors were a source of food for Mediterranean people for millennia. Archeological middens on Croatian islands revealed seabird bones among other animal remains from 4800 BC (Della Casa and Bass 2001). During Roman times, people devoured avian species and many bird populations diminished or disappeared due to excessive hunting, loss of wetland and forest habitat, and the introduction of domestic animals to islands [depleted] (Hughes 1994). A large variety and quantity of birds from peacocks to songbirds were sold on markets, cranes, storks, and flamingos were kept in aviaries, raptors for falconry, and flamingo tongues were considered a delicacy (Hughes 1994). Swans were also a delicacy from antiquity to the renaissance and avidly hunted together with other waterfowl (Knauer 2003). In the Middle Ages and the eighteenth to nineteenth centuries, most birds were excessively hunted for their meat, eggs, feathers, or as a sport throughout Europe and the Western World (Lotze 2005; Collar and others 2007). Beautifully plumed birds were in high fashion, and herons, egrets, and many other species were killed in the thousands for the millinery and fashion trade (Collar and others 2007). Such excessive exploitation together with habitat loss depleted many bird populations since at least Classic times [depleted] (Hughes 1994; Knauer 2003), and by the late nineteenth to early twentieth century, many species were reduced to very low numbers throughout Europe [rare] (BLI 2004; Collar and others 2007). In the twentieth century, continued habitat loss and pollution, especially pesticide use such as DDT, continued to threaten a wide range of birds, and excessive hunting and trapping still occurs today with up to 1 billion birds killed annually in the Mediterranean basin (Blondel and Aronson 1999).

In the Northern Adriatic, many larger bird species are rare today. The crane (*Grus grus*) has been extirpated as a breeding bird in southern Europe over the past 200–400 years (USGS 2006), and last bred in the Adriatic in the early 1940s, yet is a regular migrant with hope of re-colonization [rare] (Tout 1995). The white pelican (*Pelecanus onocrotalus*) may still occur in winter [rare], but the Dalmatian pelican (*P. crispus*) no more [extinct] (Jonsson 1992). The greater flamingo (*Phoenicopterus rubber*) only remains in the Po Delta [rare] (Jonsson 1992). In addition to exploitation and habitat loss, raptors such as white-tailed (*Haliaeetus albicilla*) and spotted eagle (*Aquila clanga*) have been threatened by pesticides and illegal traffic for falconry and exhibition centers (Blondel and Aronson 1999), and are rare today [rare] (BLI 2004). Several geese species and whooper swans (*Cygnus cygnus*) again overwinter around the Adriatic, albeit many in very low numbers [rare] (Jonsson 1992; BLI 2004). The Po Delta contains important breeding colonies for many rare migratory and non-migratory birds including several shorebirds, terns, gulls, cormorants, herons, egrets, glossy ibis, and ducks (Cencini 1998; BLI 2004). Many of the species mentioned are listed as endangered or threatened throughout Europe (Table 3), and although overall conservation efforts increase, the classification and protection of Important Bird Areas in Italy is still lagging behind (BLI 2004).

Historical Changes in Sea Turtles

The history of sea turtles in the Mediterranean probably follows the general trend in the Atlantic Ocean and worldwide (MTSG 1999). Until the eighteenth to nineteenth centuries, sea turtles were highly abundant with some populations numbering into the millions, yet intense hunting for food, skins and shells, destruction of nesting habitats, and by-catch in fisheries have drastically reduced their numbers [depleted]. Today, most sea turtle populations worldwide are depleted, declining, or locally extinct and all species are endangered [rare] (Table 3; MTSG 1999). Historical trends in Mediterranean green turtles (*Chelonia mydas*) have been traced on nesting beaches in Turkey: in 1879–1919 there were approximately 3,500 nesting females, which declined to around 1,000 in 1978–1982 and about 230 in 1998–2001, a 93% decline (MTSG 2004). Today, green turtles are limited to eastern Turkey and Cyprus, although there have been occasional recent sightings in the Adriatic Sea (CNHM 2009).

The Northern Adriatic contains important foraging and overwintering habitat for loggerhead turtles, *Caretta caretta* (Casale and others 2004). In the late nineteenth century, sea turtles were not uncommon (Faber 1883), and loggerhead turtles were often caught by Adriatic fishermen with individuals larger than 100 kg (CNHM 2009). In the twentieth century, sharp declines in turtles were observed due to by-catch and destruction of breeding sites (Blondel and Aronson 1999; Casale and others 2004). In the 1990s, incidental catches of at least 2,500 turtles per year were estimated for the eastern Adriatic Sea and surveys identified 166 observations of 1,286 turtles including loggerhead, leathery (*Dermochelys coriacea*), and green turtles (CNHM 2009).

Historical Changes in Fish

Seafood has been a major protein source for Mediterranean people since at least classical times (Hughes 1994). Fish remains constituted 10–40% of the bone assemblages in Greek caves from 5000 to 4000 BC (Galil 2004), and were found on Croatian islands from 4800 BC (Della Casa and Bass 2001). Tuna species were intensely fished in the Adriatic from the seventh century BC (Volpi 1996). In Roman and Greek times, fishing became a significant economic activity with more than 120 species of economic importance and depicted in Roman fish mosaics including sharks, rays, sardines, anchovies, and a variety of flatfish and groundfish (Radcliffe 1921; Hughes 1994; Galil 2004). Urban tastes supported a large fishing industry, favorite species being red mullet (*Mullus barbatus*), parrot wrasse (*Scarus cretensis*), sturgeon (*Accipenser* spp.), grouper (*Epinephelus* spp.), turbot (*Psetta maxima*), brill (*Scophthalmus rhombus*), common bass (*Dicentrarchus labrax*), seabream (*Sparus aurata*), hake (*Merluccius merluccius*), sole (*Solea vulgaris*), and European eel (*Anguilla anguilla*) (Hughes 1994; Galil 2003). With seagoing vessels for hook-and-line and net fishing, ancient fishermen produced large catches, but the limiting factor was preservation and storage (Bekker-Nielsen 2005). The rhombus (flounder) was imported from Ravenna, the larger mullet was one of the most expensive dainties, and 6,000 moray eels (*Muraena helena*) were dispatched for a victory feast of Julius Caesar (Guhl and Koner 1875; Galil 2003). Bluefin tuna (*Thunnus thynnus*) filled Roman trap nets (Block 2000) and fishermen erected towers on shore to sight tuna schools (Hughes 1994). Tuna and anchovies (*Engraulis encrasicolus*) were used to produce salt-fish (tarichos) and fish sauce (garoum) (Trakadas 2006). Yet complaints of depleting fisheries and increasing prices occurred on Roman markets, and by the first century AD, Italy had outfished its coastal waters [depleted] and expanded to Sicily and Corsica (Radcliffe 1921; Corcoran 1957; Hughes 1994; Trakadas 2006). Certain fishing techniques were therefore prohibited, local stocks were boosted with transplants, and fish were raised commercially (Galil 2003). Because it is unclear which and how many species were depleted, we assumed this affected the most valued species mentioned above (Appendix 3 in Supplemental Material).

After the collapse of the Roman Empire, marine resources likely recovered. However, strong human population growth in Medieval times and thereafter (Figure 1B) resulted in the renewed depletion of fisheries in coastal waters such as Venice lagoon in the thirteenth century [depleted] (Neil 2002). ''Valli'' (caged lagoon parts) were introduced to catch and culture diadromous fish such as trout (Hofrichter 2002). Sturgeons were highly valued, massively overfished (Hofrichter 2002), and their river habitat affected by deforestation and sediment loading (Hoffmann 1996). In the nineteenth century, river alterations, damming, and pollution put sturgeons further at risk, and populations strongly declined throughout the twentieth century (Hofrichter 2002). Today, all sturgeon species are endangered [rare] in the Mediterranean (Table 3, EEA 1999). In the Adriatic, only the Adriatic sturgeon (*Accipenser naccarii*) may still breed between Venice and Greece (Frid and others 2003) and occur in the Po River (EEA 1999), whereas the Beluga (*Huso huso*) and European sturgeon (*A. sturio*) are regionally extinct [extinct] (Billard and Lecointre 2001; Dulvy and others 2003). The European eel also strongly declined in the Adriatic Sea and throughout Europe since the 1980s (EEA 1999) and is listed as critically endangered today [rare] (IUCN 2010). Adriatic official catches of eel declined from more than 1000 to less than 50 t y^{-1} from the 1970s to the 2000s (Figure 2A).

Bluefin tuna has been an important part of Mediterranean culture for 12,000 years (Block 2000). For millennia, the fishery was coastal, subsistence, and small-scale, but fishing in the Adriatic intensified since the seventh century BC (Volpi 1996), and systematic exploitation of tuna along the Dalmatian coast occurred since the fourteenth century for consumers in Venice and inland Croatia (Block 2000; Hoffmann 2001). From 1650 to 1950, tuna trap catches throughout the Mediterranean fluctuated with changing temperatures (Ravier and Fromentin 2004), but declines since 1950 have been attributed to over-exploitation (MacKenzie and others 2009). Purse seining strongly increased fishing in open waters but many coastal trap fisheries closed down due to declining catches. Today, the Atlantic-Mediterranean bluefin tuna stock is considered overfished (Table 4) and at risk of collapse with a 90% decline in adult biomass within three generations [rare] (MacKenzie and others 2009). Other tunas and bonitos are also heavily exploited and some stocks are considered overexploited or depleted in the Mediterranean (FAO 2005). Swordfish (*Xiphias gladius*) catches strongly increased in the Mediterranean since the 1960s,

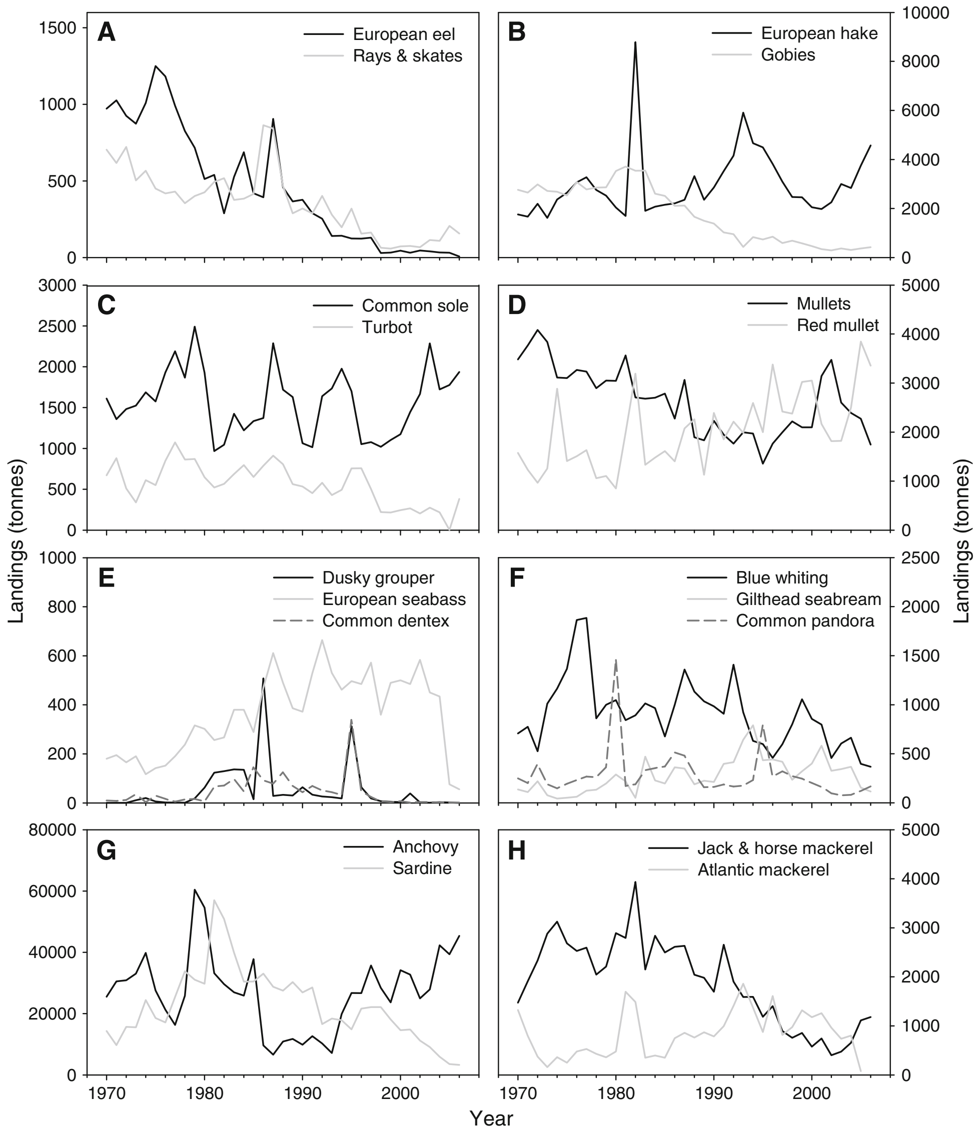

Figure 2. Official commercial fish landings in the Adriatic Sea by the Italian fleet from 1970-2006 for **A** diadromous fish and elasmobranchs, **B-F** demersal stocks, and **G-H** pelagic stocks as reported to FAO (FAO-FishStat 2010).

peaked at greater than 20,000 t in 1988, followed by declines to 14,000 t in 2007. Abundance also declined, with relative CPUE peaking at 3 in 1979, 2 in 1985, and 1 in 1989 but remaining at 0.5 since and the stock is considered overfished [depleted] (Table 4, ICCAT-SCRS 2009).

In general, fishing activities were highly developed and diversified in the Adriatic Sea throughout history, yet remained close to shore. In the nineteenth century, fishing was still performed with sailing vessels, yet concerns regarding the impact of several fishing gears on species and juvenile fish were raised by scientists and politicians at the time (Faber 1883; Botter and others 2006). In the late nineteenth century, fishing capacity grew exponentially, became motorized in the early twentieth century, and expanded offshore and into deeper waters after World War II (Libralato and others 2004; Raicevich and others 2004; Vrgoc and others 2004). Official catches of many species peaked in the 1980s to 1990s and declined since (Figure 2). Today, 70% of economically important and 44% of all exploited stocks are considered overexploited and outside safe limits (Table 4; EEA 2002), and the severe impacts of fishing on target and non target species, habitats and ecosystems are widely recognized (Tudela 2004).

Many elasmobranchs were quite common in the Adriatic in the nineteenth century (Faber 1883) but experienced strong population declines through direct fishing and increasingly bycatch in gillnet, trawl, and longline fisheries (Dulvy and others 2003; Ferretti and others 2008; Fortibuoni and others 2008). Hammerhead (*Sphyrna* spp.),

Table 4. Commercial Pelagic and Demersal Fish Stocks Considered Safe or Overfished and Outside Safe Biological Limits in the Adriatic Sea (EEA 2002)

Habitat	Commercial stocks	Status
Pelagic	Anchovy	Overfished
	Horse mackerel	Safe
	Mackerel	Safe
	Sardinella	Safe
	Pilchard (Sardine)	Safe
	Sprat	Safe
	Bluefin tuna	Overfished
	Swordfish	Overfished
Demersal	European hake	Overfished
	Blue whiting	Overfished
	European seabass	Overfished
	Seabream	Overfished
	Red mullet	Overfished
	Gray mullet	Overfished
	Flatfish	Overfished
	Common sole	Overfished
	Bogue	Safe
	Megrim	Overfished
	Greater forkbeard	Overfished
	Gurnads	Overfished
	Poor cod	Overfished

blue (*Prionace glauca*), mackerel (*Isurus oxyrinchus*, *Lamna nasus*), and thresher sharks (*Alopias vulpinus*) declined by 96–99% in the Mediterranean over the past 50–200 years [rare] (Ferretti and others 2008). White sharks (*Carcharodon carcharias*) were commonly sighted in the Adriatic Sea until the 1970s, but have strongly declined to critically endangered levels [rare] (Table 3; McPherson and Myers 2009). Many other pelagic and demersal sharks, skates and rays have strongly declined in the twentieth century, landings of rays and skates declined more than 80% since the 1980s [depleted] (Figure 2A), and several species are locally extinct or rare today (Appendix 3 in Supplemental Materials; Dulvy and others 2003; Ferretti and others 2010).

One of the most abundant demersal species, European hake (*Merluccius merluccius*), has been highly exploited over past centuries, but especially since the 1960s (Vrgoc and others 2004). Research surveys in the Adriatic revealed declines in CPUE from 6 to 3 kg/h trawls between 1948 and 1982, official catches peaked in the 1980s and 1990s with subsequent declines (Figure 2B), and the species is considered overfished [depleted] (Table 4). Many other demersal fish have also shown declining CPUE between 1948 and 1982 (for example, red mullet and common pandora both from 2.5 to 1.4 kg/h, FAO 1984; anglerfish from 4.2 to 1 kg/km^2, Vrgoc and others 2004) or declining catches in recent years (for example, turbot, gobies, blue whiting, Figure 2; Coll and others 2010c), and are considered overfished [depleted] (Table 4). Others (for example, common dentex, common pandora) have shown very low official catches recently [depleted] (Figure 2), and the dusky grouper may be locally extinct [rare] (Dulvy and others 2003). Species that occupy wetlands such as soles, mullets, and seabreams have further been affected by habitat loss (Blondel and Aronson 1999). In general, official commercial catches and CPUE of demersal fish have strongly declined in recent decades throughout the Adriatic despite increasing fishing effort (Bombace 1992; Vrgoc and others 2004; Coll and others 2010c).

Small pelagic fish stocks have also been important and highly exploited since ancient times, yet declined during the 1980s partly due to overfishing. Sardine (*Sardina pilchardus*) catches peaked at 59,000 t in 1981 but decreased to less than 10,000 t in the 2000s [depleted] (Figure 2G). Sardine biomass peaked at 390,000 t in 1982, declining to 100,000–160,000 in 1992–1996 [depleted], although the stock is not considered overfished (Table 4; Santojanni and others 2005). Anchovy (*Engraulis encrasicolus*) biomass peaked at 370,000 t in 1978, followed by a 10-fold decrease to 35,000 t in 1987, the so-called anchovy collapse. However, biomass increased to 88,000 t in 1995 (Santojanni and others 2003), and catches increased since the 1990s (Figure 2G), although the stock is still considered overfished [depleted] (Table 4). Catches of jack and horse mackerels (*Trachurus picturatus*, *T. trachurus*) have also strongly declined since the early 1980s as have Atlantic mackerels (*Scomber scombrus*) since the early 1990s [depleted] (Figure 2H).

Historical Changes in Invertebrates

Shellfish have been heavily exploited throughout Mediterranean history (Hughes 1994). Early settlers on the Dalmatian islands in 4800 BC intensively collected oysters, mussels, limpets, whelks, and top shells, which were common in shallow waters and used for food, jewellery, accessories, and buttons (Ceron-Carrasco and Bass 2001). Roman fish mosaics depict highly valued taxa including squid, octopus, lobster, shrimp, oysters, and sea urchins (Galil 2004), and industrial exploitation of luxury items took place for purple dye snails (Koutsoubas and others 2007), red coral for jewellery (Bresc 2000), and sponges for bathing (Pronzato and Manconi 2008). Many benthic species were likely affected since Roman times by either exploitation or changes in water quality, especially increasing sediment loads (see below).

Oysters (*Ostrea adriatica, O. edulis*) were among the most economically important edible mollusks throughout history (Guhl and Koner 1875). They were highly popular since Greek and Roman times as a health food and aphrodisiac (Galil 2003). Since the fifth century BC, Romans cultured oysters, which were carefully tended and protected, and began importing wild ones from the North Sea, because the local supply could not meet demand [depleted] (Eyton 1858; Hofrichter 2002; Galil 2003). Wild oysters were overexploited in the Mediterranean by 1930 [rare; Hofrichter 2002) and today's official catches in the Adriatic are negligible (FAO-FishStat 2010). After disease destroyed cultured European oysters in the 1950s, the aquaculture industry introduced Pacific oysters (*Crassostrea gigas,*), with major production centers in the Po Delta, Venice lagoon and along the Croatian coast (Hofrichter 2002).

Mussels, clams, and scallops have also been fished since ancient times. Exploitation intensified in the twentieth century with the increase in bottom trawling and hydraulic dredges that have strong negative effects on epibenthic communities (Council of Europe 1994; Newell and Ott 1999). Since 1970, commercial landings of striped venus (*Venus gallina*) and Mediterranean mussel (*Mytilus galloprovinzialis*) showed fluctuating trends (Figure 3A), although CPUE declined (Bombace 1992). Scallop (*Pecten jacobaeus*) fisheries increased after a mass mortality in 1983, but intense trawling prevented the reestablishment of scallop beds and abundance declined (Newell and Ott 1999). Overall, suspension feeders have strongly declined due to overharvesting, disturbance by bottom fishing operations and mass-mortalities due to anoxia [depleted] (Council of Europe 1994; Newell and Ott 1999).

Muricid gastropods (*Hexaplex trunculus*, *Bolinus brandaris*) were heavily exploited during ancient and Roman times for the production of purple dye to decorate royal garments as well as seafood (Ziderman 1990; Koutsoubas and others 2007). Edible murex snails were obtained along the coast of Dalmatia in the first century AD (Plinii Secundi 1513), and industrial exploitation occurred throughout the Mediterranean with at least 16 major production centers for purple dye, likely causing resource depletion (Ceron-Carrasco and Bass 2001). Murex snails have been among the most important commercial mollusks in the Mediterranean over past centuries (Koutsoubas and others 2007) and are still sold as a culinary delicacy on Adriatic fish markets (Ziderman 1990). Since the 1960s, severe oxygen depletion has caused several mass-mortalities of fish, shrimp, and benthic fauna [depleted] in the Adriatic Sea, including murex snails and other gastropods, bivalves, sponges, brittle stars, holothurians, and echinoids (Stachowitsch 1991). In the Gulf of Trieste, severe anoxia in 1983 destroyed greater than 50% of epifaunal biomass in 2 days, and more than 90% within 4 days, with slow recovery [depleted] (Stachowitsch 1984).

Crustaceans have also been valued since at least Roman times (Galil 2004), but there is not much historical information. Fishery landings since 1970 suggest that Adriatic landings of Norway lobster

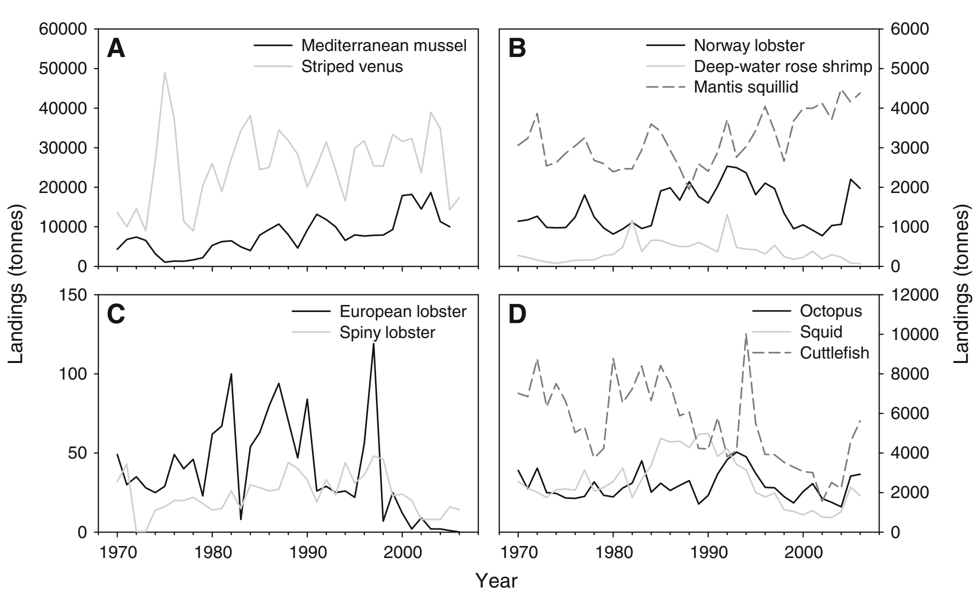

Figure 3. Official commercial invertebrate landings in the Adriatic Sea by the Italian fleet from 1970 to 2006 for **A** bivalves, **B-C** crustaceans, and **D** cephalopods as reported to FAO (FAO-FishStat 2010).

(*Nephrops norvegicus*) increased from the 1980s until the mid 1990s up to 2500 t y^{-1}, followed by a decrease to 1200 t y^{-1} in the early 2000s (Figure 3B) [depleted] (FAO-FishStat 2010). Landings of deepwater rose shrimp (*Parapenaeus longirostris*) increased to more than 1300 t in 1992, but remained below 400 t y^{-1} since the late 1990s. Similarly, landings of European lobster (*Homarus gammarus*) and spiny lobster (*Palinurus elephas*) increased to 48 and 119 t y^{-1} in the 1990s, respectively, but declined to below 20 t y^{-1} [depleted] and less than 10 t y^{-1} [rare] afterwards (Figure 3C). Only landings of mantis squid (*Squilla mantis*) have remained high (Figure 3B).

Trawl fisheries for cephalopods including octopus (*Eledone cirrhosa*, *E. moschata*, *Octopus vulgaris*), cuttlefish (*Sepia officinalis, S. elegans*), and squids (*Loligo vulgaris, Illex coindetii*) showed fluctuating CPUE trends between 1972 and 1997, with negative trends in the most valued cuttlefish (Vrgoc and others 2004) and recent signs of overexploitation (AdriaMed 2003). Italy has the greatest share of cephalopod official catches in the Adriatic Sea, which have increased to up to 18,000 t y^{-1} in 1994, following by declines to below 8,000 t y^{-1} in the early 2000s [depleted] (FAO-FishStat 2010). Declines in recent years (mean 2000–2006) from peak catches were most severe in squids (75%) and cuttlefishes (68%), followed by octopuses (48%), although 2005 and 2006 showed some increases (Figure 3D).

An important fishery for sponges occurred since Phoenician, Egyptian, and Greek times for use in bathing, medicine, and art (Pronzato 1999). During Roman times, large quantities of sponges were exported to Greece (Pronzato and Manconi 2008). Up to 1840, the entire world trade of sponges was centered on the Mediterranean. Traditional fishing involved initially free-divers, which were replaced by hard-hat divers in suits in the late nineteenth century resulting in greatly increased yields. In the 1920s, dragging was introduced to harvest sponges from deeper banks (Pronzato 1999). Prior to World War II, world sponge production averaged 1346 t y^{-1}, which declined to only 220–250 t y^{-1} afterwards [depleted] (Pronzato 1999). Overfishing and disease strongly depleted sponges in the 1970s–1980s and commercial sponges practically disappeared on most exploited banks [rare]. Today, *Spongia officinalis* and *S. agricina* are listed as threatened, and aquaculture is seen as a potential alternative (Pronzato 1999; Hofrichter 2002).

Red coral (*Corallium rubrum*) has been of commercial importance for jewellery since Greek and Roman times (Bresc 2000). In recent decades, coral exploitation by trawling is progressively restricting their occurrence, and the total catch reported to FAO declined from 98 t in 1978 to 40 t in 2008 [depleted], with the biggest shares from Italy and Spain (FAO 2010). Other corals (for example, gorgonians) have also experienced major declines over past decades due to pollution, trawling, and algal overgrowth [depleted] (Hofrichter 2002). For example, greater than 90% of *Cladocora caespitose* colonies, the only reef-building coral in the Adriatic, died en masse on a 150 km^2 reef in the Central Adriatic from 2001 to 2005 [rare] (Kružić and Požar-Domac 2007).

Historical Changes in Vegetation

In ancient times, the coastlands of the Po Delta were described as a continuous, almost impassable sequence of lagoons, marshes, and rivers (Cencini 1998). Most wetlands have subsequently been filled by sediment or reclaimed by humans for settlements and agricultural land. Today, 98% of freshwater and greater than 70% of salt marshes that existed in the early 1900s within the ancient Po Delta have been reclaimed (Cencini 1998). Reclamation ended by the 1960s and protection increased since the 1980s. With its remaining 50,000 ha of fresh- and saltwater marshes, the Po Delta is still among the largest wetland areas in Italy and among the most important in the Mediterranean basin (Cencini 1998).

Human influence on the Po River and its wetlands probably began during the Neolithic when population growth and the development of human activities strongly increased [abundant] (Marchetti 2002). Major wetland draining began in Etruscan times (fifth century BC) and accelerated in Roman times (Marchetti 2002). After the collapse of the Roman Empire wetlands recovered [abundant], but drainage was renewed in the Middle Ages [depleted] (Blondel and Aronson 1999). In Venice lagoon, draining of intertidal mudflats and saltmarshes, and canal and dike construction increased since 800 AD (Neil 2002), and upland deforestation and agriculture enhanced sediment erosion and burial of marshes (Appuhn 1999). Human modification of the Po River and Delta also increased (Gandolfini and others 1982). In 1604, the river mouth was redirected southward to prevent sediment infilling near Venice Lagoon (Stefani and Vincenti 2005). Wetland loss accelerated during the nineteenth century with the help of machinery and to eradicate malaria. Overall, of the approximately 25,000 km^2 of wetlands that existed in Italy alone during Roman times, only 7000 km^2 remained in the early 1900s, and 1000 km^2 today, a total loss of 96% [rare] (Figure 4; Airoldi and Beck 2007).

Submerged macrophytes including seagrasses and macroalgae were dominant primary producers in shallow waters of the Northern Adriatic, yet have become much less abundant over the last century (Newell and Ott 1999), and today's seafloor habitats drastically differ from the past (Barmawidjaja and others 1995; Airoldi and Beck 2007). They were probably first affected by increased sediment loads through deforestation and land reclamation during Roman and Medieval times [abundant] (Appuhn 1999). In Venice lagoon, seagrass beds were buried by sediments in Medieval times (Appuhn 1999). Off the Po Delta, a considerable decrease in epiphytic foraminifera from 1840 to 1870 (Figure 4) indicated a significant loss of seagrasses, likely caused by increased sediment and nutrient loads from Po River [depleted] (Barmawidjaja and others 1995). Since the 1850s, former prairies of endemic *Posidonia oceanica* have retreated from several areas and are now virtually extinct in the Northern Adriatic [rare] (Airoldi and Beck 2007). A 190 km^2 bed in front of Marano and Grado lagoons disappeared during the 1970s (Newell and Ott 1999). Heavy overgrowth with annual green algae (*Ulva* spp.) due to nutrient enrichment preceded the retreat (Ott 1992).

An impoverishment of macroalgae was found from the late 1800s to the 1960s, most pronounced for red and least for green algae, and further deterioration of fucoid and red algae occurred in the 1960s–1970s (Munda 2000). In Venice lagoon, many species declined to virtual extinction; although 141 algal species were found in 1938, these decreased to 116 species in 1962, 107 in 1987, and 96 in 1991 (Airoldi and Beck 2007).

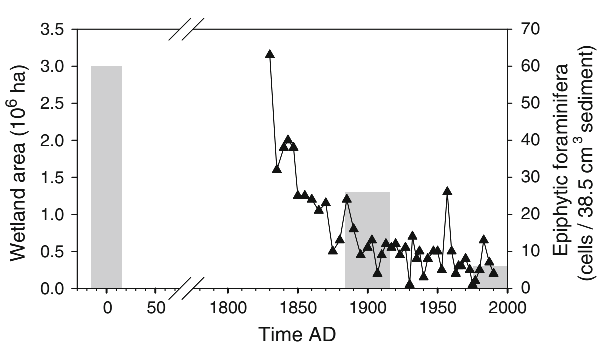

Figure 4. Historical changes in the extent of wetlands (*gray bars*, Airoldi and Beck 2007) and the occurrence of seagrasses and other macrophytes in the Adriatic Sea measured by the abundance of epiphytic foraminifera as a proxy in sediment cores (*triangles*, Barmawidjaja and others 1995).

Extensive stands of kelp (*Cystoseira* spp.) existed until the 1960s down to 15-m depth (Newell and Ott 1999), but precipitously declined in 1968–1972 and have been replaced by barren rock inhabited by black sea urchins (*Paracentrotus lividus*, Ott 1992). Of 7 *Cystoseira* and 1 *Sargassum* species that occurred in the 1940s around Monte Conero in Italy only 4 remained in 1960 and 2 in 1990, and 70% of the still existing *Cystoseira* forests disappeared during 2002–2005 [depleted] (Perkol-Finkel and Airoldi 2010).

Historical Changes in Water Quality

Human actions in the Po Delta including deforestation, wetland drainage, and sediment erosion have been traced back 2500 years (Cencini 1998) and such actions increased during Roman and Medieval times in the Po Delta (Marchetti 2002) and Venice lagoon (Appuhn 1999). Sediment core data indicated relatively stable concentrations of coccolithophorids over past millennia until the late nineteenth century when concentrations started to increase (Figure 2A; Puškaric and others 1990). Diatoms and silicious plankton also increased during the twentieth century due to increased nutrient loads and shifts from benthic to pelagic production, with ebridians (eutrophication indicators) strongly increasing after 1950 (Figure 5A). Nutrient loads in the Po River doubled from 1968 to 1980, river mouth concentrations of nitrogen increased about 3-fold and phosphate about 2.75-fold (Marchetti and others 1989), whereas fertilizer use increased 7.14-fold for nitrogen and 2.33-fold for phosphorus (Justić and others 1987). Foraminifera abundance strongly declined after 1850, whereas eutrophic species such as *Nonionella turgida* increased in the twentieth century (Figure 5B; Barmawidjaja and others 1995). From 1830 to 1990, dinoflagellates increased in total abundance as well as the ratio of heterotroph:autotroph species (Figure 5C; Sangiorgi and Donders 2004). Eutrophic species increased from the 1930s onwards, causing red tides and toxic blooms in recent decades. From 1962 to 1981, primary production in mid Adriatic waters increased around 3.5-fold, whereas the diatom:dinoflagellate ratio declined greater than 5-fold (Marasović and others 2005). Although eutrophication levels were still high during the early 1990s, they partly decreased in recent years due to changes in environmental policy (Sangiorgi and Donders 2004).

Mucilage-forming phytoplankton blooms have occurred in the Adriatic Sea periodically since the 1700s. Based on Vollenweider and others (1995),

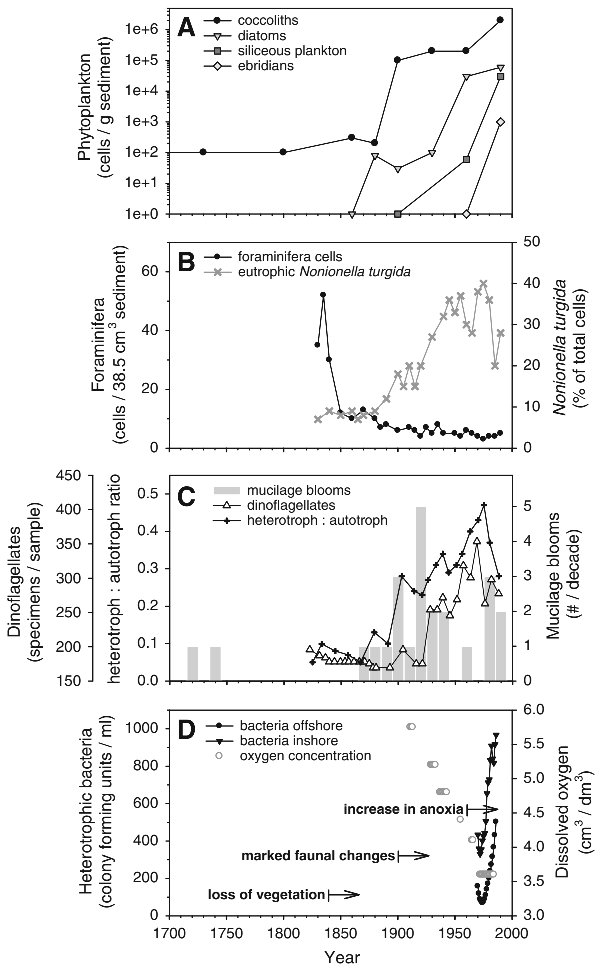

Figure 5. Historical changes in plankton and water quality in the Adriatic Sea based on sediment core and hydrographic data. Changes in **A** abundance of different phytoplankton groups (Puškaric and others 1990), **B** abundance of all foraminifera and percent contribution of *Nonionella turgida*, an indicator species of eutrophic conditions (Barmawidjaja and others 1995), **C** abundance of dinoflagellates, their heterotroph:autotroph ratio (Sangiorgi and Donders 2004), and occurrence of mucilage blooms (Vollenweider and others 1995), and **D** heterotrophic bacterial abundance at an inshore and an offshore station (Krstulovic and Solic 1990), dissolved oxygen concentration in the bottom layer during summer (Justić and others 1987), and general eutrophication sequence (Barmawidjaja and others 1995). See text for details.

we calculated the number of blooms per decade from 1729 to 1991 suggesting increasing frequency and severity in the twentieth century (Figure 5C). Recent blooms were reported for 1997, 2000, and 2002 (Fonda Umani 2004), and have also been linked to increasing sea surface temperature (Danovaro and others 2009). Since 1975, red tides by dinoflagellates have also been observed regularly in coastal waters (Fonda Umani 2004).

Algal blooms last for short periods after which time the dead organic matter is decomposed by bacteria that deplete ambient oxygen levels. Dissolved oxygen concentrations in bottom layers of the Northern Adriatic decreased since the early twentieth century (Figure 5D), and frequent summer and fall anoxic events have caused mass mortalities of benthic fauna since 1960 (Justić and others 1987). Heterotrophic bacteria in offshore and coastal waters strongly increased since 1970 (Figure 5D; Krstulovic and Solic 1990). Also, species richness of hydromedusae with bottom-dwelling life stages (Anthomedusae, Leptomedusae) strongly decreased, possibly linked to oxygen limitation, whereas species without bottom-dwelling stages (Trachymedusae, Narcomedusae) showed no changes (Benović and others 1987). Outbreaks of jellyfish and tunicates have also been linked to eutrophication, overfishing, and invasions (Boero 2001; Malej and Malej 2004).

The general eutrophication sequence (Figure 5D; Barmawidjaja and others 1995) started with a reduction in submerged aquatic vegetation in 1840 and large-scale losses since the 1860s. Eutrophication gradually increased in the 1880s, changes in marine fauna were noticed around 1900, and marked faunal transitions started in the 1920s. Since the 1940s, eutrophication strongly increased with enhanced occurrence of anoxia in the 1960s, reaching its maximum in the 1980s, and slight reductions in the 1990s.

Synthesis of Historical Changes in Abundance, Diversity, and Ecosystem Structure

Overall trends in the relative abundance of 24 functional and 6 taxonomic groups are presented in Appendix 3 (Supplementary material) and Figure 6A. Before classical times no signs of species depletion were found despite subsistence use of a wide range of species. This dramatically changed with rising human population and demand for food and luxury products during Roman times. Based on our literature search, we found evidence for local depletions of birds and fish and some declines in invertebrates and plants (Figure 6A). After the collapse of the Roman Empire, many marine resources may have recovered, as shown for terrestrial resources and coastal wetlands (Blondel and Aronson 1999). However, expanding human population and associated pressures in Medieval times reversed this trend and further declines occurred in

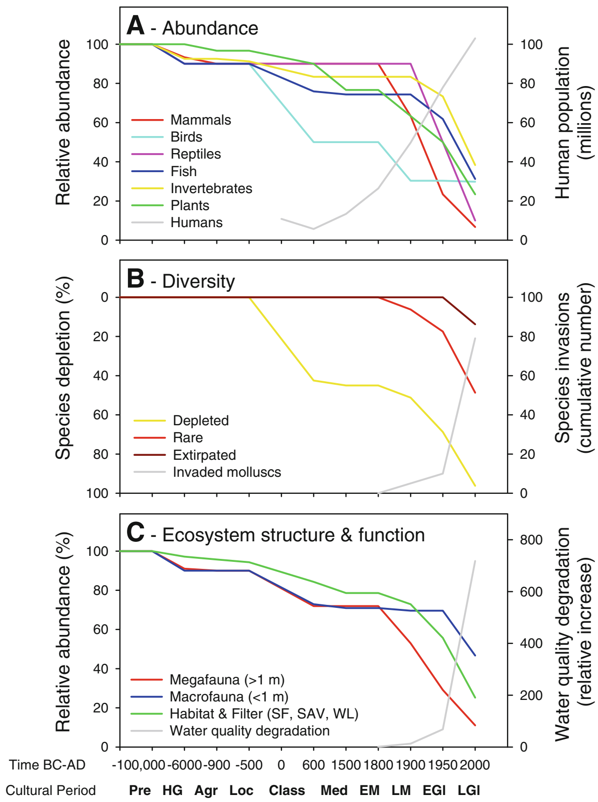

Figure 6. Synthesis of trajectories of change in **A** relative abundance of different taxonomic groups and humans, **B** species diversity as cumulative percent depletions and number of invasions, and **C** relative abundance of different ecosystem components in the Adriatic Sea over historical time BC–AD and cultural periods (see Table 2 for abbreviations). Year 0 was included as a reference. Axes for *colored lines* are on the *left*, axes for *gray lines* on the *right*. The timeline for species invasions refers to mollusk invasions in the Mediterranean as a whole; all other data refer to the Adriatic Sea. See text for details.

plants (Figure 6A). In the nineteenth to twentieth centuries, strong declines occurred across all taxonomic groups with increasing commercialization, industrialization, urbanization, and human demand. Only bird populations stabilized in the twentieth century with increasing conservation efforts, whereas mammals and reptiles were depleted the most (Figure 6A).

Changes in species diversity were reflected in the number of species that became depleted, rare, or extirpated over time (Figure 6B). Depleted species may still be abundant enough to fulfill their ecological roles, but a 50–90% reduction in number or biomass of some taxa substantially alters community structure. Formerly abundant species that became rare (>90% decline) are likely no longer able to fulfill their ecological roles and may be considered ecologically extinct. Extirpated species are locally or regionally lost, but if they are not globally extinct there is still potential for reintroduction. Our data indicate that species depletions increased during Roman times, rare species appeared in the nineteenth century, and extirpated species in the 20th twentieth century (Figure 6B). Today, 98% of formerly important species are depleted with 37% rare (cumulative 48% including rare species; Figure 6B) and 11% extirpated. However, there have also been species gains: by 2002, 41 invasions (13 macroalgae, 27 invertebrates, 1 fish) via ships were recorded in the Northern Adriatic (Occhipinti-Ambrogi 2002). There was no timeline of invasions for the Adriatic, but mollusk invasions in the Mediterranean increased to 79 from 1877 to 2000 (Zenetos and others 2004; Figure 6B). Invasions occurred mainly in small, low-trophic level species whereas losses occurred in larger mammals, birds, and fish, thereby shifting local diversity patterns.

Changes in species abundance and diversity affect ecosystem structure and functioning. We found that large predators and consumers (>1-m body size, megafauna) became more severely depleted (to 11% of former abundance) than smaller macrofauna (<1 m, 47%), especially in the nineteenth to twentieth centuries (Figure 6C). Also, species providing 3D habitat and filter capacity have been severely reduced to 25% of former abundance. This loss in essential ecosystem functions likely contributed to the decline in water quality (Figure 6C).

Historical Food-Web Changes

The historical changes outlined above are reflected in our binary food webs from different cultural periods in terms of (i) changes in human exploitation patterns by targeting more species groups over time, (ii) the addition of discards from industrial fishing in the twentieth century, and (iii) changes in species composition due to those becoming rare (<10%) or extinct (monk seal) (Table 5). For each food web for the 10 historical periods and 4 modelling scenarios we calculated 14 food-web properties (Appendix 4 in Supplemental Materials) and compared the observed changes over time with expected trends of degradation (Table 6), which agreed in 71–86% of cases. The two scenarios excluding species that became functionally extinct (<10%) independent of human presence (FW_E) or absence (FW_WoH&E) best agreed with the expected trends of degradation,

Table 5. List of Functional Groups (FG) and Species in Food Webs Representing Different Historical Periods

FG	Name of group	Species	Pre	HG	Agr	Loc	Class	Med	EM	LM	EGl	LGl
1	Large whales	Sperm and fin whales	P	P	P	P	P	P	P	P	<10%	<10%
2	Small whales	Dolphins	P	P	P	P	P	P	P	P	P	<10%
3	Pinnipeds	Monk seal	P	P	P	P	P	P	P	P	<10%	E
4	Raptors	Eagles	P	P	P	P	P	P	P	<10%	<10%	<10%
5	Seabirds	Pelicans, gulls, cormorants, terns, shearwater	P	P	P	P	P	P	P	P	P	P
6	Shorebirds	Sandpipers, stilts, avocets, plovers	P	P	P	P	P	P	P	P	P	P
7	Waterfowl and Waders (2), carnivores	Crane, greater flamingo, eiders, seaducks, herons, egrets, ibises	P	P	P	P	P	P	P	P	P	P
8	Waterfowl and Waders (1), herbivores	Geese, swans, dabbling ducks	P	P	P	P	P	P	P	P	P	P
9	Sea turtles (1), carnivores	Sea turtles	P	P	P	P	P	P	P	P	P	<10%
10	Sea turtles (2), herbivores	Green turtle	P	P	P	P	P	P	P	P	P	<10%
11	Diadromous fish	Sturgeons, eels, trouts	P	P	P	P	P	P	P	P	P	P
12	Groundfish (1), large carnivores	Grouper, seabass, hake, moray eel	P	P	P	P	P	P	P	P	P	P
13	Demersal sharks and rays	Sharks, rays and skates	P	P	P	P	P	P	P	P	P	P
14	Groundfish (2), small carnivores	Flatfish, mullets, whiting, reef fish	P	P	P	P	P	P	P	P	P	P
15	Groundfish (3), small herbivores	Salema	P	P	P	P	P	P	P	P	P	P
16	Tunas and swordfish	Tunas, swordfish	P	P	P	P	P	P	P	P	P	P
17	Large predatory sharks	Pelagic sharks	P	P	P	P	P	P	P	P	P	<10%
18	Large filter-feeding fish	Basking shark, whale shark, sunfish	P	P	P	P	P	P	P	P	P	P
19	Small pelagic fish (1), carnivore	Jacks, mackerels	P	P	P	P	P	P	P	P	P	P
20	Small pelagic fish (2), omnivore	Sardines, anchovies, sprats	P	P	P	P	P	P	P	P	P	P
21	Cephalopods	Octopus, squid, cuttlefish	P	P	P	P	P	P	P	P	P	P
22	Demersal crustaceans	Crabs, lobsters	P	P	P	P	P	P	P	P	P	P
23	Pelagic crustaceans	Shrimps	P	P	P	P	P	P	P	P	P	P
24	Echinoderms	Sea urchins, sea stars, echiurids	P	P	P	P	P	P	P	P	P	P
25	Benthic snails	Whelks, limpets, top shells	P	P	P	P	P	P	P	P	P	P
26	Bivalves	Mussels, clams, scallops	P	P	P	P	P	P	P	P	P	P
27	Oysters	Oysters	P	P	P	P	P	P	P	P	<10%	<10%
28	Corals	Corals, gorgonians	P	P	P	P	P	P	P	P	P	P
29	Sponges and ascidians	Sponges, ascidians	P	P	P	P	P	P	P	P	P	<10%
30	Hydrozoans	Jellyfish	P	P	P	P	P	P	P	P	P	P
31	Polychaetes	Various species	P	P	P	P	P	P	P	P	P	P
32	Zooplankton	Various species	P	P	P	P	P	P	P	P	P	P
33	Macroalgae	Macroalgae, kelp	P	P	P	P	P	P	P	P	P	P
34	Seagrasses	Seagrasses	P	P	P	P	P	P	P	P	P	<10%
35	Phytoplankton	Diatoms, dinoflagellates	P	P	P	P	P	P	P	P	P	P
36	Detritus	Dead organic matter	P	P	P	P	P	P	P	P	P	P
37	Discards	Organic matter from fishing									P	P
38	Imports	Proportion of diet imported	P	P	P	P	P	P	P	P	P	P
39	Humans	Fishing, hunting, harvesting		P	P	P	P	P	P	P	P	P

See Table 2 for abbreviations.
P = present; <10% = rare; E = extinct; gray cells = exploited by humans.

Table 6. Calculated Food-web Properties, Their Expected Direction of Change Towards Degradation Over Time in Terms of (a) Overexploitation of High Trophic Levels and (b) Simplification of Food-web Structure (Coll and others 2008), and Observed Changes in the 4 Modelling Scenarios

Food-web properties		Expected direction	FW_all	FW_WoH	FW_E	FW_WoH&E
(a) Overexploitation of high trophic levels (TL)						
Fraction of top predators (species with prey but no predators)	%T	Decrease	D	D	D	D*
Fraction of intermediate predators (species with both prey and predators)	%I	Increase / Decrease	ID	D	ID	ID
Fraction of basal species (species with predators but no preys)	%B	Increase	I	I	I	I
Fraction of herbivore species (species that feed on basal species)	%H	Increase	D	D	I*	I*
Generality (number of prey per species and standard deviation)	GenSD	Increase	I	I	I*	I*
Vulnerability (number of predators per species and standard deviation)	VulSD	Decrease	D	I	D	ID
Mean trophic level of the community (short-weighted or average prey trophic level)	SWTL	Decrease	D	D	D	D
(b) Simplification of food-web structure						
Linkage density (all trophic links (L) divided by species or ecological groups (S))	L/S	Decrease	I	D	ID	D
Connectance (proportion of actual to all possible links (L/S^2), 0 = no species preys on any species, 1 = every species preys on every species)	C	Decrease	ID	D	I	I
Fraction of omnivorism (species that feed on more than 1 trophic level)	%Omn	Decrease	D	D	ID	D
Fraction of cannibalism (species that feed directly on its own species)	%Can	Increase	D	D	I	I
Fraction in loop (Species involved in looping by appearing in a food chain twice)	%Loop	Decrease	D	D*	I	I
Mean short-weighted chain length (mean number of links in every possible food chain or sequence of links connecting top to basal species)	ChLen	Decrease	D	D	D	D
Trophic path length (characteristic path length or the mean shortest path length between species pairs)	Path	Decrease	D	I	D	D
Percent accordance with expected direction			78.57	71.43	85.71	85.71

*I = increase; D = decrease; ID = first increase then decrease; gray cells = observed changes follow expected trend; * = changes reversed in the last period.*

thus most reflecting the overexploitation of high trophic levels and simplification of food-web structure over time.

Specifically, the fraction of top predators (%T) and the mean trophic level of the community (SWTL) decreased, whereas the fraction of basal species (%B) and number of prey per species (generality, GenSD) increased, suggesting an overexploitation of higher trophic levels and a change of the food web towards smaller organisms (Table 6). Also, the fraction of intermediate predators (%I) first increased (likely due to predation release) and later decreased (due to direct exploitation), and the number of predators per species (vulnerability, VulSD) decreased in 3 of 4 scenarios. The fraction of herbivores (%H) did follow the expected increase in 2 scenarios. All these trends indicate that the food webs became ''shorter'' and ''fatter'' over time.

A simplification of food-web structure over time was indicated by a general decrease in the mean number of links in every possible food chain (mean short-weighted chain length, ChLen), the linkage density (L/S), trophic path length (Path), and the fraction of omnivores (%Omn) (Table 6). Also, the proportion of actual to all possible links (connectance, C) and the fraction of species involved in looping (%Loop) decreased and those involved in cannibalism (%Can) increased as expected in 2 scenarios (Table 6). All these trends suggest that food webs became less connected and complex and more simplified over time.

The cluster analysis and ANOSIM comparison of food webs indicated strong structural changes over time. When including all functional groups and humans (FW_All scenario; Figure 7A), the beginning of human exploitation separated the Prehuman from the hunter–gatherer and agriculture periods, whereas expanding exploitation patterns significantly separated these from a cluster of Classic to Late Modern periods ($R = 0.62$, $P = 0.017$), and again from the Early and Late Global periods ($R = 1$, $P = 0.002$). This scenario reflects the presence of different functional groups and expanding exploitation (gray cells in Table 5) over time and suggests significant changes in food-web structure between clusters due to human presence, increasing overexploitation of high trophic levels and structural simplification as outlined above. The exclusion of humans as a functional group (FW_WoH; Figure 7B) only resulted in the significant separation of the Early and Late Global periods from all earlier periods ($R = 1$, $P = 0.022$). This was largely driven by the removal of extinct species (monk seal) and addition of fishing discards as an additional source of organic matter. Thus, the consequences of human exploitation (discards, extinctions) have altered food-web structure even if humans were not considered part of the food web itself. When functionally extinct species (<10%) were removed, there was a further distinct split between the Early and Late Global periods (FW_E; Figure 7C) when compared to the FW_All scenario (Figure 7A). This scenario reflects the increasing number of rare species in the second half of the twentieth century (Table 5) on top of the expanding exploitation by humans, and suggests that functional extinctions cause further changes in food-web structure in terms of overexploitation of high trophic levels and structural simplification. Excluding the exploitation effect from the FW_E scenario by removing humans from the food web (FW_WoH&E; Figure 7D) clearly separated the Late Modern, Early and Late Global from earlier periods ($R = 0.833$, $P = 0.008$) and each other. This means that every functional extinction changes food-web structure, with the number of functional extinctions and their consequences increasing over time, leaving the Late Global food web the most degraded.

Changes in food-web composition (that is, the presence/absence of functional groups) also had consequences on the robustness of food webs to simulated species loss. In the scenarios just representing presence/absence of all functional groups (FW_All) and all except humans (FW_WoH), secondary extinctions started at a similar number of species removed (value on *x*-axis) for all periods (Figure 8A, B), suggesting similar vulnerability to species loss. However, the Late and Early Global periods had the highest number of secondary extinctions and were the first to collapse (reaching the diagonal line) when greater than 50% of species were removed, which is an extreme scenario. This difference must have been caused by the absence of extinct species and presence of discards, which represent the main change in species composition in the Early and Late Global compared to earlier periods. In contrast, in the scenarios excluding functional extinctions (FW_E, FW_WoH&E) food webs of all periods collapsed at a similar number of species removals (Figure 8C, D), however, in both scenarios secondary extinctions started at a much lower number of species removed in the Late Global than all other periods. This suggests that the high number of functional extinctions in the Late Global period makes food webs more vulnerable to early secondary extinctions.

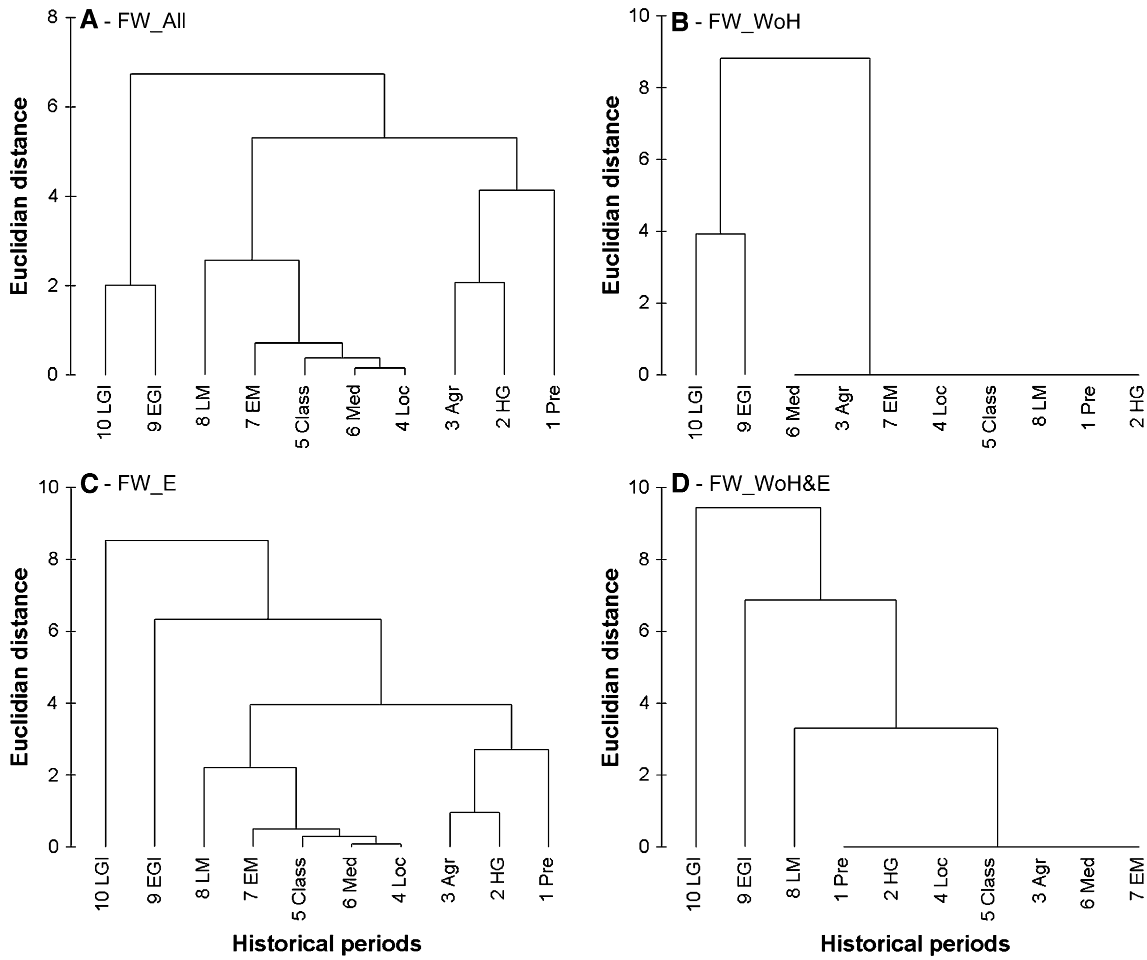

Figure 7. Hierarchical clustering based on Euclidean distances of food webs from the 10 cultural periods (see Table 2 for abbreviations) and four modelling scenarios: **A** all functional groups (FW_All), **B** all functional groups except humans (FW_WoH), **C** all functional groups excluding functional extinctions (FW_E), and **D** all functional groups excluding humans and functional extinctions (FW_WoH&E).

Discussion

The Adriatic Sea has witnessed a long history of human-induced changes in individual animal populations, habitats, and water quality as well as species diversity, food-web structure and ecosystem functioning. Our compilation of historical records, estimation of trajectories of change, and modelling of food-web alterations together provide new insight into ecosystem changes that have occurred in the Adriatic Sea over past centuries and millennia. Moreover, it provides a baseline to compare more recent ecosystem changes against (Coll and others 2010b). We show that the loss and depletion of many large predators and consumers has degraded the diversity, complexity, and connectivity of food webs with consequences for their functioning and robustness against further species loss. Moreover, habitat loss and pollution have further altered ecosystem functioning and degraded the living conditions and recovery potential for many species. Because most species are still present, although in much reduced abundance, there are still options and hope for recovery and restoration. However, this requires concerted management and conservation efforts of surrounding countries, a new balance between exploitation and conservation, and a shift towards rebuilding natural resources and ecosystems that will support human well-being in the future (Lotze and others 2006; Worm and others 2009).

Historical Changes in the Adriatic Sea

It is well documented that Romans severely overexploited terrestrial resources, with evident deforestation and game depletion all around the Mediterranean (Hughes 1994; Blondel and Aron-

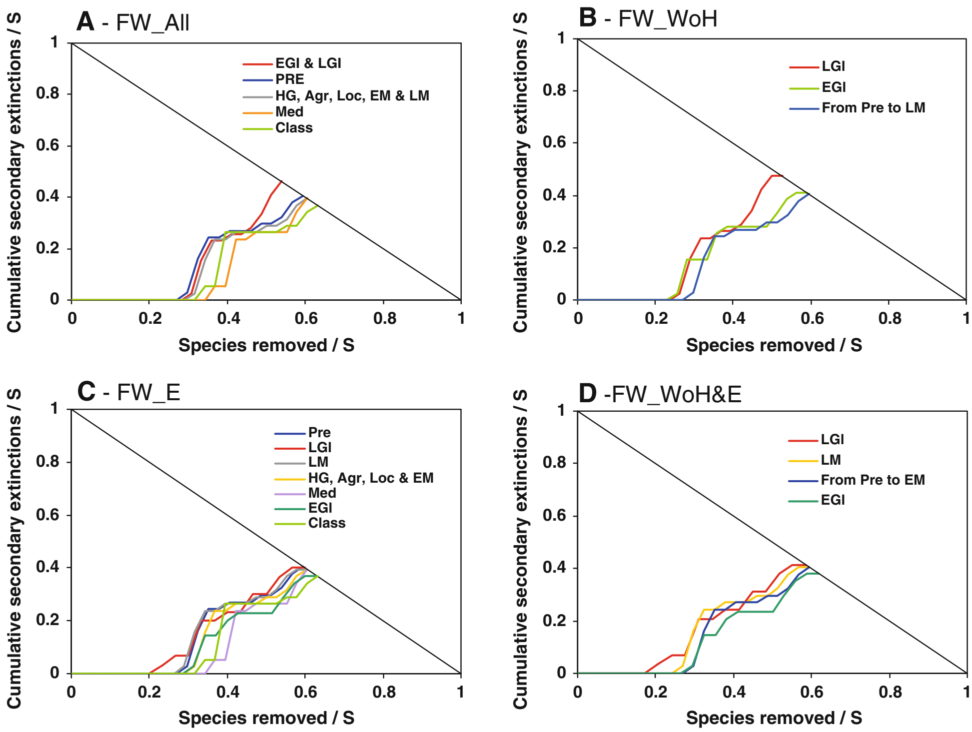

Figure 8. Robustness of food webs from different cultural periods (see Table 2 for abbreviations) and modelling scenarios (**A–D**, see Figure 7) to simulated species extinctions. Shown are the cumulative secondary extinctions resulting from simulated removals of the most connected species in each food webs.

son 1999; Hofrichter 2002). Our records also indicate the depletion of coastal marine resources such as wetlands, oysters, fish, and birds. There is increasing evidence from around the world that even small-scale subsistence exploitation by ancient or modern people can result in strong resource depletion (Rick and Erlandson 2008; Lotze and Worm 2009). Thus, given their large human population, well-developed technology, transport, and trade it is likely that Romans had substantial impact on marine resources and coastal ecosystems (Radcliffe 1921; Hughes 1994). After the collapse of the Roman Empire, many marine-like terrestrial resources may have recovered (Blondel and Aronson 1999; Hofrichter 2002), only to be reversed again by intensified population growth in Medieval times. Since then, exploitation, habitat loss, pollution, invasions, and other human impacts have further intensified over time and expanded from coastal to increasingly offshore areas (Tudela 2004; Lotze and others 2006; Coll and others 2010b). Although changes in environmental properties such as water temperature have been shown to drive long-term fluctuations in some populations (for example, bluefin tuna, Ravier and Fromentin 2004), the overwhelming effect of human impacts caused most of the observed depletions in recent centuries such as the decline of bluefin tuna (MacKenzie and others 2009). Similar trajectories of change have been found in other estuarine and coastal ecosystems worldwide. However, they started much earlier in the Adriatic Sea due to the long history of human influence and have led to a more severe ecosystem degradation (Lotze and others 2006).

Our food-web analysis showed how historical changes in human exploitation and the local or functional extinction of marine species were translated into changes in food-web structure and functioning. Increasing food-web degradation over time was reflected by overexploitation of higher trophic levels and simplification of food-web structure. Similar results have been found in more detailed food-web studies from recent decades (Coll and others 2008). This study shows that structural changes started at least in the nineteenth century (Late Modern) and accelerated in the twentieth century (Early and Late Global) with an increasing number of species becoming rare and thus functionally extinct. Resulting changes in food-web composition reduced the robustness to simulated species loss especially in the most recent period (Late Global), which has important implications for ecosystem management. Because our food-web analysis was constrained by limited historical data availability and only reflected changes in functional group presence but not abundance or biomass, our results are likely conservative. The inclusion of other species that have been depleted (often at higher trophic levels) or increased (for example, jellyfish or invasive species, often at lower trophic levels) over time would have likely enhanced food-web degradation.

The historical changes described for the Adriatic Sea probably reflect past changes in other areas of the Mediterranean and Black Seas (Bekker-Nielsen 2005; Sala 2004; Gertwagen and others 2008). In many places around the Mediterranean basin, evidence of Roman fishing and fish processing has been found (Trakadas 2006) and fishing has severely depleted ecosystems (Stergiou and Koulouris 2000; Tudela 2004). The Adriatic and Catalan Sea ecosystems of the 1970s and 1990s were found to be similarly degraded in terms of their structure, functioning and resilience, yet they were more degraded when compared to regions outside the Mediterranean such as the Benguela, Caribbean, and US shelf ecosystems (Coll and others 2008). The Adriatic and Catalan Seas were also ranked highest in fishing impacts when trend and state indicators were compared with 17 other exploited ecosystems around the world (Coll and others 2010a). Therefore, changes described here for the Adriatic Sea may reflect general historical changes in the Mediterranean, and forecast changes in other marine ecosystems with advancing degradation.

Conservation, Recovery, and Rebuilding

Our historical records indicated overall stabilizing trends in Adriatic bird populations in the twentieth century, yet we did not find clear signs of recovery in other taxonomic groups (Figure 6A). In other estuaries and coastal seas, reduced or banned exploitation, habitat protection, and pollution control have helped several species to recover, with most recoveries evident in birds and pinnipeds (Lotze and others 2006). In the Adriatic, many species of rare birds now find refuge in protected areas such as the *Parco del Delta del Po*, yet this may not be sufficient to increase their overall population size. Today, there are about 12 marine protected areas in the Northern Adriatic but many are relatively small and coastal, and they greatly vary in regulations and goals (Turk and Odorico 2009). Although no-take marine protected areas in the Mediterranean and Adriatic have been shown to enhance the abundance and biomass of target species (Guidetti and Sala 2007; Turk and Odorico 2009) and maintain food-web structure (Libralato and others 2010), existing protected areas are often too small and too recent, or human pressures in surrounding areas too high to enable large-scale recovery of marine populations. Thus, targeted conservation and environmental protection measures are needed outside protected areas to allow endangered, rare, or depleted populations to rebound, for example bluefin tuna (MacKenzie and others 2009) or marine mammals (Notarbartolo-Di-Sciara and others 2008). In the Mediterranean Sea (IMEDES 1999), as in other parts of the world (Worm and others 2009), the reduction of exploitation pressure has enabled some fish populations and community biomass to rebuild. This has been achieved through a combination of management tools including quota, effort and gear restrictions, closed areas, fisheries certification, catch shares, and community co-management. However, if species such as the monk seal, the Dalmatian pelican, and several fishes in the Northern Adriatic have already been locally extirpated, only natural or human-aided reintroduction will bring these populations back, as reported in other regions (Lotze 2005).

ACKNOWLEDGMENTS

We are grateful to S. Kidwell, M. Kirby, H. Lenihan, S. Raicevich, and F. Ferretti for historical information, and to T. Romanuk for advice on food-web modelling. Financial support was provided by the National Center for Ecological Analysis and Synthesis' Long-term Marine Records working group, the Census of Marine Life's FMAP project, and post-doctoral fellowships to M.C. from the Spanish Ministry of Science and Technology and the Marie-Curie International Outgoing Fellowships (IOF; Call: FP7-PEOPLE-2007-4-1-IOF) to ECOFUN.

REFERENCES

AdriaMed. 2003. Aspects of Fish Markets in the Adriatic Sea. AdriaMed Tech Doc 10:152.

Airoldi L, Beck MW. 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanogr Mar Biol Annu Rev 45:345–405.

Appuhn KR 1999. Environmental politics and state power in early modern Venice, 1300-1650. Ph.D. thesis. Evanston: Northwestern University. 269 pp.

Barmawidjaja DM, van der Zwaan GJ, Jorissen FJ, Puškaric S. 1995. 150 years eutrophication in the northern Adriatic Sea: evidence from a benthic foraminiferal record. Mar Geol 122:367–84.

Bearzi G, Reeves RR, Notarbartolo-di-Sciara G, Politi E, Cañadas A, Frantzis A, Mussi B. 2003. Ecology, status and conservation of short-beaked common dolphins. Mamm Rev 33:224–52.

Bearzi G, Holcer D, Notarbartolo di Sciara G. 2004. The role of historical dolphin takes and habitat degradation in shaping the present status of northern Adriatic cetaceans. Aquat Conserv Mar Freshw Ecosyst 14:363–79.

Bekker-Nielsen T. 2005. The technology and productivity of ancient sea fishing. In: Bekker-Nielsen T, Ed. Ancient fishing and fish processing in the Black Sea region. Aarhus (DK): Aarhus University Press. p 83–95.

Benović A, Justić D, Bender A. 1987. Enigmatic changes in the hydromedusan fauna of the northern Adriatic Sea. Nature 326:597–600.

Billard R, Lecointre G. 2001. Biology and conservation of sturgeon and paddlefishes. Rev Fish Biol Fisheries 10:335–92.

BLI (BirdLife International). 2004. Birds in Europe: population estimates, trends, and conservation status. BirdLife Conserv Ser 12:374.

Block BA. 2000. Of tuna and tonnarotti. Science 289:876–7.

Blondel J, Aronson J. 1999. Biology and wildlife in the Mediterranean Region. Oxford: Oxford University Press. p 352.

Bode M. 2002. Wale und Walfang in der Antike. Laverna 13:1–23.

Boero F. 2001. Adriatic ecological history: a link between jelly outbreaks, red tides, mass mor- talities, overfishing, mucilages, and thaliacean plakton? CIESM Workshop Ser 14:44–6.

Bombace G. 1992. Fisheries of the Adriatic Sea. In: Colombo G, Ferrari I, Ceccherelli VU, Rossi R, Eds. Marine eutrophication and population dynamics. Fredensborg: Olsen and Olsen. p 379–89.

Botter L, Giovanardi O, Raicevich S. 2006. Chioggia's fleet fishery migration in the Adriatic Sea between 19th and the early 20th century. J Mediterr Stud 16:27–44.

Brambati A. 1992. Origin and evolution of the Adriatic Sea. In: Colombo G, Ferrari I, Ceccherelli VU, Rossi R, Eds. Marine Eutrophication and Population Dynamics. Fredensborg: Olson and Olson. p 327–46.

Bresc H. 2000. Pêche et commerce du corail en Méditerranée de l'Antiquitè au Moyen Age. In: Morel JP, Rondi-Costanzo C, Ugolini D, Eds. Corallo di ieri, corallo di oggi. Scienze e materiali del patrimonio culturale 5. Bari: Edipuglia. p 41–53.

Casale P, Laurent L, De Metrio G. 2004. Incidental capture of marine turtles by the Italian trawl fishery in the north Adriatic Sea. Biol Conserv 119:287–95.

Cencini C. 1998. Physical processes and human activities in the evolution of the Po delta, Italy. J Coastal Res 14:774–93.

Ceron-Carrasco R, Bass B. 2001. Molluscan exploitation patterns: evidence of the uses of the immediate environment at Susac. In: Society for American Archaeology 66th Annual Meeting, 18–22 April 2001, New Orleans.

Christensen V, Guenette S, Heymans JJ, Walters CJ, Watson R, Zeller D, Pauly D. 2003. Hundred-year decline of North Atlantic predatory fishes. Fish Fish 4:1–24.

Clarke KR, Gurley RN. 2006. PRIMER v6: user manual/tutorial (Plymouth Routines in Multivariate Ecological Research). Plymouth: Primer-E Ltd. p 190.

CNHM (Croatian Natural History Museum). 2009. Adriatic Marine Turtle Program. http://www.hpm.hr/turtles/kor-uvod.htm.

Coll M, Lotze HK, Romanuk TN. 2008. Structural degradation in Mediterranean Sea food webs: Testing ecological hypotheses using stochastic and mass-balance modelling. Ecosystems 11:939–60.

Coll M, Shannon LJ, Yemane D, Link JS, Ojaveer H, Neira S, Jouffre D, Labrosse P, Heymans JJ, Fulton EA, Shin Y-J. 2010a. Ranking the ecological relative status of exploited marine ecosystems. ICES J Mar Sci 67:769–86.

Coll M, Piroddi C, Kaschner K, Ben Rais Lasram F, Steenbeek J, Aguzzi J, Ballesteros E, Nike Bianchi C, Corbera J, Dailianis T, Danovaro R, Estrada M, Froglia C, Galil BS, Gasol JM, Gertwagen R, Gil J, Guilhaumon F, Kesner-Reyes K, Kitsos M-S, Koukouras A, Lampadariou N, Laxamana E, López-Fé de la Cuadra CM, Lotze HK, Martin D, Mouillot D, Oro D, Raicevich S, Rius-Barile J, Saiz-Salinas JI, San Vicente C, Somot S, Templado J, Turon X, Vafidis D, Villanueva R, Voultsiadou E. 2010b. The biodiversity of the Mediterranean Sea: estimates, patterns and threats. PLoS ONE 5(8):e11842.

Coll M, Santojanni A, Palomera I, Arnesi E. 2010c. Ecosystem assessment of the North-Central Adriatic (Mediterranean Sea): towards a multivariate reference framework. Mar Ecol Progr Ser 417:193–210.

Collar NJ, Long AJ, Robles Gil P, Rojo J. 2007. Birds and people: bonds in a timeless journey. Mexico City: CEMEX-Agrupacion Sierra Madre-BirdLife International. p 360.

Corcoran TH. 1957. The Roman fishing industry of the late republic and early empire. Ph.D. thesis. Evanston: Northwestern University. 189p.

Council of Europe. 1994. Protection of coastal areas of the Adriatic Sea. Strassbourg: Council of Europe. 164 pp.

Danovaro R, Fonda Umani S, Pusceddu A. 2009. Climate change and the potential spreading of marine mucilage and microbial pathogens in the Mediterranean Sea. PLoS ONE 4:e7006.

Della Casa P, Bass B. 2001. Archaeological evidence from the Island of Susac, Croatia. Preliminary Report, Department of Prehistory, University of Zurich. http://www.prehist.uzh.ch/forschung/susac/susacset1.html.

Dulvy N, Sadovy Y, Reynolds JD. 2003. Extinction vulnerability in marine populations. Fish Fish 4:25–64.

Dunne JA, Williams RJ, Martinez ND. 2002a. Food-web structure and network theory: The role of connectance and size. Proc Natl Acad Sci 99:12917–22.

Dunne JA, Williams RJ, Martinez ND. 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol Lett 5:558–67.

Dunne JA, Williams RJ, Martinez ND, Wood RA, Erwin DH. 2008. Compilation and network analyses of Cambrian food webs. PLoS Biol 6:e102.

EEA (European Environment Agency). 1999. State and pressures of the marine and coastal Mediterranean environment. Environ Assess Ser 5:44p.

EEA (European Environment Agency). 2002. Indicator fact sheet: Fish stocks outside safe biological limits. Copenhagen: European Environmental Agency. p 8.

Evans PGH. 1987. The natural history of whales and dolphins. New York: Facts on File Publications. p 343.

Eyton TC. 1858. A history of the oyster and the oyster fisheries. London: Van Voorst. p 40.

Faber GL. 1883. The fisheries of the Adriatic and the fish thereof. London: Bernard Quarich. p 292.

FAO. 1984. Report of the third technical consultation on the stock assessment in the Adriatic. FAO Fisheries Reports R290, 255 pp.

FAO. 2005. Review of the state of world marine fishery resources. FAO Fish Tech Paper 457:235p.

FAO. 2010. *Corallium rubrum*, Species Fact Sheets, Fisheries and Aquaculture Department, FAO. http://www.fao.org/fishery/species/3611/en.

FAO-FishStat. 2010. Mediterranean and Black Sea (GFCM) capture production 1970-2006 (Released 2010). Regional dataset for Adriatic Sea (Region 2.1). Available at ftp://ftp.fao.org/fi/stat/windows/fishplus/gfcm.zip.

Ferretti F, Myers RA, Serena F, Lotze HK. 2008. Loss of large predatory sharks from the Mediterranean Sea. Conserv Biol 22:952–64.

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK. 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13:1055–71.

Fonda Umani S. 2004. Northern Adriatic Sea, Chapter 18. Wassmann P, Olli K, Eds. Drainage basin nutrient inputs and eutrophication: an integrated approach. http://lepo.it.da.ut.ee/~olli/eutr/html/htmlBook.html.

Fortibuoni T, Giovanardi O, Libralato S, Raicevich S, Solidoro C. 2008. Integrating historical naturalists' descriptions and statistical-scientific data to describe changes in fish assemblages over the last two centuries in the Northern Adriatic Sea. ICES CM 2008/R: 14.

Frid C, Hammer C, Law R, Loeng H, Pawlak JF, Reid PC, Tasker M. 2003. Environmental Status of the European Seas. ICES CIEM Report. 75 pp.

Galil BS. 2003. A sea of stone—biodiversity and history. Biomare Newslett 3:7.

Galil BS. 2004. Of fish bones and mosaics—the fisheries of the ancient Mediterranean. HMAP 1st Mediterranean Workshop. 20–22 Sept 2004. Institute of Marine Science, Barcelona. Spain.

Gandolfini G, Mordenti A, Paganelli L. 1982. Composition and longshore dispersal of sands from the Po and Adige rivers since pre-Etruscan age. J Sediment Petrol 57:797–805.

Gertwagen R, Raicevich S, Fortibuoni T, Giovanardi O. 2008. Il Mare Com'era. Chioggia: Istituto Superiore per la Protezione e la Ricerca Ambientale. p 219.

Guhl E, Koner W. 1875. The Life of the Greeks and Romans. London: Chapman and Hall. p 636.

Guidetti P, Sala E. 2007. Community-wide effects of marine reserves in the Mediterranean Sea. Mar Ecol Prog Ser 335:43–56.

Haywood J. 1997. Atlas of world history. Abingdon: Andromeda Oxford. p 256.

Hoffmann RC. 1996. Economic development and aquatic ecosystems in Medieval Europe. Am Hist Rev 101:631–69.

Hoffmann RC. 2001. Frontier foods for late Medieval consumers: culture, economy, ecology. Environ Hist 7:131–67.

Hofrichter R. 2002. Das mittelmeer: fauna, flora, oekologie. Teil I—Allgemeiner Teil. Heildelberg, Berlin: Spektrum Akademischer Verlag. p 608.

Hughes JD. 1994. Pan's Travail. Environmental Problems of the Ancient Greeks and Romans. Baltimore: Hopkins University Press. p 277.

ICCAT-SCRS. 2009. Mediterranean swordfish. In: International Commission for the Conservation of Atlantic Tunas (ICCAT), Standing Committee on Research and Statistics (SCRS), Madrid (Spain): Report for biennial period 2008-09, Part II Vol. 2, pp 174–180

IMEDES 1999. The Castellón trawling project (1961–1966): teachings for a sustainable fisheries management. IMEDES, COPEMED and FAO special publication. 173 pp.

IUCN. 2010. The IUCN Red List of threatened species. Available at: www.iucn.org.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–38.

Johnson WM, Karamanlidis AA, Dendrinos P, Fernández de Larrinoa P, Gazo M, González LM, Güçlüsoy H, Pires R, Schnellmann M. 2009. Monk seal fact sites: Mediterranean Monk Seal (*Monachus monachus*). http://www.monachus-guardian.org/factfiles/medit01.htm.

Jonsson L. 1992. Die Voegel Europas und des Mittelmeerraumes. Kosmos Naturfuehrer. Stuttgart: Franck-Kosmos. p 559.

Justić D, Legovic T, Rottini-Sandrini L. 1987. Trends in oxygen content 1911–1984 and occurrence of benthic mortality in the Northern Adriatic Sea. Estuar Coast Shelf Sci 25:435–45.

Knauer ER. 2003. Fishing with cormorants: a note on Vittore Carpaccio's hunting on the lagoon—Critical Essay. Apollo, September 2003.

Koutsoubas D, Galinou-Mitsoudi S, Katsanevakis S, Leontarakis P, Metaxatos A, Zenetos A. 2007. Bivalve and gastropod molluscs of commercial interest for human consumption in the Hellenic Seas. In: Papaconstantinou C, Zenetos A, Tserpes G, Vassilopoulou V, Eds. State of the Hellenic Fisheries. Athens: HCMR Publications. p 70–84.

Kovačević Z. 2002. History and political ecology of the Adriatic Sea. Religion, Science and the Environment: Adriatic Sea Symposium. 8 pp. http://www.rsesymposia.org/themedia/File/1151678043-Kovacevic.pdf.

Krstulovic N, Solic M. 1990. Long-term study of heterotrophic bacteria as indicators of eutrophication of the open middle Adriatic Sea. Estuar Coast Shelf Sci 30:611–17.

Kružić P, Požar-Domac A. 2007. Impact of tuna farming on the banks of the coral *Cladocora caespitosa* in the Adriatic Sea. Coral Reefs 26:665.

Lahmeyer J. 2006. Population statistics: Growth of the population per country in a historical perspective, including their administrative divisions and principal towns. http://www.populstat.info/.

Libralato S, Raicevich S, Pranovi F, Giovanardi O. 2004. Fisheries and state of the ecosystem: what about the Adriatic Sea? HMAP 1st Mediterranean Workshop. 20–22 Sept 2004. Barcelona: Institute of Marine Science.

Libralato S, Coll M, Tempesta M, Santojanni A, Spoto M, Palomera I, Arneri E, Solidoro C. 2010. Food-web traits of protected and exploited areas of the Adriatic Sea. Biol Conserv 143:2182–94.

Lotze HK. 2005. Radical changes in the Wadden Sea fauna and flora over the last 2000 years. Helgoland Mar Res 59:71–83.

Lotze HK, Worm B. 2009. Historical baselines for large marine animals. Trends Ecol Evol 24:254–62.

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–9.

MacKenzie BR, Mosegaard H, Rosenberg AA. 2009. Impending collapse of bluefin tuna in the northeast Atlantic and Mediterranean. Conserv Lett 2:25–34.

Malej A, Malej A Jr. 2004. Invasion of the jellyfish Pelagia noctiluca in the Northern Adriatic: a non-success story. In: Dumond H, Shiganova TA, Nierman U, Eds. Aquatic Invasions in the Black, Caspian and Mediterranean Seas. Kluwer: Academic Publishers. p 273–85.

Marasović I, Ninčević Z, Kušpilić G, Marinović S, Marinov S. 2005. Long-term changes of basic biological and chemical parameters at two stations in the middle Adriatic. J Sea Res 54:3–14.

Marchetti M. 2002. Environmental changes in the central Po Plain (northern Italy) due to fluvial modifications and anthropogenic activities. Geomorphology 44:361–73.

Marchetti R, Provini A, Crosa G. 1989. Nutrient load carried by the River Po into the Adriatic Sea, 1968–1987. Mar Pollut Bull 20:168–72.

Marini L. 1998. Cetaceans in the Italian Seas: a brief review. Aubert M, Riddel M, editors. Actes du Colloque. International ''La Méditerranée, la mer et l'homme''. RIMMO, Cagnes-su-Mer et Antibes, 6–7 Novembre 1998, pp 88–90.

Maschner HDG, Betts MW, Cornell J, Dunne JA, Finney B, Huntly N, Jordan JW, Misarti N, Reedy-Maschner KL, Russell R, Tews A, Wood S, Benson B. 2009. An introduction to the biocomplexity of Sanak Island, Western Gulf of Alaska. Pac Sci 63:673–709.

McEvedy C, Jones R. 1978. Atlas of World Population History. London: Penguin Books. p 368.

McPherson J, Myers RA. 2009. How to infer population trends in sparse data: examples with opportunistic sighting records for great white sharks. Divers Distrib 15:880–9.

MTSG. 2004. 2004 Global status assessment, Green turtle (*Chelonia mydas*). The IUCN Species Survival Commission, Red List Programme. Cambridge: IUCN. p 71.

MTSG (Marine Turtle Specialist Group). 1999. A Global strategy for the conservation of marine turtles. The IUCN Species Survival Commission. Cambridge: IUCN.

Munda IM. 2000. Long-term marine floristic changes around Rovinj (Istrian coast, North Adriatic) estimated on the basis of historical data from Paul Kuckuck's field diaries from the end of the 19th century. Nova Hedwigia 71:1–36.

Neil DT. 2002. A thousand years of human-coastal interactions in Venice: lessons from the serene republic. Coast Coast 2002:318–21.

Newell RIE, Ott JA. 1999. Macrobenthic communities and eutrophication. In: Malone TC, Malej A, Harding LWG Jr, Smodlaka N, Turner RE, Eds. Ecosystems at the land-sea margin, drainage basin to coastal sea. Washington (DC): American Geophysical Union. p 265–94.

Notarbartolo-Di-Sciara G, Agardy T, Hyrenbach D, Scovazzid T, Klaveren PV. 2008. The Pelagos Sanctuary for Mediterranean marine mammals. Aquat Conserv Mar Freshw Ecosyst 18:367–91.

Occhipinti-Ambrogi A. 2002. Susceptibility to invasion: assessing scale and impact of alien biota in the Northern Adriatic. CIESM Workshop Monogr 20:67–73.

Ott JA. 1992. The Adriatic benthos: problems and perspectives. In: Colombo G, Ferrari I, Ceccherelli VU, Rossi R, Eds. Marine eutrophication and population dynamics. Fredensborg: Olsen and Olsen. p 367–78.

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–8.

Pauly D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol Evol 10:430.

Perkol-Finkel S, Airoldi L. 2010. Loss and recovery potential of marine habitats: an experimental study of factors maintaining resilience in subtidal algal forests at the Adriatic Sea. PLoS ONE 5:e10791. doi:10.1371/journal.pone.0010791.

Perry SL, DeMaster DP, Silber GK. 1999. The great whales: history and status of six species listed as endangered under the U.S. Endangered Species Act of 1973. Mar Fish Rev Sp Issue 61:1–74.

Pinardi N, Arneri E, Crise A, Ravaioli M, Zavatarelli M. 2006. The physical, sedimentary and ecological structure and variability of shelf areas in the Mediterranean Sea. Robinson AR, Brink KH, editors. The Sea Vol. 14. Cambridge: Harvard University Press. p1243-1330.

Plinii Secundi C. 1513. Naturalis historiae. Libri XXXVII. Venice, Italy

Pronzato R. 1999. Sponge-fishing, disease and farming in the Mediterranean Sea. Aquat Conserv Mar Freshw Ecosyst 9:485–93.

Pronzato R, Manconi R. 2008. Mediterranean commercial sponges: over 5000 years of natural history and cultural heritage. Mar Ecol 29:146–66.

Puškaric S, Berger GW, Jorissen FJ. 1990. Successive appearance of subfossil phytoplankton species in Holocene sediments of the Northern Adriatic and its relation to the increased eutrophication pressure. Estuar Coastal Shelf Sci 31:177–87.

Radcliffe W. 1921. Fishing from the earliest times. Chicago: Ares. p 478.

Raicevich S, Libralato S, Giovanardi O, Pranovi F. 2004. Historical data of ecosystem driving forces and anthropogenic disturbance in the Northern Adriatic Sea. HMAP 1st Mediterranean Workshop. 20–22 Sept 2004. Institute of Marine Science, Barcelona. Spain.

Ravier C, Fromentin J-M. 2004. Are the long-term fluctuations in Atlantic bluefin tuna (*Thunnus thynnus*) population related to environmental changes? Fish Oceanogr 13:145–60.

Rick TC, Erlandson JM. 2008. Human impacts on ancient marine ecosystems: a global perspective. Berkely: University of California Press. p 319.

Roopnarine PD, Angielczyk KD, Wang SC, Hertog R. 2007. Trophic network models explain instability of Early Triassic terrestrial communities. Proc R Soc B 274:2077–86.

Sala E. 2004. The past and present topology and structure of Mediterranean subtidal rocky-shore food webs. Ecosystems 7:333–40.

Sangiorgi F, Donders TH. 2004. Reconstructing 150 years of eutrophication in the north-western Adriatic Sea (Italy) using dinoflagellate cysts, pollen and spores. Estuar Coast Shelf Sci 60:69–79.

Santojanni A, Arneri E, Barry C, Belardinelli A, Cingolani N, Giannetti G, Kirkwood G. 2003. Trends of anchovy (*Engraulis encrasicolus* L.) biomass in the northern and central Adriatic Sea. Sci Marina 67:327–40.

Santojanni A, Cingolani N, Arneri E, Kirkwood G, Belardinelli A, Giannetti G, Colella S, Donato F, Barry C. 2005. Stock assessment of sardine (*Sardina pilchardus* Walb.) in the Adriatic Sea, with an estimate of discards. Scientia Marina 69:603–17.

Sergeant D, Ronald K, Boulva J, Berkes F. 1979. The recent status of *Monachus monachus* the Mediterranean Monk Seal. In: Ronald K, Duguy R, Eds. The Mediterranean monk seal. Oxford: Pergamon Press. p 31–54.

Stachowitsch M. 1984. Mass mortality in the Gulf of Trieste: the course of community destruction. Mar Ecol 5:243–64.

Stachowitsch M. 1991. Anoxia in the Northern Adriatic Sea: rapid death, slow recovery. Geol Soc Lond Sp Publ 58:119–29.

Stefani M, Vincenti S. 2005. The interplay of eustasy, climate and human activity in the late Quaternary depositional evolution and sedimentary architecture of the Po Delta system. Mar Geol 222–223:19–48.

Stergiou KI, Koulouris ML. 2000. Fishing down the marine food webs in the Hellenic Seas. CIESM Workshop Monogr 12:73–8.

Tout P. 1995. Birds of the Northern Adriatic Region. http://www.istrianet.org/istria/fauna/birds/birds-adriatic.htm.

Trakadas LA. 2006. Exhausted by fishermen's nets': Roman sea fisheries and their management. J Mediterr Stud 16:259–72.

Tudela S. 2004. Ecosystem effects of fishing in the Mediterranean: an analysis of the major threats of fishing gear and practices to biodiversity and marine habitats, General Fisheries Commission for the Mediterranean. Stud Rev 74:44.

Turk R, Odorico R. 2009. Marine protected areas in the Northern Adriatic. Varstvo Narave 22:33–45.

USGS (U.S. Geological Survey). 2006. The cranes: status survey and conservation action plan Eurasian crane (*Grus grus*). U.S. Department of the Interior, U.S. Geological Survey. http://www.npwrc.usgs.gov/resource/birds/cranes/grusgrus.htm.

Vollenweider RA, Montanari G, Rinaldi A. 1995. Statistical inferences about the mucilage events in the Adriatic Sea, with special reference to recurrence patterns and claimed relationship to sun activity cycles. Sci Total Environ 165:213–24.

Volpi LB. 1996. La spettacolare pesca del tonno nel golfo di Trieste. Trieste: Mladika.

Vrgoc N, Arneri E, Jukic-Peladic S, Krstulovic Sifner S, Mannini P, Marceta B, Osmani K, Piccinetti C, Ungaro N. 2004. Review of current knowledge on shared demersal stocks of the Adriatic Sea. FAO-Adriamed Tech Doc 12:105p.

Watermeyer KE, Shannon LJ, Griffiths CL. 2008. Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. Afr J Mar Sci 30:351–82.

Whitehead H. 2002. Estimates of the current global population size and historical trajectory for sperm whales. Mar Ecol Prog Ser 242:295–304.

Williams RJ, Martinez ND. 2000. Simple rules yield complex food webs. Nature 404:180–3.

Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, Fogarty MJ, Fulton EA, Hutchings JA, Jennings S, Jensen OP, Lotze HK, Mace PM, McClanahan TR, Minto C, Palumbi SR, Parma AM, Ricard D, Rosenberg AA, Watson R, Zeller D. 2009. Rebuilding global fisheries. Science 325:578–85.

Zavatarelli M, Raicich F, Bregant D, Russo A, Artegiani A. 1998. Climatological biogeochemical characteristics of the Adriatic Sea. J Mar Syst 18:227–63.

Zenetos A, Gofas S, Russo G, Templado J. 2004. CIESM Atlas of Exotic Species in the Mediterranean 3: Molluscs. Monaco: CIESM.

Ziderman I. 1990. Seashells and ancient purple dyeing. Biblical Archaeol 53:98–101.