Marine extinctions - patterns and processes

Executive Summary[1]

This synthesis, sketched during the course of the meeting, was developed in the following months on the basis of further inputs received by the participants, under the coordination of Ferdinando Boero, James Carlton and Frédéric Briand. The latter reviewed and edited the entire volume, whose physical production was carried out by Valérie Gollino.

1. Introduction

The study of extinction in the sea is fraught with challenges. On the one hand species long thought extinct are re-discovered or otherwise "resurrected" on a regular basis (Keith and Burgman, 2004; Scheffers *et al.*, 2011). On the other hand, it seems probable that many species believed to still exist in our oceans may have long since gone extinct. Further, a robust understanding of the processes that may be currently driving species to, and over, the extinction cliff, often remains elusive, especially for those species where obtaining rigorous population and distribution estimates is expensive, arduous and problematic.

To cast a light on the current processes and extent of marine extinctions, CIESM invited a selected group of 16 specialists from various disciplines – ranging from marine biology, community dynamics, population genetics, paleontology, fishery science, historical ecology and evolution (see list at end of volume). They were welcomed in the futuristic Center of Arts and Sciences of Valencia by CIESM Director General, Dr Frédéric Briand, who started by thanking Dr Daniel Garcia Parraga for hosting this 45th Workshop of the Commission in 'his' splendid Oceanogràfic building, collaborator Dr Paula Moschella for her efforts in the logistic preparation, and last but not least Dr Ferdinando Boero, Chair of CIESM Committee on marine ecosystems, for suggesting this exciting, timely theme and for agreeing to act as discussion moderator/ stimulator.

In his opening remarks, Frédéric Briand focused on a number of issues and open questions which the four-day exploratory meeting would explore in earnest, such as the proximate / ultimate causes of extinction, the spatio-temporal scale of the process, the relevance or not of rarity, the available evidence from past extinction events, the tools and models available to assess the current rates of extinction, the risks of a sixth forthcoming wave of extinction, and appropriate conservation measures to reduce man's acceleration of the process. Ferdinando Boero followed, highlighting the difficulty of securing reliable, quantitative data on a scientific question so elusive as biodiversity changes in the vast marine realm, before inviting participants to present their paper.

Red *vs* black lists

Species particularly vulnerable to human impacts raise most concern about mass extinction. A great deal indeed of recent published works has addressed the potential for habitat destruction,

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[1] to be cited as:
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water quality degradation, overfishing, climate change, and other processes to push species to the brink (Pew Oceans Commission, 2003). While there are enduring, long-term challenges in determining the threatened, endangered, and extinct status of terrestrial and freshwater species (Scheffers *et al.*, 2011), these challenges are vastly more exacerbated in the world's oceans.

Species lists

Naming species is probably the first form of culture, and it is even written in the Genesis that "the Creator brought animals to the first human to see what name he would have given to them". The task of naming species is still unfinished. Estimates say that about two million species have been named, and that there are almost six or more millions that are still unnamed. Some scientists even estimated how many of these unknown species are becoming extinct before we are even aware of their existence. Strange enough, it is presumed that unknown species are becoming extinct, while there is little proof that the known ones are really extinct!

The inventory of the natural capital

Producing a rigorous catalogue of threatened, endangered, or extinct species is a challenge in the absence of detailed knowledge of regional marine biota. Few such thorough inventories exist, and *no inventories* are known to us that accurately reflect the current knowledge of systematics, distribution, biology (including life cycles), and ecology (such as the place in a trophic network) of all marine species within a region – admittedly a daunting task. Checklists alone do not reveal the population status of the vast majority of species or when they were last seen. For European seas, there is the European Register of Marine Species http://www.marbef.org/data/erms.php, for example, and, broader still, the Ocean Biogeographic Information System (http://www.iobis.org/). For most species on these lists, non-specialists would be surprised to learn that we know little more than their morphology and have only a coarse-grained view of their distribution. If, and where, populations have declined or disappeared for, literally, hundreds of thousands of marine species, is simply not known, a reality which may be obscured by the apparent existence of extensive "data bases" on the world's marine biodiversity.

Biodiversity increase: real or artefact?

The first species lists contained just a small fraction of biodiversity. Species numbers have been growing as long as new species were described or newly recorded for a given place. So, the number of species is in continuous increase. This is happening both globally and locally. The arrival of many non indigenous species in the Mediterranean, for instance, is leading to a marked increase in the species numbers that are making up the biodiversity of the basin. Some of these species are labelled as "worst aliens" and their presence is considered as negative, although their very presence represents an increase in species numbers. One of the features of these "worst aliens" is their negative impact on native species that should be pushed on the verge of extinction by the newcomers. The newcomers, however, often arrive and become established because of physical conditions changes (e.g. due to global warming) to the detriment of native species that are not tolerant enough to withstand the new situation. Under such circumstances, pre-adapted species to the new conditions might take the place of the original, now "maladapted ones". In this case the substitution of the native species by the non native ones merely reflets changing environmental conditions. Whatever the cause, it is anyway important to remain aware of possible extinctions, if only to demonstrate that we are really going through a biodiversity crisis.

This enterprise is possible, and our workshop aimed at showing its feasibility while taking the Mediterranean Sea as a paradigm for the world ocean, and by tackling the problem of extinction both from a paleontological and a neontological point of view, putting in contact fields of expertise that rarely do interact.

Marine *vs* terrestrial extinctions

Concern about extinction is widespread and leaves almost no room for doubt. But if the question is posed about naming extinct species, the first ones that come to mind are usually the dodo and the great auk (not to mention dinosaurs), while names do not come to mind when asked to list extinct marine species. Unfortunately such lists do exist, even though they do not contain "charismatic" species, i.e. the popular animals that are familiar to the public at large. The bias towards these species is, however, not justified when the problem of extinction is tackled from a scientific point of view.

The number of marine species is much lower than that of terrestrial ones, even if the diversity of body plans (e.g. phyla) is much higher in the sea than on land. The insects, making up almost half of known species, are paradigmatic in this respect, while having relatively few marine representatives. The phyla of the interstitial fauna, for example, are almost exclusively marine and, as such, constitute a great contribution to the diversity of life at higher levels of organization. The lower species diversity of marine life, if compared to terrestrial one, is often explained by the high connectivity characterizing marine environments, with lower chances of population segregation, leading to allopatric speciation. The barriers separating terrestrial habitats have no comparison in the marine realm. Local extinction is of course possible, but the wider distribution of marine species is conducive to the survival of marine forms in other places.

Marine extinctions, for these reasons are far more difficult to establish than those affecting terrestrial groups.

Peculiarities of the Mediterranean Sea

After the Messinian crisis, about six million years ago, the Mediterranean biota became established by recolonisation through the strait of Gibraltar. In different geological periods, species with different features entered the basin. Species of cold affinity entered during the cold periods, whereas species of warm affinity entered during warmer periods. Large seasonal fluctuations in temperature allowed for the survival of both contingents, if their life cycles and histories involved periods of activity (during the favourable season) and periods of rest (during the unfavourable one). At present, the Mediterranean biota in surface waters, does have a tropical nature in the summer and a temperate nature in the winter. The Mediterranean is also characterized by a high rate of endemism. The entrance of species is rather easy, near the surface, due to the presence of a surface current entering from the Atlantic. The outgoing current is deeper and surface species might find it difficult to get out, while having good chances of getting in. Under these circumstances, the Mediterranean behaves as a trap that lets species in but prevents them from getting out. This situation is conducive to the high rates of endemism that characterize the Mediterranean Sea biota. These species are liable of extinction due to environmental change and, since they are not present elsewhere, local extinction might be equal to final extinction.

The Mediterranean Sea, thus, is a paradigmatic area to study the impact of environmental change on species survival. This advantage, however, is to be considered with care. The history of marine taxonomy views the Mediterranean as a very important centre, due to the concentration of taxonomic efforts both in the past and in the present. New species, described from the Mediterranean, and thus having this sea as their type locality, might be newcomers that were unknown in their original area of distribution, and were ‘discovered’ by local taxonomists upon their arrival, just as the recently described jellyfish species *Marivagia stellata* and *Rhopilema nomadica*. These species most probably entered in the Mediterranean through the Suez Canal and were non-described in their native area due to lack of taxonomic expertise, soon to be detected once they reached an area “patrolled” by active taxonomists. For taxonomy, the Mediterranean is the type locality of these species, but this does not reflect their actual distribution.

Rarity

Most species are poorly known simply because they are inconspicuous and the perception of their existence is based on just a few records, sometimes even just one: the original description. These species are labelled as rare, while this may be simply due to insufficient sampling or lack of expertise. The processes leading to extinction imply a decrease in number, and it seems logical that rare species are in a risky situation, due to the scarcity of their populations. But, since most species are rare, and just a few are abundant at a given period in the history of a biota, rarity is not a risky condition per se. The alternation of periods of abundance and rarity, in fact, might be the main motor of species diversification, through flush and crash phenomena that represent sudden pressures of natural selection on species populations. During the periods of flush, species are represented by a multitude of individuals, but these cannot persist for long, due to the overexploitation they exert on the very resources that should sustain them. The collapse of these populations (the crash) removes maladapted individuals and enhances the surviving ones that survived just due to genetic makeups conducive to ecological success. In light of these considerations, rarity is not a sufficient precondition to extinction.

2. Assessing extinction – what can we learn from paleontology?

Patterns seen in the past are becoming increasingly important for predicting the future. This is especially true for marine extinctions, for which the fossil record provides invaluable data on multiple temporal and spatial scales while evidence for modern extinctions comes largely from terrestrial environments. A major limitation of using the fossil record in a straightforward way is its incompleteness and the vast time scales on which global patterns are usually being assessed. The incompleteness and many other issues related to sampling can be overcome by applying rigorous methods of sampling standardization on fossil occurrences combined with appropriate counting methods (Alroy *et al.*, 2001; Alroy, 2008; Alroy *et al.*, 2008). The vast time scales can be used as an advantage because we can observe the fate of fossil lineages from their origin until final extinction. Paleontologists can thus assess extinction rates and their selectivity directly, without relying on inferences of extinction risk as used in the IUCN Red List. In addition, deep time patterns inform us about the natural variability of species abundances (if indirectly) and geographic ranges. In linking taxonomic and ecological information paleontologists can thus evaluate a number of key questions such as:

2.1 Which traits render a species prone to extinction?

The suite of factors that paleontologists have identified is very similar to that offered by neontologists (McKinney, 1997; Kiessling, this volume). Examples are specialization, mode of life, mode of reproduction, and abundance traits. Most of these traits have long been identified as important determinants of extinction risk in a qualitative way, but more recent studies have helped to assess their relative importance. For example, while body size, abundance and geographic range have all been linked to extinction risk, geographic range is the only one of these factors that directly controls extinction risk (Harnik, 2011). The other two factors are only indirectly linked to extinction risk.

As clear from the IUCN Red List, rarity does not necessarily mean enhanced extinction risk because rarity is a natural state for many species (Mace *et al.*, 2008). A recent study using the entire marine fossil record confirmed that among the various forms of rarity low population size has the weakest effect on extinction risk, whereas restricted geographic range is the most important driver followed by narrow habitat breadth (Harnik *et al.*, 2012a,b). Abundance has a U-shaped relationship with extinction risk in fossil marine bivalves. Very rare and very abundant taxa show elevated extinction rates, whereas extinction risk is minimized at intermediate abundances (Simpson and Harnik, 2009). The common notion of specialist species being at greater risk of extinction than generalists holds true, but there are issues with defining what a specialist really is. The fossil record shows that habitat specialists are at a greater risk of extinction but also have greater chances of speciation (Kiessling and Aberhan, 2007a; Colles *et al.*, 2009).

Several additional traits that increase extinction risk in marine animals have been identified, based on fossil invertebrates. An important trait is low metabolic rate and the formation of heavy skeletons, which increased extinction risk during times of massive changes in ocean chemistry such as ocean acidification (Kiessling and Simpson, 2011; Knoll and Fisher, 2011). The general notion that marine animal species are less extinction-prone than terrestrial animal species is supported by the fossil record (McKinney, 1998). However, this does not imply that marine species are less at risk today, because the fossil record also tells us that during mass extinctions marine taxa were hit as hard as terrestrial taxa (Benton, 1995).

2.2 What besides magnitude distinguishes background extinctions from a mass extinction?

Paleontologists have long emphasized the dichotomy between background extinctions and mass extinctions (Jablonski, 1986a). Mass extinctions are defined by extinction magnitudes that are significantly above background extinctions, which declined over the course of the Phanerozoic eon (the last 540 million years) (Kiessling, this volume). There is no arbitrary choice of a proportion of taxa becoming extinct but experience shows that the traditional Big Five mass extinction of the Phanerozoic (Raup and Sepkoski, 1982) wiped out more than 40% of marine genera and probably more than 70% of marine species. Some rules that govern survival during normal times do not apply during global catastrophes. An important example is geographic range, which facilitates survival during background times but not during mass extinctions (Kiessling and Aberhan, 2007b; Payne and Finnegan, 2007). This is probably due to the global scope of environmental changes that lead to mass extinctions, whereas background extinctions were triggered by biotic interactions and regional environmental change. Other traits governing survival during background times may also become ineffectual during mass extinctions (Jablonski and Raup, 1995) but the selectivity of mass extinctions can be used efficiently to assess their specific causes (Smith and Jeffery, 1998; Kiessling *et al.*, 2007; Knoll *et al.*, 2007). The difference in selective regimes between background and mass extinctions has probably been overemphasized in the past. The question if we are already approaching a mass extinction event (Barnosky *et al.*, 2011) is still important to put the current biodiversity crisis in a geological context, but not crucial to assess extinction risk of extant species with the help of the fossil record.

2.3 What are the natural causes of extinction?

All ancient mass extinctions are associated with massive perturbations of the global carbon cycle and rapid climate change. The ultimate triggers of ancient mass extinctions range from slow processes such as plate tectonics to shock events such as meteorite impacts and are thus very different from the entirely anthropogenic driver today. However, the time scales involved in actually triggering marine extinctions were perhaps not as different as commonly assumed. It is more the failure to resolve the duration of ancient extinctions than factual evidence for prolonged crises that led to the notion of vastly different time scales involved in extinctions now and then. Probabilistic approaches rendered it likely that marine extinctions occurred in pulses, not only during mass extinctions but also during background intervals (Foote, 2005). Rapid climate change is a component of all mass extinctions although the causes and pace of climate change varied considerably. The massive release of greenhouse gases due to volcanism is seen as a crucial trigger of two out of three mass extinctions in the last 250 Myr and the most recent of these (the end-Cretaceous mass extinction) was probably caused by a meteorite impact (see Kiessling, this volume).

2.4 What is the natural variability of population sizes?

Defining natural baselines is among the central tasks of the emerging field of conservation paleobiology (Dietl and Flessa, 2011). What was natural in the coastal oceans (Jackson, 2001) is a key question for which paleo-ecological data can be especially useful. Studies from shallow time are useful to assess natural variations in population size. The purpose of previous studies was largely to monitor economically important or hazardous species over time scales beyond historical records (Walbran *et al.*, 1989; Valdés *et al.*, 2008), to assess changes in productivity (Kowalewski *et al.*, 2000) or to separate invasive from native species (van Leeuwen *et al.*, 2008). Fossil data can enhance our knowledge on the natural variability of population sizes and should thus be included in the assessments of extinction risk for recent species, especially in the marine realm, where knowledge is so poor compared with terrestrial records.

Box 1. Confidence in extinction.

How long must a species go unseen before it can safely be declared extinct? This is a difficult question, which cannot be answered with a simple number that is valid for all species. A conspicuous species that is regularly sighted will need less time to be declared extinct with confidence than an inconspicuous species that is only identified by specialists. Complete certainty on species extinction is virtually impossible to achieve as demonstrated by repeated sightings of presumably extinct species. In the most extreme case, the time span between last sighting and re-discovery can span millions of years as exemplified by the gap of presumed coelacanth extinction in the Late Cretaceous (ca. 80 myr) and the discovery of living *Latimeria* in the 1930s. The problem of when a species should be considered extinct has thus concerned both biologists and palaeontologists (Strauss and Sadler, 1989; Carlton *et al.*, 1999).

Paleontologists have developed tools to quantify the confidence with which a species can be considered extinct. Those models were first applied to stratigraphic sections (Strauss and Sadler, 1989) and later to global taxonomic ranges (Marshall, 1990; Marshall, 1994). Biologists have adopted and further developed these approaches. Current approaches on the temporal distribution of sighting records are rather complex and require advanced statistical knowledge (Solow and Roberts, 2003; Solow, 2005; Collen *et al.*, 2010).

We recommend using an adjusted version of Marshall's (1990) simple equation as a first approximation for poorly documented marine groups because this can be applied with ease by taxonomists and it does not require information about the temporal distribution of sightings.

The confidence (C) of the declaration of a species being extinct at a given time is calculated by

$$C = 1 - (G/R + 1)^{-(H-1)}$$

where

G = number of years since last sighting
R = years between first record (the date of first collection) and the last sighting
H = number of individual years in which there is a record

A species could be declared extinct if the confidence is 95% or greater. An 80% confidence should be be taken as a critical values warranting closer inspection.

This said, we caution that this formula is only applicable to larger well-known species for which it can be demonstrated that both the historical and modern-day record is thorough and rigorous. For most species, data relative to sightings are an artifact of a combination of sampling intensity (either spatially or temporally) with the ability of workers to identify a species. Many species in many community samples simply go unidentified because no taxonomists are available, and thus we have no ability to assess the continued presence, or presumptive absence, of a vast number of species. Thousands and thousands of marine species – especially protists, invertebrates, and smaller algae – have gone unreported for decades or centuries since their first descriptions, simply because no one has sought them out again. As pointed out by Boero (2011) how many inconspicuous species have probably gone in complete indifference? Current knowledge depends on whether anyone has actually sampled or identified these species over subsequent years. The modern-day record demonstrates that even large, once-abundant species (e.g. sharks, see Soldo, this volume) can simply disappear without notice, suggesting that documenting the disappearance of uncommon and smaller species is a fundamental challenge.

3. PREDICTING RISK OF EXTINCTION

3.1 Overexploitation

Over-extraction of marine resources, habitat destruction, water quality, climate change and invasive species are together threatening the marine biota and marine ecosystems. Due to rapid coastal urbanization and industrialization, point and non-point source land and urban runoff has rendered what were once natural, diverse estuaries, bays, and lagoons – but are now marinas, busy harbors, and industrial wastelands – nearly biologically depauperate. For many locations we have poor historical data on overfishing / overexploitation, except on hunting of marine species of megafauna. Many populations and species of marine mammals (see Panigada and Pierantonio, this volume), seabirds, and marine turtles are now at a fraction of their former pre-exploitation abundance levels and listed as threatened in the IUCN Red List (Dulvy *et al.*, 2009).

Marine fish and shellfish (including molluscs and crustacean) species have also experienced large reductions in abundance from former levels since medieval times (Hoffmann, 2005), with industrial-scale fisheries commencing in the late 19th and early 20th centuries. The Food and Agriculture Organization of the United Nations (FAO), in charge of collecting world fishery landings statistics and summarizing the status of global fisheries, calculated that in 2009 over 87% of the commercially important fish stocks were already either fully exploited, or overexploited (FAO, 2012). However, the FAO global status assessment covers only a small number of exploited fish resources, leaving out hundreds of species, and thousands of populations for which there are not official statistics, particularly excluding bycatch species and species exploited by artisanal and subsistence fisheries (Zeller and Pauly, 2007).

There have been also multiple attempts to quantify the impacts of fishing on several groups of data-rich species, commonly large predatory fishes, with the objective of providing a more accurate picture of their trajectories and reductions from known historical levels (historical baselines). Hutchings and Reynolds (2004) examined data of 230 marine fish populations in the North Atlantic and estimated a reduction of 83% in adult biomass from known historic levels. The adult biomass of scombrids species (tunas and mackerels) is estimated to have decreased globally on average by 60% since the 1950s, with temperate tuna exhibiting the largest declines in biomass (on average 80% reductions) (Juan-Jorda *et al.*, 2011). Similarly, large pelagic shark populations have declined by more than 75% in the Northwest Atlantic Ocean and over 90% in the Gulf of Mexico (Baum *et al.*, 2003; Baum and Myers, 2004).

Although these global or regional synthesis studies provide a more accurate picture of the biomass trajectories of commercially important fish populations, the reality is that biomass estimates and the current exploitation status for the large majority of fish species are still uncertain or unknown globally. We still rely on the FAO landings fish statistics, rather than population biomass estimates, to illustrate the impacts of fisheries on marine living resources within the last 50-60 years of industrialized fisheries. Global fisheries landings reveal that the average trophic level of the global catch has declined over time, suggesting that predatory fishes have been sequentially declining as fisheries started to also target middle and lower trophic fish species, an indication that both fishing down and through marine food-webs is occurring (Pauly *et al.*, 1998; Essington, 2006).

Long term trends of global fish landings also signal that fish resource are exhaustible. Since the 1980s, fish landing have leveled off (if China statistics are included) or have slowly decreased (if China statistics are excluded), suggesting that food webs are becoming simplified and that it is getting harder to extract fish from the oceans despite all the technological developments (Watson and Pauly, 2001; Pauly *et al.*, 2005). At the same time there is increasing evidence that jellyfish abundance is increasing worldwide (Brotz *et al.*, 2012), and that fishing – by removing the natural predators of jellyfish species – might be in part responsible for this trend (Purcell *et al.*, 2007). The impacts of reducing large amounts of biomass from the oceans and the indirect effects of overfishing on the structure and functioning of marine ecosystems are still poorly understood (Scheffer *et al.*, 2005). One of the best documented cases of cascading effects induced by overfishing is the Canadian cod collapse and its effects all the way down the foodweb (Frank *et al.*, 2005). There is growing evidence that changes at the top of the food chain can provoke sudden ecosystem changes, sometimes referred as regime shifts, and that such changes in ecological state may be irreversible once over some tipping points (Casini *et al.*, 2008).

Factors contributing to overfishing

Multiple factors have been identified as main drivers contributing to overfishing, thus jeopardizing the sustainable management of marine ecosystems and increasing the rates of extinction of marine species. The following drivers have been identified as the four largest contributors to overfishing: 1) fish subsides; 2) overcapacity in fisheries; 3) growing demand and price of marine products; and 4) illegal fishing (Pauly and Alder, 2005; Sumaila *et al.*, 2008; Pauly, 2009). Subsidies, in most cases facilitated by governments, are considered to be the most significant drivers of overfishing. Subsidies typically contribute to the development of bigger and more efficient fleets, increase fishing effort and the net profits of fishers, thus sustaining fishing fleets that otherwise would not be economically viable (Sumaila *et al.*, 2010). Second, the current fleet overcapacity is at least two and a half times greater than required to bring long-term catches at a sustainable rate (Pauly, 2009). Third, global human population growth connected with an increase in demand and price values of marine products are also contributing to overfishing. Some species can reach high prices in the international markets, creating incentives for overfishing. For example, in 2011 a single Pacific bluefin tuna was sold for more than 400,000$ in Tokyo market. Although the value of this particular fish does not represent the average sale value of bluefin tunas in the global markets, it clearly illustrates the inflated values reached by some fish species, which generate high pressures and incentives for overfishing. Fourth, illegal, unreported and unregulated (IUU) fisheries also fuel the problem of overfishing. It has been estimated that between $10bn and $23,5 bn (between 11 and 26 million tones) are lost annually worldwide due to current illegal and unreported fishing (Agnew *et al.*, 2009). Although there have been some attempts to halt and reduce IUU fisheries, control and surveillance of fisheries worldwide continue to be a challenge.

From collapse to extinction

Although there are numerous examples of marine populations and species that have suffered declines of 80-90% or more from pre-exploitation abundance and numerous examples of fish collapses precipitating closure of fisheries, it has been widely assumed (and still held) that marine species are less vulnerable to fishing exploitation and less prone to extinction than terrestrial species. This assumption arises in part from two reasons. First, few marine species (relative to terrestrial species) have been documented to have become globally extinct in the last century and those now extinct had relatively small ranges (Dulvy *et al.*, 2009). Second, the intrinsic biology of marine species, particularly the biology of teleost fish with large fecundities combined with their widespread distributions and high abundances, has led to the wrong assumption that marine fish species are more resilient to fishing impacts and therefore less vulnerable to extinction than other non-fish marine species or terrestrial species.

Recently these perceptions have been challenged and questioned by many (Hutchings, 2001; Sadovy, 2001; Dulvy *et al.*, 2003). Marine extinctions are now believed to be underestimated because of low detection abilities and the general lack of information of the status of the majority of marine species (Dulvy *et al.*, 2009; Carlton, this volume). There are many examples of local extinctions of marine species and the reporting of local marine extinction is increasing over time. Given that local extinctions are the first step towards global extinction, the importance of local extinctions cannot be underestimated. Large reductions of biomass to very low levels, triggered by overfishing and fragmented habitats caused by destructive fishing methods, are two factors likely to lead to numerous local extinctions, especially in species with the most intrinsic vulnerable life histories, such as the long-lived, slow growing and fragile species (Sadovy and Cheung, 2003). Moreover, the widely-held belief that large fecund fishes are more resilient to overexploitation lacks any scientific support. Instead, there is increasing agreement that highly fecund fishes (largely teleost) are not more resilient to overexploitation or extinctions than terrestrial mammals (Hutchings *et al.*, 2012). There is a need to focus on fragmented populations and populations with low abundance levels induced by fishing. At these stages, the loss of genetic diversity, decompensation (Allee effects) and inbreeding depression in fragmented and small populations might drive species to the brink of extinction (Briggs, 2010).

Besides fishes, several valued benthic invertebrates, such as bath sponges and corals have been subjected to harvesting for centuries by humans (for details see Voultsiadou *et al.,* this volume). The commercial value of such species commonly increases as they become less abundant and this, in turn, leads to even more intensive harvesting and poaching. Thus, they may not necessarily become economically extinct before their local or regional extinction, as is assumed for fish stocks (Dulvy *et al*., 2003). Moreover, the withdrawal of these organisms can have an increased impact on the benthic marine ecosystem, since they act as ecosystem engineers (Coleman and Williams, 2002) enhancing the complexity of the substratum available to other organisms. Bath sponge and red coral populations are exhibiting a continuously declining trend reaching local extinction in several areas, which demands urgent monitoring and conservation interventions.

One of the best known examples of fish stock collapse is the case of Atlantic northwest cod fishery. This fishery, which existed for more than half of a millennium and shaped the coastal communities of the eastern Canadian cost, was stopped by the Canadian Government in 1992. The Atlantic northwest cod fishery was, for centuries, based on fishing gear used on restricted fishing grounds. Thus, catches were limited, allowing normal reproduction of the cod. From the mid 20th century cod fishery started to be more industrialized in terms of using new technology: dimensions of trawls, and consequently its catchability, were increased; more powerful and bigger trawlers, equipped with radars, sonders and sonars, were used. Use of new technology expanded old fishing grounds, especially to deeper areas, while CPUE, measured by a time of towing and area covered was increased enormously. Huge increase of catches, which during 1970's peaked to 810,000 tons, resulted in partial collapse of the northwest cod fishery. Although the fishery was supervised and managed, the exact state of the cod stock was not recognized at that time as management measures were set, based on defective calculations of maximum sustainable yield. Fishing continued, as the government, responding to pressure from the fishing industry, failed to intervene. An additional problem, not taken into account, was ecological: increase of catches of cod was followed by a huge increase of bycatch, consising of non-commercial, but ecologically very important fish. The collapse was catastrophic: Atlantic northwest cod stock fell to 1% of earlier biomass level and Canadian government declared a complete moratorium on the cod fishery. More than 40,000 workers from the fishing industry became unemployed and the cod stock has still not recovered.

Due to a lack of management interest for chondrichthyan species, and although these species are much more vulnerable to overfishing (see Soldo, this volume), well-documented cases of chondrichthyan stocks' collapses are rare. Of those, the case of the porbeagle shark fishery – *Lamna nasus* – is perhaps the best known. In the Northeast Atlantic porbeagle has been fished by the fleets of many European countries. The fishery began when Norway started targeting porbeagle in the 1930s using long lines. Fishery reopened after the Second World War and catches reached a peak of 6,000t in 1947. Although porbeagle was a target species, there has never been any restriction on fishing effort. From 1953 to 1960 the fishery collapsed and resulted in the redirection of fishing effort by Norwegian and Danish long line shark fishing vessels into the Northwest Atlantic. That fishery was only sustained for six years before collapsing in the 1960s. In the Northeast Atlantic current biomass and numbers are showing a decline of 94% and 93%, respectively, while in the Mediterranean Sea, the porbeagle is on the verge of regional extinction, with a calculated population decline of over 99,99% since the 1950s.

Prey depletion *vs* direct targeting

Prey depletion may lead to nutritional stresses for marine vertebrates. Trites and Donnelly (2003) described how marine mammals may respond to systematic lack of food, providing evidence of e.g. reduced birth rates and body size and increased newborn and juvenile mortality. Changes in the behavior have also been described, with animals performing longer feeding dives, together with physiological alterations. Prey depletion may cause a reduction in reproductive rates and this may represent one of the principal factors causing population decline in marine mammals. However, the decline of a population may be caused by a series of effects (see Panigada and Pierantonio, this volume), acting in synergy, and singling out each cause may prove rather difficult.

Intensive and poorly regulated fishing efforts in the Mediterranean Sea (CIESM, 2000; FAO, 2000) may lead to ecological extinctions, caused by the dramatic impact that overfishing has on stocks (e.g. Pauly and Palomares, 2005; Stergiou and Koulouris, 2000) and ecosystems (Jackson *et al.*, 2001). Prey depletion, caused by overfishing, is considered as one of the principal causes for the decline of coastal odontocete species, such as the short-beaked common dolphin (*Delphinus delphis*) (Bearzi *et al.*, 2003; Panigada and Pierantonio, this volume).

Alien species and extinctions

To date no introduced species is known to have caused the extinction of another species in the sea. As noted in this Monograph, however, the record of extinctions is so poorly known that it is risky to assume that non-indigenous species have not led to global extinctions, especially given the vast number of invasions in regions such as the Mediterranean Sea (over 600 species! CIESM, 2001/2002 ; Galil, 2012) and San Francisco Bay (Cohen and Carlton, 1995). This said, many hundreds of species of non-indigenous protists, invertebrates, algae, and fish have caused the severe decline of many native species (reviewed in part in Rilov and Crooks, 2009), such that celebrating the lack of evidence of global extinction at the hands of invasions is of little comfort. Chapman *et al.* (2012) have detailed an extraordinary example of the arrival of a non-native parasite that has rendered a large marine benthic thalassinid extinct in many bays along the Pacific coast of North America in the past 20 years. While this decapod is not globally extinct, their work serves as a potential harbinger of the full-court press of invasions now underway around the world, and as a model for what may have occurred, unnoticed, in the past.

Minimum viable population size

The mimimum viable population size is the number of individuals under which the population is supposed to become extinct in the wild. It is often defined as the population size necessary to ensure between 90 and 95 percent probability of survival between 100 to 1,000 years. It depends on numerous factors such as the reproduction system of the species (for instance consanguinity is increased for smaller populations), the ecology of the species and the environment variability, and the past history (when a population or a species survived severe past bottlenecks, the consequent inbreeding has more chances to survive in future since it purged its deleterious alleles). This is very difficult to estimate, and requires computer simulations based on demographic and environmental data parameters which need to be obtained by field studies. Most of these influential factors will affect genetic diversity. Consequently population genetics provides very powerful (and indirect) tools to estimate effective sizes of populations and species (see Chenuil, this volume).

3.2 What do we need to build reliable models and scenarios?

Metapopulation theory – both from a population genetics and ecological dynamics point of view – is rich in predictions and scenarios. Yet most predictions are largely focused on one level of organization (i.e., genetics or ecology) and remain to be tested (Lande, 1988; Hanski, 2011). This is unfortunate because we are witnessing an explosion of better and more accurate models, high-resolution data, and increasing computer power and storage but all of them remain highly independent in most scientific disciplines (Jones *et al.*, 2006). Thus, common sense suggests that the first thing we need for building reliable models is to join efforts, combine a suite of realistic scenarios with different levels of complexity, high-resolution data and quantitative methods to compare models, and infer the processes that may help us to anticipate species extinction or diversity loss in specific features of natural metapopulations (Beaumont, 2010).

Merging realistic models, high-resolution data and quantitative methods is challenging but it can have useful consequences to train our intuition about extinction processes. For example, results coming from theory suggest that demographic thresholds – critical population values below which the population goes extinct – are particularly relevant to anticipate extinctions (Nee, 1994). These thresholds – highly related to the minimum viable population size (see Chenuil, this volume) – are normally derived after different types of disturbances that reduce the fraction of available patches in a metapopulation context. It has been observed that these thresholds may change with the level of spatial resolution, the complexity of the food web, and the effect of environmental variability acting on networks of patches (Ovaskainen *et al.*, 2002). Changes in the thresholds – as in the minimum viable population size – may also be a function of the shape or the topology of the populations in the spatial landscape, or the life-history traits and these and additional factors make predictions to anticipate an extinction extremely difficult (Hanski and Ovaskainen, 2000).

Currently, the idea of a threshold in metapopulations is quite a general concept but the conditions under which this may occur seem rather context-dependent and taxon-specific. Which highlights the importance of connecting informed theory, using empirical estimations from data across disciplines and taxa. In this regard, concepts like the threshold in a population is helpful to distinguish linear from nonlinear processes or the speed of a population to go extinct.

The vulnerability of a species to extinction is determined by its degree of exposure to extrinsic threats, such as fishing, habitat destruction or climate change, and its intrinsic sensitivity to the threatening process. The intrinsic sensitivity of a species to external threats is determined by the species characteristics, such as life history and ecology, which underlie the productivity of the species and its capacity to recover from known threats. The presumed resilience of marine species to become extinct compared with terrestrial species in contemporary times has been questioned. Given the current exceedingly high extinction rates of species, more than ever there is an increasing need to understand which biological and ecological factors are more likely to determine which species will be able to adapt to current threats and which will go extinct. Moreover, the vulnerabilities of species to extinction are known to vary across marine taxa and across different types of threat, yet the intrinsic taxonomic and ecological correlates of extinction risk remain poorly understood across marine taxa and across different types of threat.

Life history theory suggests that species with ‘slow’ life histories characterized by large longevities, slow growth, late maturation and slow fecundities, should be at greater risk of extinction than species with “fast” life histories characterized with the opposite suite of traits. While there are some empirical studies in marine mammals and fishes testing this hypothesis, empirical testing of this hypothesis lags for the majority of the marine invertebrate groups. The most useful biological predictor of extinction risk in marine fishes is large body size and second in importance, age at maturity. Maximum body size is the most reliable correlate of marine fish species vulnerability to fishing, suggesting that it might be the most reliable predictor of species declines, recoveries and threat status in marine fishes. Age at maturity is the most consistent and reliable biological correlate of species intrinsic sensitivity, suggesting that age at maturity might be the most reliable predictor of marine fish species maximum per-capita growth rates (for details see Juan-Jordá *et al.*, this volume). In marine mammals, larger body mass at weaning, fewer births per year, smaller geographical range sizes, small social groups and the taxonomic group have been identified as the most useful predictors of extinction risk globally. In contrast, the biological and ecological correlates of extinction risk in marine invertebrates are poorly known. More worrying, current risk assessments or the risk status for the majority of invertebrate groups (e.g. echinoids, bivalves, etc.) are lacking or are very uncertain. For invertebrate groups, we rely on the knowledge of the extinction rates in the fossil record, i.e., what paleontologists have identified as the most important biological and ecological factor of extinction risk in the fossil record.

Overexploitation and habitat destruction have been identified as major causes of local and global marine extinctions in the recent and current history. Over the coming century, marine species will be faced with additional threats derived from changes in ocean temperature and changes in ocean chemistry which might interact and intensify the effects of overexploitation and habitat destruction. To date the majority of empirical studies have focused on identifying what life history and ecological traits of species are most useful to predict extinction risk. However, under the effect of current changes in ocean temperature and ocean chemistry, there is an urgent need to undertake comparative studies across taxa to identify what physiological characteristics of the species, such as their thermal tolerance limits and CO_2 tolerance limits, are determinant to predict their capacity to acclimatize and adapt to different scenarios of ocean warming and ocean acidification and thus determine what species might be able to adapt and which species might go extinct.

Genetic diversity, bottlenecks, genetic drift, founder effects. Extinction or adaptation (acclimatation).

Adaptation corresponds to the increase in frequency of genes providing an increased survival and reproduction under prevailing environmental conditions. In the absence of genetic diversity adaptation cannot occur. Furthermore when genetic diversity is low, homozygous genotypes become more frequent including for deleterious recessive alelles (inbreeding depression). Thus the genetic diversity of natural populations, which can be assessed easily and non-invasively, with molecular markers (Chenuil, 2006), can be used as a proxy to vulnerability, to which it is inversely correlated.

3.3 Genetic warning signals (loss of genes)

When monitoring a population via mere counting of individuals observed in the field, a loss of genetic diversity, thus an increase in vulnerability can be overlooked, because populations can recover after a perturbation although their adaptation potential decreases after each perturbation (Chenuil, this volume).

Frequency of mass mortalities, anoxic crisis

Besides harvesting pressure, mortality from disease is an important ongoing threat for marine populations and can be evaluated as a warning signal of potential local extinction. Several severe incidents have been reported during the past decades (Webster, 2007; Garrabou *et al.*, 2009), affecting mostly sessile invertebrates, such as bath sponges and Anthozoans in the Mediterranean Sea. Mass mortality events have been associated to environmental temperature anomalies that promote stress and consequently chemical and microbial shifts in the affected organisms (Webster *et al.*, 2008; Lejeusne *et al.*, 2010). Thus, they are expected to be more intense and recurring within a reportedly increasing warming trend (Coma *et al.*, 2009). Monitoring disease incidents, especially in the most sensitive areas, e.g. the southeastern Mediterranean, is an urgent priority.

3.4 From local to global extinction

Along with other traits that can cause a higher extinction risk, a geographical range size of certain species is one of the most important. It can be presumed that large and abundant populations with global distribution will not be significantly influenced by local or regional extinctions, but what about a species with small populations and geographically restricted distribution, such as marine mammals and chondrichthyan fish (see Panigada and Pierantonio; Soldo in this volume)? Evidently, the importance of a broad distribution in permitting a large population size, or as a buffer against habitat loss or overfishing, is such that it transcends biological differences among taxonomic groups, as well as differences in the threatening processes among regions (Cardillo *et al.*, 2008). On the other hand, patchy populations (i.e. those with high amounts of dispersal among local populations) are most likely to exhibit an increase in synchrony following extinction.

Numerous species in the wild can be modeled as metapopulations, which are a set of local populations that may undergo local extinction, and that exchange migrants. Population genetics again allows estimating connectivity among demes (local populations), an important parameter related to the risk of global extinction. The risk of local extinction can in some cases be estimated by genetic diversity, but if environmental stochasticity is high and demes small, genetic diversity is of poor use.

4. Management issues (and recommendations)

MPAs

Marine Protected Areas (MPAs) have been used as a measure for the protection of endangered species or populations (see Voultsiadou *et al.*, this volume), or of sensitive ecosystems. Additionally, MPAs can contribute to the conservation of representative habitats which support rich diversity (e.g. Mediterranean coralligenous assemblages and *Posidonia* meadows), nursery grounds and Essential Fish Habitats, as well as undisturbed pristine sites. The latter can recover from or adapt more easily to natural and anthropogenic phenomena, such as the temperature rise, and can be used as reference sites for monitoring relevant unprotected areas. MPAs can also provide spillover effects to the surrounding areas (PISCO, 2011).

In 2010 5,800 MPAs existed globally, covering 1,2% of the ocean, while only 0,1% encompass fully protected no-take Marine Reserves (PISCO, 2011). A major impediment to marine conservation is the ineffective management and surveillance of MPAs: a number of cases are just ‘paper parks’, where no management measures have been implemented (Abdulla *et al.*, 2008). The critical need for the establishment of networks of Marine Reserves, high seas MPAs, and ‘Marine Peace Parks’ globally has been underlined by scientists (Coll *et al.*, 2012), scientific commissions (CIESM, 2011), NGOs (Greenpeace, 2006; OCEANA, 2011), and Conventions (see Giakoumi *et al.*, 2012 for an analytical listing). The 2003 IUCN World Parks Congress goal for protecting 20-30% of the world's oceans within representative Networks of MPAs by 2012 has been largely ignored and the Convention on Biological Diversity Meeting in Nagoya (2010) set the target to protect 10% of each coastal and marine ecoregion by 2020.

Fisheries management (no take areas, nursery areas, spawning areas, quotas)
Multiple management tools exist to meet combined fisheries and conservation objectives and reach consensus towards sustainable use of marine resources. Quota restrictions, gear modifications, temporal and spatial area closures, no take areas, community management, creation of economic incentives are all examples of traditional management tools that work towards restoring depleted populations, ultimately protecting them from local or global extinctions. Experience has shown that combining diverse management actions can lead to successful management of marine resources, keeping in mind that the best combination of management actions depends on the resource and on the local context.

Large shark monitoring in the Adriatic started in late 1990s by collecting the data from marine police, harbor offices and fishermen. Later, by advertising the monitoring in marine journals and other media, the monitoring was enriched by data compiled by the broader interested public. Currently, it constantly provides data not only on large sharks, which remain the main goal of the monitoring, but also on other marine organisms, especially rare and new species for the Adriatic.

Remedial actions

Better use of fisheries statistics (data*)*
Collection of scientific data has a long history. Nowadays most of the data are stored electronically and can be easily available thru web-based datasets such as the Global Biodiversity Information Facility [GBIF, www.gbif.org]. Until recently most of the scientific data were stored in paper format, in local libraries, limiting their dissemination and accessibility. Given the increasing rates of loss in biodiversity and extinction risk globally, it is essential to design strategies to digitally recover historical datasets, particularly the recovery of long-term and large scale historical surveys. Historical data can provide valuable information to construct baselines of species distribution, abundance and biodiversity, which is critical to monitor the extinction rate of species. We recommend and encourage any efforts to recover and restore historical data sets and facilitate their accessibility. Successful projects have shown that the cost of recovering data is a small percentage of the initial project costs. In addition, there have been numerous global strategies to construct global datasets such as the GBIF to encourage free and open access to valuable scientific data. We believe that scientific data should always be easily available and accessible and that a standard practice of any scientific project should be to ensure that no data is lost to future generation of scientists.

Issue proper legislation and enforce it (no paper parks)
Marine Protected Areas (MPAs) have been set up to protect vulnerable species and ecosystems, to conserve biodiversity and minimize extinction risk, to re-establish ecosystem integrity, to segregate uses to avoid user conflicts and to enhance the productivity of fish and marine invertebrate populations around a reserve (Pauly *et al.*, 2002; Hooker and Gerber, 2004).

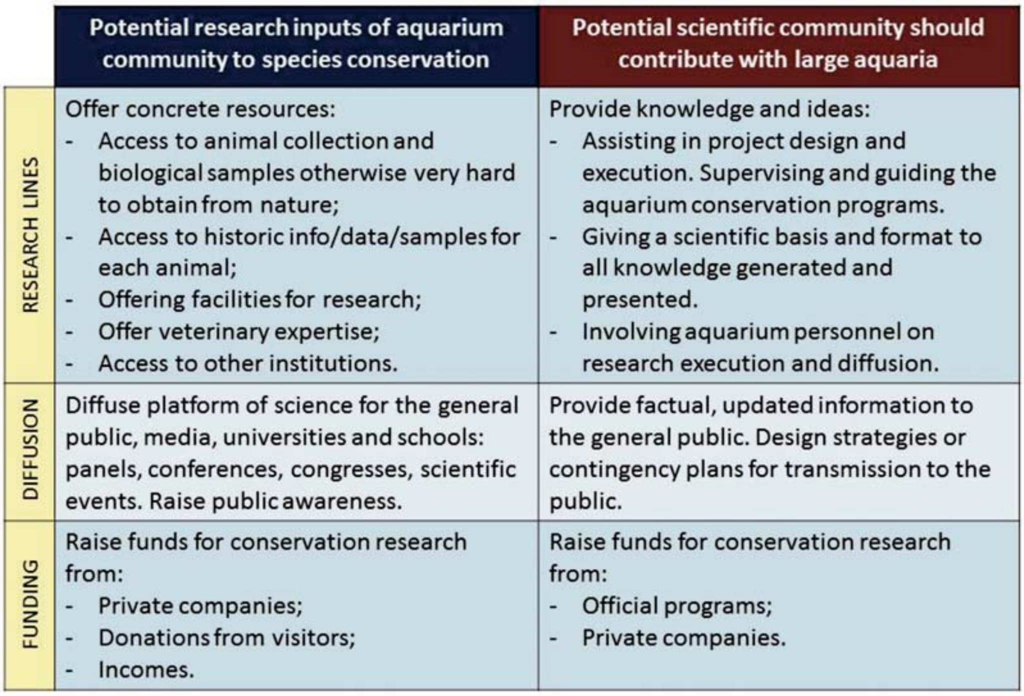
One of the crucial feature making a Marine Protected Area efficient is the establishment, maintenance and economical support of a proper management body. Without appropriate management plans, coupled with enforcement and compliance efforts to ensure that rules are respected and measures are correctly implemented, the risk that the MPA will be perceived only as a "paper park" is more than concrete (Notarbartolo di Sciara, 2008; Reeves, 2000).

Systematic monitoring programs, long-term goals, enforcement policy, public awareness efforts are among the tasks to include in a proper and effective management plan; these objectives should be assessed at regular intervals, to make sure the institutional aims of the Marine Protected Area are addressed and achieved.

Strengthen *ex situ* conservation
As shown in Box 2, much remains to be done to enhance useful synergies between the research community and large public aquaria. While these offer an unequalled showcase for displaying

recent scientific findings to a large audience, they also allow easy access to the animals for non-invasive research, for the study of aging, behaviour, lymphocytes, etc.

Box 2. The potential role of public aquaria for *ex situ* conservation by Daniel Garcia Parraga



	Potential research inputs of aquarium community to species conservation	Potential scientific community should contribute with large aquaria
RESEARCH LINES	Offer concrete resources: - Access to animal collection and biological samples otherwise very hard to obtain from nature; - Access to historic info/data/samples for each animal; - Offering facilities for research; - Offer veterinary expertise; - Access to other institutions.	Provide knowledge and ideas: - Assisting in project design and execution. Supervising and guiding the aquarium conservation programs. - Giving a scientific basis and format to all knowledge generated and presented. - Involving aquarium personnel on research execution and diffusion.
DIFFUSION	Diffuse platform of science for the general public, media, universities and schools: panels, conferences, congresses, scientific events. Raise public awareness.	Provide factual, updated information to the general public. Design strategies or contingency plans for transmission to the public.
FUNDING	Raise funds for conservation research from: - Private companies; - Donations from visitors; - Incomes.	Raise funds for conservation research from: - Official programs; - Private companies.

Some success stories

Marine turtles

The present status of the Mediterranean population of the loggerhead marine turtle *Caretta caretta*, an endangered species under strict protection (e.g. Barcelona and Bern Conventions, CITES), can serve as an example of effective monitoring and conservation efforts. Extensive research, including beach monitoring, tagging, and public awareness for more than 20 years in the main Mediterranean nesting areas (i.e. the western coast of Greece and Cyprus), has been carried out mostly by environmental organizations (Margaritoulis, 2005). In spite of difficulties due to ineffective enforcement of the legislation and incidental capture of turtles in fishing gear, encouraging trends of populations recovery have been observed in areas where conservation measures are applied (for details see Voultsiadou *et al.,* this volume). Stabilization of population numbers and increase of annual birth rate have been also recorded for the monk seal *Monachus monachus* in the Northern Sporades, Aegean Sea, since monitoring efforts started in the area (see Dendrinos *et al.*, 2007).

Sharks in Croatia

Chondrichthyans, especially sharks, have suffered huge declines in the Adriatic, as well as in whole Mediterranean area. In the absence of usually required stock assessment data, chondrichthyans were simply not managed. Now, Croatia has chosen to apply the precautionary approach to chondrichthyan management, based on existing available data (see Soldo, this volume). As a result, 23 chondrichthyan species (16 of them large sharks, mainly highly migratory species) have been granted strict protected status by Croatia in past five years, the highest level of protection in the country.

Rebuilding stocks of East Atlantic and Mediterranean bluefin tuna?

The overexploitation of East Atlantic and Mediterranean bluefin tuna is well documented, reflecting many problems found in the world fisheries, i.e. severe overexploitation driven by high market value, an open access in international waters where in the absence of control, regulations are easy to ignore. Recent indications of improvement in Atlantic bluefin tuna stock status (Porch and Fromentin, 2013) due to the imposition of strict fishery regulations, following intense mediatic pressure by concerned NGOs, illustrates that despite many sources of uncertainty in the projections of future trends, the management of a heavily exploited fish stock can still show hopes for recovery when there is a strong political will.

Marine extinctions - patterns and processes

Executive Summary[1]

This synthesis, sketched during the course of the meeting, was developed in the following months on the basis of further inputs received by the participants, under the coordination of Ferdinando Boero, James Carlton and Frédéric Briand. The latter reviewed and edited the entire volume, whose physical production was carried out by Valérie Gollino.

1. Introduction

The study of extinction in the sea is fraught with challenges. On the one hand species long thought extinct are re-discovered or otherwise "resurrected" on a regular basis (Keith and Burgman, 2004; Scheffers *et al.*, 2011). On the other hand, it seems probable that many species believed to still exist in our oceans may have long since gone extinct. Further, a robust understanding of the processes that may be currently driving species to, and over, the extinction cliff, often remains elusive, especially for those species where obtaining rigorous population and distribution estimates is expensive, arduous and problematic.

To cast a light on the current processes and extent of marine extinctions, CIESM invited a selected group of 16 specialists from various disciplines – ranging from marine biology, community dynamics, population genetics, paleontology, fishery science, historical ecology and evolution (see list at end of volume). They were welcomed in the futuristic Center of Arts and Sciences of Valencia by CIESM Director General, Dr Frédéric Briand, who started by thanking Dr Daniel Garcia Parraga for hosting this 45th Workshop of the Commission in 'his' splendid Oceanogràfic building, collaborator Dr Paula Moschella for her efforts in the logistic preparation, and last but not least Dr Ferdinando Boero, Chair of CIESM Committee on marine ecosystems, for suggesting this exciting, timely theme and for agreeing to act as discussion moderator/ stimulator.

In his opening remarks, Frédéric Briand focused on a number of issues and open questions which the four-day exploratory meeting would explore in earnest, such as the proximate / ultimate causes of extinction, the spatio-temporal scale of the process, the relevance or not of rarity, the available evidence from past extinction events, the tools and models available to assess the current rates of extinction, the risks of a sixth forthcoming wave of extinction, and appropriate conservation measures to reduce man's acceleration of the process. Ferdinando Boero followed, highlighting the difficulty of securing reliable, quantitative data on a scientific question so elusive as biodiversity changes in the vast marine realm, before inviting participants to present their paper.

Red *vs* black lists

Species particularly vulnerable to human impacts raise most concern about mass extinction. A great deal indeed of recent published works has addressed the potential for habitat destruction,

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[1] to be cited as:
Boero F., Carlton J., Briand F., Kiessling W., Chenuil A., Voultsiadou E., Twitchett, R., Soldo A., Panigada S., Juan-Jorda M.J., Melian C.J., Cury P. and P. Moschella. 2013. Executive Summary pp. 5 - 19 *in* CIESM Workshop Monograph n° 45 [F. Briand, ed.] Marine extinctions - patterns and processes, 188 p., CIESM Publisher, Monaco.

water quality degradation, overfishing, climate change, and other processes to push species to the brink (Pew Oceans Commission, 2003). While there are enduring, long-term challenges in determining the threatened, endangered, and extinct status of terrestrial and freshwater species (Scheffers *et al.*, 2011), these challenges are vastly more exacerbated in the world's oceans.

Species lists

Naming species is probably the first form of culture, and it is even written in the Genesis that "the Creator brought animals to the first human to see what name he would have given to them". The task of naming species is still unfinished. Estimates say that about two million species have been named, and that there are almost six or more millions that are still unnamed. Some scientists even estimated how many of these unknown species are becoming extinct before we are even aware of their existence. Strange enough, it is presumed that unknown species are becoming extinct, while there is little proof that the known ones are really extinct!

The inventory of the natural capital

Producing a rigorous catalogue of threatened, endangered, or extinct species is a challenge in the absence of detailed knowledge of regional marine biota. Few such thorough inventories exist, and *no inventories* are known to us that accurately reflect the current knowledge of systematics, distribution, biology (including life cycles), and ecology (such as the place in a trophic network) of all marine species within a region – admittedly a daunting task. Checklists alone do not reveal the population status of the vast majority of species or when they were last seen. For European seas, there is the European Register of Marine Species http://www.marbef.org/data/erms.php, for example, and, broader still, the Ocean Biogeographic Information System (http://www.iobis.org/). For most species on these lists, non-specialists would be surprised to learn that we know little more than their morphology and have only a coarse-grained view of their distribution. If, and where, populations have declined or disappeared for, literally, hundreds of thousands of marine species, is simply not known, a reality which may be obscured by the apparent existence of extensive "data bases" on the world's marine biodiversity.

Biodiversity increase: real or artefact?

The first species lists contained just a small fraction of biodiversity. Species numbers have been growing as long as new species were described or newly recorded for a given place. So, the number of species is in continuous increase. This is happening both globally and locally. The arrival of many non indigenous species in the Mediterranean, for instance, is leading to a marked increase in the species numbers that are making up the biodiversity of the basin. Some of these species are labelled as "worst aliens" and their presence is considered as negative, although their very presence represents an increase in species numbers. One of the features of these "worst aliens" is their negative impact on native species that should be pushed on the verge of extinction by the newcomers. The newcomers, however, often arrive and become established because of physical conditions changes (e.g. due to global warming) to the detriment of native species that are not tolerant enough to withstand the new situation. Under such circumstances, pre-adapted species to the new conditions might take the place of the original, now "maladapted ones". In this case the substitution of the native species by the non native ones merely reflets changing environmental conditions. Whatever the cause, it is anyway important to remain aware of possible extinctions, if only to demonstrate that we are really going through a biodiversity crisis.

This enterprise is possible, and our workshop aimed at showing its feasibility while taking the Mediterranean Sea as a paradigm for the world ocean, and by tackling the problem of extinction both from a paleontological and a neontological point of view, putting in contact fields of expertise that rarely do interact.

Marine *vs* terrestrial extinctions

Concern about extinction is widespread and leaves almost no room for doubt. But if the question is posed about naming extinct species, the first ones that come to mind are usually the dodo and the great auk (not to mention dinosaurs), while names do not come to mind when asked to list extinct marine species. Unfortunately such lists do exist, even though they do not contain "charismatic" species, i.e. the popular animals that are familiar to the public at large. The bias towards these species is, however, not justified when the problem of extinction is tackled from a scientific point of view.

The number of marine species is much lower than that of terrestrial ones, even if the diversity of body plans (e.g. phyla) is much higher in the sea than on land. The insects, making up almost half of known species, are paradigmatic in this respect, while having relatively few marine representatives. The phyla of the interstitial fauna, for example, are almost exclusively marine and, as such, constitute a great contribution to the diversity of life at higher levels of organization. The lower species diversity of marine life, if compared to terrestrial one, is often explained by the high connectivity characterizing marine environments, with lower chances of population segregation, leading to allopatric speciation. The barriers separating terrestrial habitats have no comparison in the marine realm. Local extinction is of course possible, but the wider distribution of marine species is conducive to the survival of marine forms in other places.

Marine extinctions, for these reasons are far more difficult to establish than those affecting terrestrial groups.

Peculiarities of the Mediterranean Sea

After the Messinian crisis, about six million years ago, the Mediterranean biota became established by recolonisation through the strait of Gibraltar. In different geological periods, species with different features entered the basin. Species of cold affinity entered during the cold periods, whereas species of warm affinity entered during warmer periods. Large seasonal fluctuations in temperature allowed for the survival of both contingents, if their life cycles and histories involved periods of activity (during the favourable season) and periods of rest (during the unfavourable one). At present, the Mediterranean biota in surface waters, does have a tropical nature in the summer and a temperate nature in the winter. The Mediterranean is also characterized by a high rate of endemism. The entrance of species is rather easy, near the surface, due to the presence of a surface current entering from the Atlantic. The outgoing current is deeper and surface species might find it difficult to get out, while having good chances of getting in. Under these circumstances, the Mediterranean behaves as a trap that lets species in but prevents them from getting out. This situation is conducive to the high rates of endemism that characterize the Mediterranean Sea biota. These species are liable of extinction due to environmental change and, since they are not present elsewhere, local extinction might be equal to final extinction.

The Mediterranean Sea, thus, is a paradigmatic area to study the impact of environmental change on species survival. This advantage, however, is to be considered with care. The history of marine taxonomy views the Mediterranean as a very important centre, due to the concentration of taxonomic efforts both in the past and in the present. New species, described from the Mediterranean, and thus having this sea as their type locality, might be newcomers that were unknown in their original area of distribution, and were 'discovered' by local taxonomists upon their arrival, just as the recently described jellyfish species *Marivagia stellata* and *Rhopilema nomadica*. These species most probably entered in the Mediterranean through the Suez Canal and were non-described in their native area due to lack of taxonomic expertise, soon to be detected once they reached an area "patrolled" by active taxonomists. For taxonomy, the Mediterranean is the type locality of these species, but this does not reflect their actual distribution.

Rarity

Most species are poorly known simply because they are inconspicuous and the perception of their existence is based on just a few records, sometimes even just one: the original description. These species are labelled as rare, while this may be simply due to insufficient sampling or lack of expertise. The processes leading to extinction imply a decrease in number, and it seems logical that rare species are in a risky situation, due to the scarcity of their populations. But, since most species are rare, and just a few are abundant at a given period in the history of a biota, rarity is not a risky condition per se. The alternation of periods of abundance and rarity, in fact, might be the main motor of species diversification, through flush and crash phenomena that represent sudden pressures of natural selection on species populations. During the periods of flush, species are represented by a multitude of individuals, but these cannot persist for long, due to the overexploitation they exert on the very resources that should sustain them. The collapse of these populations (the crash) removes maladapted individuals and enhances the surviving ones that survived just due to genetic makeups conducive to ecological success. In light of these considerations, rarity is not a sufficient precondition to extinction.

2. Assessing extinction – what can we learn from paleontology?

Patterns seen in the past are becoming increasingly important for predicting the future. This is especially true for marine extinctions, for which the fossil record provides invaluable data on multiple temporal and spatial scales while evidence for modern extinctions comes largely from terrestrial environments. A major limitation of using the fossil record in a straightforward way is its incompleteness and the vast time scales on which global patterns are usually being assessed. The incompleteness and many other issues related to sampling can be overcome by applying rigorous methods of sampling standardization on fossil occurrences combined with appropriate counting methods (Alroy *et al.*, 2001; Alroy, 2008; Alroy *et al.*, 2008). The vast time scales can be used as an advantage because we can observe the fate of fossil lineages from their origin until final extinction. Paleontologists can thus assess extinction rates and their selectivity directly, without relying on inferences of extinction risk as used in the IUCN Red List. In addition, deep time patterns inform us about the natural variability of species abundances (if indirectly) and geographic ranges. In linking taxonomic and ecological information paleontologists can thus evaluate a number of key questions such as:

2.1 Which traits render a species prone to extinction?

The suite of factors that paleontologists have identified is very similar to that offered by neontologists (McKinney, 1997; Kiessling, this volume). Examples are specialization, mode of life, mode of reproduction, and abundance traits. Most of these traits have long been identified as important determinants of extinction risk in a qualitative way, but more recent studies have helped to assess their relative importance. For example, while body size, abundance and geographic range have all been linked to extinction risk, geographic range is the only one of these factors that directly controls extinction risk (Harnik, 2011). The other two factors are only indirectly linked to extinction risk.

As clear from the IUCN Red List, rarity does not necessarily mean enhanced extinction risk because rarity is a natural state for many species (Mace *et al.*, 2008). A recent study using the entire marine fossil record confirmed that among the various forms of rarity low population size has the weakest effect on extinction risk, whereas restricted geographic range is the most important driver followed by narrow habitat breadth (Harnik *et al.*, 2012a,b). Abundance has a U-shaped relationship with extinction risk in fossil marine bivalves. Very rare and very abundant taxa show elevated extinction rates, whereas extinction risk is minimized at intermediate abundances (Simpson and Harnik, 2009). The common notion of specialist species being at greater risk of extinction than generalists holds true, but there are issues with defining what a specialist really is. The fossil record shows that habitat specialists are at a greater risk of extinction but also have greater chances of speciation (Kiessling and Aberhan, 2007a; Colles *et al.*, 2009).

Several additional traits that increase extinction risk in marine animals have been identified, based on fossil invertebrates. An important trait is low metabolic rate and the formation of heavy skeletons, which increased extinction risk during times of massive changes in ocean chemistry such as ocean acidification (Kiessling and Simpson, 2011; Knoll and Fisher, 2011). The general notion that marine animal species are less extinction-prone than terrestrial animal species is supported by the fossil record (McKinney, 1998). However, this does not imply that marine species are less at risk today, because the fossil record also tells us that during mass extinctions marine taxa were hit as hard as terrestrial taxa (Benton, 1995).

2.2 What besides magnitude distinguishes background extinctions from a mass extinction?

Paleontologists have long emphasized the dichotomy between background extinctions and mass extinctions (Jablonski, 1986a). Mass extinctions are defined by extinction magnitudes that are significantly above background extinctions, which declined over the course of the Phanerozoic eon (the last 540 million years) (Kiessling, this volume). There is no arbitrary choice of a proportion of taxa becoming extinct but experience shows that the traditional Big Five mass extinction of the Phanerozoic (Raup and Sepkoski, 1982) wiped out more than 40% of marine genera and probably more than 70% of marine species. Some rules that govern survival during normal times do not apply during global catastrophes. An important example is geographic range, which facilitates survival during background times but not during mass extinctions (Kiessling and Aberhan, 2007b; Payne and Finnegan, 2007). This is probably due to the global scope of environmental changes that lead to mass extinctions, whereas background extinctions were triggered by biotic interactions and regional environmental change. Other traits governing survival during background times may also become ineffectual during mass extinctions (Jablonski and Raup, 1995) but the selectivity of mass extinctions can be used efficiently to assess their specific causes (Smith and Jeffery, 1998; Kiessling *et al.*, 2007; Knoll *et al.*, 2007). The difference in selective regimes between background and mass extinctions has probably been overemphasized in the past. The question if we are already approaching a mass extinction event (Barnosky *et al.*, 2011) is still important to put the current biodiversity crisis in a geological context, but not crucial to assess extinction risk of extant species with the help of the fossil record.

2.3 What are the natural causes of extinction?

All ancient mass extinctions are associated with massive perturbations of the global carbon cycle and rapid climate change. The ultimate triggers of ancient mass extinctions range from slow processes such as plate tectonics to shock events such as meteorite impacts and are thus very different from the entirely anthropogenic driver today. However, the time scales involved in actually triggering marine extinctions were perhaps not as different as commonly assumed. It is more the failure to resolve the duration of ancient extinctions than factual evidence for prolonged crises that led to the notion of vastly different time scales involved in extinctions now and then. Probabilistic approaches rendered it likely that marine extinctions occurred in pulses, not only during mass extinctions but also during background intervals (Foote, 2005). Rapid climate change is a component of all mass extinctions although the causes and pace of climate change varied considerably. The massive release of greenhouse gases due to volcanism is seen as a crucial trigger of two out of three mass extinctions in the last 250 Myr and the most recent of these (the end-Cretaceous mass extinction) was probably caused by a meteorite impact (see Kiessling, this volume).

2.4 What is the natural variability of population sizes?

Defining natural baselines is among the central tasks of the emerging field of conservation paleobiology (Dietl and Flessa, 2011). What was natural in the coastal oceans (Jackson, 2001) is a key question for which paleo-ecological data can be especially useful. Studies from shallow time are useful to assess natural variations in population size. The purpose of previous studies was largely to monitor economically important or hazardous species over time scales beyond historical records (Walbran *et al.*, 1989; Valdés *et al.*, 2008), to assess changes in productivity (Kowalewski *et al.*, 2000) or to separate invasive from native species (van Leeuwen *et al.*, 2008). Fossil data can enhance our knowledge on the natural variability of population sizes and should thus be included in the assessments of extinction risk for recent species, especially in the marine realm, where knowledge is so poor compared with terrestrial records.

Box 1. Confidence in extinction.

How long must a species go unseen before it can safely be declared extinct? This is a difficult question, which cannot be answered with a simple number that is valid for all species. A conspicuous species that is regularly sighted will need less time to be declared extinct with confidence than an inconspicuous species that is only identified by specialists. Complete certainty on species extinction is virtually impossible to achieve as demonstrated by repeated sightings of presumably extinct species. In the most extreme case, the time span between last sighting and re-discovery can span millions of years as exemplified by the gap of presumed coelacanth extinction in the Late Cretaceous (ca. 80 myr) and the discovery of living *Latimeria* in the 1930s. The problem of when a species should be considered extinct has thus concerned both biologists and palaeontologists (Strauss and Sadler, 1989; Carlton *et al.*, 1999).

Paleontologists have developed tools to quantify the confidence with which a species can be considered extinct. Those models were first applied to stratigraphic sections (Strauss and Sadler, 1989) and later to global taxonomic ranges (Marshall, 1990; Marshall, 1994). Biologists have adopted and further developed these approaches. Current approaches on the temporal distribution of sighting records are rather complex and require advanced statistical knowledge (Solow and Roberts, 2003; Solow, 2005; Collen *et al.*, 2010).

We recommend using an adjusted version of Marshall's (1990) simple equation as a first approximation for poorly documented marine groups because this can be applied with ease by taxonomists and it does not require information about the temporal distribution of sightings.

The confidence (C) of the declaration of a species being extinct at a given time is calculated by

$C = 1 - (G/R + 1)^{-(H-1)}$

where

G = number of years since last sighting
R = years between first record (the date of first collection) and the last sighting
H = number of individual years in which there is a record

A species could be declared extinct if the confidence is 95% or greater. An 80% confidence should be be taken as a critical values warranting closer inspection.

This said, we caution that this formula is only applicable to larger well-known species for which it can be demonstrated that both the historical and modern-day record is thorough and rigorous. For most species, data relative to sightings are an artifact of a combination of sampling intensity (either spatially or temporally) with the ability of workers to identify a species. Many species in many community samples simply go unidentified because no taxonomists are available, and thus we have no ability to assess the continued presence, or presumptive absence, of a vast number of species. Thousands and thousands of marine species – especially protists, invertebrates, and smaller algae – have gone unreported for decades or centuries since their first descriptions, simply because no one has sought them out again. As pointed out by Boero (2011) how many inconspicuous species have probably gone in complete indifference? Current knowledge depends on whether anyone has actually sampled or identified these species over subsequent years. The modern-day record demonstrates that even large, once-abundant species (e.g. sharks, see Soldo, this volume) can simply disappear without notice, suggesting that documenting the disappearance of uncommon and smaller species is a fundamental challenge.

3. PREDICTING RISK OF EXTINCTION

3.1 Overexploitation

Over-extraction of marine resources, habitat destruction, water quality, climate change and invasive species are together threatening the marine biota and marine ecosystems. Due to rapid coastal urbanization and industrialization, point and non-point source land and urban runoff has rendered what were once natural, diverse estuaries, bays, and lagoons – but are now marinas, busy harbors, and industrial wastelands – nearly biologically depauperate. For many locations we have poor historical data on overfishing / overexploitation, except on hunting of marine species of megafauna. Many populations and species of marine mammals (see Panigada and Pierantonio, this volume), seabirds, and marine turtles are now at a fraction of their former pre-exploitation abundance levels and listed as threatened in the IUCN Red List (Dulvy *et al.*, 2009).

Marine fish and shellfish (including molluscs and crustacean) species have also experienced large reductions in abundance from former levels since medieval times (Hoffmann, 2005), with industrial-scale fisheries commencing in the late 19th and early 20th centuries. The Food and Agriculture Organization of the United Nations (FAO), in charge of collecting world fishery landings statistics and summarizing the status of global fisheries, calculated that in 2009 over 87% of the commercially important fish stocks were already either fully exploited, or overexploited (FAO, 2012). However, the FAO global status assessment covers only a small number of exploited fish resources, leaving out hundreds of species, and thousands of populations for which there are not official statistics, particularly excluding bycatch species and species exploited by artisanal and subsistence fisheries (Zeller and Pauly, 2007).

There have been also multiple attempts to quantify the impacts of fishing on several groups of data-rich species, commonly large predatory fishes, with the objective of providing a more accurate picture of their trajectories and reductions from known historical levels (historical baselines). Hutchings and Reynolds (2004) examined data of 230 marine fish populations in the North Atlantic and estimated a reduction of 83% in adult biomass from known historic levels. The adult biomass of scombrids species (tunas and mackerels) is estimated to have decreased globally on average by 60% since the 1950s, with temperate tuna exhibiting the largest declines in biomass (on average 80% reductions) (Juan-Jorda *et al.*, 2011). Similarly, large pelagic shark populations have declined by more than 75% in the Northwest Atlantic Ocean and over 90% in the Gulf of Mexico (Baum *et al.*, 2003; Baum and Myers, 2004).

Although these global or regional synthesis studies provide a more accurate picture of the biomass trajectories of commercially important fish populations, the reality is that biomass estimates and the current exploitation status for the large majority of fish species are still uncertain or unknown globally. We still rely on the FAO landings fish statistics, rather than population biomass estimates, to illustrate the impacts of fisheries on marine living resources within the last 50-60 years of industrialized fisheries. Global fisheries landings reveal that the average trophic level of the global catch has declined over time, suggesting that predatory fishes have been sequentially declining as fisheries started to also target middle and lower trophic fish species, an indication that both fishing down and through marine food-webs is occurring (Pauly *et al.*, 1998; Essington, 2006).

Long term trends of global fish landings also signal that fish resource are exhaustible. Since the 1980s, fish landing have leveled off (if China statistics are included) or have slowly decreased (if China statistics are excluded), suggesting that food webs are becoming simplified and that it is getting harder to extract fish from the oceans despite all the technological developments (Watson and Pauly, 2001; Pauly *et al.*, 2005). At the same time there is increasing evidence that jellyfish abundance is increasing worldwide (Brotz *et al.*, 2012), and that fishing – by removing the natural predators of jellyfish species – might be in part responsible for this trend (Purcell *et al.*, 2007). The impacts of reducing large amounts of biomass from the oceans and the indirect effects of overfishing on the structure and functioning of marine ecosystems are still poorly understood (Scheffer *et al.*, 2005). One of the best documented cases of cascading effects induced by overfishing is the Canadian cod collapse and its effects all the way down the foodweb (Frank *et al.*, 2005). There is growing evidence that changes at the top of the food chain can provoke sudden ecosystem changes, sometimes referred as regime shifts, and that such changes in ecological state may be irreversible once over some tipping points (Casini *et al.*, 2008).

Factors contributing to overfishing

Multiple factors have been identified as main drivers contributing to overfishing, thus jeopardizing the sustainable management of marine ecosystems and increasing the rates of extinction of marine species. The following drivers have been identified as the four largest contributors to overfishing: 1) fish subsides; 2) overcapacity in fisheries; 3) growing demand and price of marine products; and 4) illegal fishing (Pauly and Alder, 2005; Sumaila *et al.*, 2008; Pauly, 2009). Subsidies, in most cases facilitated by governments, are considered to be the most significant drivers of overfishing. Subsidies typically contribute to the development of bigger and more efficient fleets, increase fishing effort and the net profits of fishers, thus sustaining fishing fleets that otherwise would not be economically viable (Sumaila *et al.*, 2010). Second, the current fleet overcapacity is at least two and a half times greater than required to bring long-term catches at a sustainable rate (Pauly, 2009). Third, global human population growth connected with an increase in demand and price values of marine products are also contributing to overfishing. Some species can reach high prices in the international markets, creating incentives for overfishing. For example, in 2011 a single Pacific bluefin tuna was sold for more than 400,000$ in Tokyo market. Although the value of this particular fish does not represent the average sale value of bluefin tunas in the global markets, it clearly illustrates the inflated values reached by some fish species, which generate high pressures and incentives for overfishing. Fourth, illegal, unreported and unregulated (IUU) fisheries also fuel the problem of overfishing. It has been estimated that between $10bn and $23,5 bn (between 11 and 26 million tones) are lost annually worldwide due to current illegal and unreported fishing (Agnew *et al.*, 2009). Although there have been some attempts to halt and reduce IUU fisheries, control and surveillance of fisheries worldwide continue to be a challenge.

From collapse to extinction

Although there are numerous examples of marine populations and species that have suffered declines of 80-90% or more from pre-exploitation abundance and numerous examples of fish collapses precipitating closure of fisheries, it has been widely assumed (and still held) that marine species are less vulnerable to fishing exploitation and less prone to extinction than terrestrial species. This assumption arises in part from two reasons. First, few marine species (relative to terrestrial species) have been documented to have become globally extinct in the last century and those now extinct had relatively small ranges (Dulvy *et al.*, 2009). Second, the intrinsic biology of marine species, particularly the biology of teleost fish with large fecundities combined with their widespread distributions and high abundances, has led to the wrong assumption that marine fish species are more resilient to fishing impacts and therefore less vulnerable to extinction than other non-fish marine species or terrestrial species.

Recently these perceptions have been challenged and questioned by many (Hutchings, 2001; Sadovy, 2001; Dulvy *et al.*, 2003). Marine extinctions are now believed to be underestimated because of low detection abilities and the general lack of information of the status of the majority of marine species (Dulvy *et al.*, 2009; Carlton, this volume). There are many examples of local extinctions of marine species and the reporting of local marine extinction is increasing over time. Given that local extinctions are the first step towards global extinction, the importance of local extinctions cannot be underestimated. Large reductions of biomass to very low levels, triggered by overfishing and fragmented habitats caused by destructive fishing methods, are two factors likely to lead to numerous local extinctions, especially in species with the most intrinsic vulnerable life histories, such as the long-lived, slow growing and fragile species (Sadovy and Cheung, 2003). Moreover, the widely-held belief that large fecund fishes are more resilient to overexploitation lacks any scientific support. Instead, there is increasing agreement that highly fecund fishes (largely teleost) are not more resilient to overexploitation or extinctions than terrestrial mammals (Hutchings *et al.*, 2012). There is a need to focus on fragmented populations and populations with low abundance levels induced by fishing. At these stages, the loss of genetic diversity, decompensation (Allee effects) and inbreeding depression in fragmented and small populations might drive species to the brink of extinction (Briggs, 2010).

Besides fishes, several valued benthic invertebrates, such as bath sponges and corals have been subjected to harvesting for centuries by humans (for details see Voultsiadou *et al.,* this volume). The commercial value of such species commonly increases as they become less abundant and this, in turn, leads to even more intensive harvesting and poaching. Thus, they may not necessarily become economically extinct before their local or regional extinction, as is assumed for fish stocks (Dulvy *et al*., 2003). Moreover, the withdrawal of these organisms can have an increased impact on the benthic marine ecosystem, since they act as ecosystem engineers (Coleman and Williams, 2002) enhancing the complexity of the substratum available to other organisms. Bath sponge and red coral populations are exhibiting a continuously declining trend reaching local extinction in several areas, which demands urgent monitoring and conservation interventions.

One of the best known examples of fish stock collapse is the case of Atlantic northwest cod fishery. This fishery, which existed for more than half of a millennium and shaped the coastal communities of the eastern Canadian cost, was stopped by the Canadian Government in 1992. The Atlantic northwest cod fishery was, for centuries, based on fishing gear used on restricted fishing grounds. Thus, catches were limited, allowing normal reproduction of the cod. From the mid 20th century cod fishery started to be more industrialized in terms of using new technology: dimensions of trawls, and consequently its catchability, were increased; more powerful and bigger trawlers, equipped with radars, sonders and sonars, were used. Use of new technology expanded old fishing grounds, especially to deeper areas, while CPUE, measured by a time of towing and area covered was increased enormously. Huge increase of catches, which during 1970's peaked to 810,000 tons, resulted in partial collapse of the northwest cod fishery. Although the fishery was supervised and managed, the exact state of the cod stock was not recognized at that time as management measures were set, based on defective calculations of maximum sustainable yield. Fishing continued, as the government, responding to pressure from the fishing industry, failed to intervene. An additional problem, not taken into account, was ecological: increase of catches of cod was followed by a huge increase of bycatch, consising of non-commercial, but ecologically very important fish. The collapse was catastrophic: Atlantic northwest cod stock fell to 1% of earlier biomass level and Canadian government declared a complete moratorium on the cod fishery. More than 40,000 workers from the fishing industry became unemployed and the cod stock has still not recovered.

Due to a lack of management interest for chondrichthyan species, and although these species are much more vulnerable to overfishing (see Soldo, this volume), well-documented cases of chondrichthyan stocks' collapses are rare. Of those, the case of the porbeagle shark fishery – *Lamna nasus* – is perhaps the best known. In the Northeast Atlantic porbeagle has been fished by the fleets of many European countries. The fishery began when Norway started targeting porbeagle in the 1930s using long lines. Fishery reopened after the Second World War and catches reached a peak of 6,000t in 1947. Although porbeagle was a target species, there has never been any restriction on fishing effort. From 1953 to 1960 the fishery collapsed and resulted in the redirection of fishing effort by Norwegian and Danish long line shark fishing vessels into the Northwest Atlantic. That fishery was only sustained for six years before collapsing in the 1960s. In the Northeast Atlantic current biomass and numbers are showing a decline of 94% and 93%, respectively, while in the Mediterranean Sea, the porbeagle is on the verge of regional extinction, with a calculated population decline of over 99,99% since the 1950s.

Prey depletion *vs* direct targeting

Prey depletion may lead to nutritional stresses for marine vertebrates. Trites and Donnelly (2003) described how marine mammals may respond to systematic lack of food, providing evidence of e.g. reduced birth rates and body size and increased newborn and juvenile mortality. Changes in the behavior have also been described, with animals performing longer feeding dives, together with physiological alterations. Prey depletion may cause a reduction in reproductive rates and this may represent one of the principal factors causing population decline in marine mammals. However, the decline of a population may be caused by a series of effects (see Panigada and Pierantonio, this volume), acting in synergy, and singling out each cause may prove rather difficult.

Intensive and poorly regulated fishing efforts in the Mediterranean Sea (CIESM, 2000; FAO, 2000) may lead to ecological extinctions, caused by the dramatic impact that overfishing has on stocks (e.g. Pauly and Palomares, 2005; Stergiou and Koulouris, 2000) and ecosystems (Jackson *et al.*, 2001). Prey depletion, caused by overfishing, is considered as one of the principal causes for the decline of coastal odontocete species, such as the short-beaked common dolphin (*Delphinus delphis*) (Bearzi *et al.*, 2003; Panigada and Pierantonio, this volume).

Alien species and extinctions

To date no introduced species is known to have caused the extinction of another species in the sea. As noted in this Monograph, however, the record of extinctions is so poorly known that it is risky to assume that non-indigenous species have not led to global extinctions, especially given the vast number of invasions in regions such as the Mediterranean Sea (over 600 species! CIESM, 2001/2002 ; Galil, 2012) and San Francisco Bay (Cohen and Carlton, 1995). This said, many hundreds of species of non-indigenous protists, invertebrates, algae, and fish have caused the severe decline of many native species (reviewed in part in Rilov and Crooks, 2009), such that celebrating the lack of evidence of global extinction at the hands of invasions is of little comfort. Chapman *et al.* (2012) have detailed an extraordinary example of the arrival of a non-native parasite that has rendered a large marine benthic thalassinid extinct in many bays along the Pacific coast of North America in the past 20 years. While this decapod is not globally extinct, their work serves as a potential harbinger of the full-court press of invasions now underway around the world, and as a model for what may have occurred, unnoticed, in the past.

Minimum viable population size

The mimimum viable population size is the number of individuals under which the population is supposed to become extinct in the wild. It is often defined as the population size necessary to ensure between 90 and 95 percent probability of survival between 100 to 1,000 years. It depends on numerous factors such as the reproduction system of the species (for instance consanguinity is increased for smaller populations), the ecology of the species and the environment variability, and the past history (when a population or a species survived severe past bottlenecks, the consequent inbreeding has more chances to survive in future since it purged its deleterious alleles). This is very difficult to estimate, and requires computer simulations based on demographic and environmental data parameters which need to be obtained by field studies. Most of these influential factors will affect genetic diversity. Consequently population genetics provides very powerful (and indirect) tools to estimate effective sizes of populations and species (see Chenuil, this volume).

3.2 What do we need to build reliable models and scenarios?

Metapopulation theory – both from a population genetics and ecological dynamics point of view – is rich in predictions and scenarios. Yet most predictions are largely focused on one level of organization (i.e., genetics or ecology) and remain to be tested (Lande, 1988; Hanski, 2011). This is unfortunate because we are witnessing an explosion of better and more accurate models, high-resolution data, and increasing computer power and storage but all of them remain highly independent in most scientific disciplines (Jones *et al.*, 2006). Thus, common sense suggests that the first thing we need for building reliable models is to join efforts, combine a suite of realistic scenarios with different levels of complexity, high-resolution data and quantitative methods to compare models, and infer the processes that may help us to anticipate species extinction or diversity loss in specific features of natural metapopulations (Beaumont, 2010).

Merging realistic models, high-resolution data and quantitative methods is challenging but it can have useful consequences to train our intuition about extinction processes. For example, results coming from theory suggest that demographic thresholds – critical population values below which the population goes extinct – are particularly relevant to anticipate extinctions (Nee, 1994). These thresholds – highly related to the minimum viable population size (see Chenuil, this volume) – are normally derived after different types of disturbances that reduce the fraction of available patches in a metapopulation context. It has been observed that these thresholds may change with the level of spatial resolution, the complexity of the food web, and the effect of environmental variability acting on networks of patches (Ovaskainen *et al.*, 2002). Changes in the thresholds – as in the minimum viable population size – may also be a function of the shape or the topology of the populations in the spatial landscape, or the life-history traits and these and additional factors make predictions to anticipate an extinction extremely difficult (Hanski and Ovaskainen, 2000).

Currently, the idea of a threshold in metapopulations is quite a general concept but the conditions under which this may occur seem rather context-dependent and taxon-specific. Which highlights the importance of connecting informed theory, using empirical estimations from data across disciplines and taxa. In this regard, concepts like the threshold in a population is helpful to distinguish linear from nonlinear processes or the speed of a population to go extinct.

The vulnerability of a species to extinction is determined by its degree of exposure to extrinsic threats, such as fishing, habitat destruction or climate change, and its intrinsic sensitivity to the threatening process. The intrinsic sensitivity of a species to external threats is determined by the species characteristics, such as life history and ecology, which underlie the productivity of the species and its capacity to recover from known threats. The presumed resilience of marine species to become extinct compared with terrestrial species in contemporary times has been questioned. Given the current exceedingly high extinction rates of species, more than ever there is an increasing need to understand which biological and ecological factors are more likely to determine which species will be able to adapt to current threats and which will go extinct. Moreover, the vulnerabilities of species to extinction are known to vary across marine taxa and across different types of threat, yet the intrinsic taxonomic and ecological correlates of extinction risk remain poorly understood across marine taxa and across different types of threat.

Life history theory suggests that species with ‘slow’ life histories characterized by large longevities, slow growth, late maturation and slow fecundities, should be at greater risk of extinction than species with “fast” life histories characterized with the opposite suite of traits. While there are some empirical studies in marine mammals and fishes testing this hypothesis, empirical testing of this hypothesis lags for the majority of the marine invertebrate groups. The most useful biological predictor of extinction risk in marine fishes is large body size and second in importance, age at maturity. Maximum body size is the most reliable correlate of marine fish species vulnerability to fishing, suggesting that it might be the most reliable predictor of species declines, recoveries and threat status in marine fishes. Age at maturity is the most consistent and reliable biological correlate of species intrinsic sensitivity, suggesting that age at maturity might be the most reliable predictor of marine fish species maximum per-capita growth rates (for details see Juan-Jordá *et al.*, this volume). In marine mammals, larger body mass at weaning, fewer births per year, smaller geographical range sizes, small social groups and the taxonomic group have been identified as the most useful predictors of extinction risk globally. In contrast, the biological and ecological correlates of extinction risk in marine invertebrates are poorly known. More worrying, current risk assessments or the risk status for the majority of invertebrate groups (e.g. echinoids, bivalves, etc.) are lacking or are very uncertain. For invertebrate groups, we rely on the knowledge of the extinction rates in the fossil record, i.e., what paleontologists have identified as the most important biological and ecological factor of extinction risk in the fossil record.

Overexploitation and habitat destruction have been identified as major causes of local and global marine extinctions in the recent and current history. Over the coming century, marine species will be faced with additional threats derived from changes in ocean temperature and changes in ocean chemistry which might interact and intensify the effects of overexploitation and habitat destruction. To date the majority of empirical studies have focused on identifying what life history and ecological traits of species are most useful to predict extinction risk. However, under the effect of current changes in ocean temperature and ocean chemistry, there is an urgent need to undertake comparative studies across taxa to identify what physiological characteristics of the species, such as their thermal tolerance limits and CO_2 tolerance limits, are determinant to predict their capacity to acclimatize and adapt to different scenarios of ocean warming and ocean acidification and thus determine what species might be able to adapt and which species might go extinct.

Genetic diversity, bottlenecks, genetic drift, founder effects. Extinction or adaptation (acclimatation).

Adaptation corresponds to the increase in frequency of genes providing an increased survival and reproduction under prevailing environmental conditions. In the absence of genetic diversity adaptation cannot occur. Furthermore when genetic diversity is low, homozygous genotypes become more frequent including for deleterious recessive alelles (inbreeding depression). Thus the genetic diversity of natural populations, which can be assessed easily and non-invasively, with molecular markers (Chenuil, 2006), can be used as a proxy to vulnerability, to which it is inversely correlated.

3.3 Genetic warning signals (loss of genes)

When monitoring a population via mere counting of individuals observed in the field, a loss of genetic diversity, thus an increase in vulnerability can be overlooked, because populations can recover after a perturbation although their adaptation potential decreases after each perturbation (Chenuil, this volume).

Frequency of mass mortalities, anoxic crisis

Besides harvesting pressure, mortality from disease is an important ongoing threat for marine populations and can be evaluated as a warning signal of potential local extinction. Several severe incidents have been reported during the past decades (Webster, 2007; Garrabou *et al.*, 2009), affecting mostly sessile invertebrates, such as bath sponges and Anthozoans in the Mediterranean Sea. Mass mortality events have been associated to environmental temperature anomalies that promote stress and consequently chemical and microbial shifts in the affected organisms (Webster *et al.*, 2008; Lejeusne *et al.*, 2010). Thus, they are expected to be more intense and recurring within a reportedly increasing warming trend (Coma *et al.*, 2009). Monitoring disease incidents, especially in the most sensitive areas, e.g. the southeastern Mediterranean, is an urgent priority.

3.4 From local to global extinction

Along with other traits that can cause a higher extinction risk, a geographical range size of certain species is one of the most important. It can be presumed that large and abundant populations with global distribution will not be significantly influenced by local or regional extinctions, but what about a species with small populations and geographically restricted distribution, such as marine mammals and chondrichthyan fish (see Panigada and Pierantonio; Soldo in this volume)? Evidently, the importance of a broad distribution in permitting a large population size, or as a buffer against habitat loss or overfishing, is such that it transcends biological differences among taxonomic groups, as well as differences in the threatening processes among regions (Cardillo *et al.*, 2008). On the other hand, patchy populations (i.e. those with high amounts of dispersal among local populations) are most likely to exhibit an increase in synchrony following extinction.

Numerous species in the wild can be modeled as metapopulations, which are a set of local populations that may undergo local extinction, and that exchange migrants. Population genetics again allows estimating connectivity among demes (local populations), an important parameter related to the risk of global extinction. The risk of local extinction can in some cases be estimated by genetic diversity, but if environmental stochasticity is high and demes small, genetic diversity is of poor use.

4. Management issues (and recommendations)

MPAs

Marine Protected Areas (MPAs) have been used as a measure for the protection of endangered species or populations (see Voultsiadou *et al.*, this volume), or of sensitive ecosystems. Additionally, MPAs can contribute to the conservation of representative habitats which support rich diversity (e.g. Mediterranean coralligenous assemblages and *Posidonia* meadows), nursery grounds and Essential Fish Habitats, as well as undisturbed pristine sites. The latter can recover from or adapt more easily to natural and anthropogenic phenomena, such as the temperature rise, and can be used as reference sites for monitoring relevant unprotected areas. MPAs can also provide spillover effects to the surrounding areas (PISCO, 2011).

In 2010 5,800 MPAs existed globally, covering 1,2% of the ocean, while only 0,1% encompass fully protected no-take Marine Reserves (PISCO, 2011). A major impediment to marine conservation is the ineffective management and surveillance of MPAs: a number of cases are just 'paper parks', where no management measures have been implemented (Abdulla *et al.*, 2008). The critical need for the establishment of networks of Marine Reserves, high seas MPAs, and 'Marine Peace Parks' globally has been underlined by scientists (Coll *et al.*, 2012), scientific commissions (CIESM, 2011), NGOs (Greenpeace, 2006; OCEANA, 2011), and Conventions (see Giakoumi *et al.*, 2012 for an analytical listing). The 2003 IUCN World Parks Congress goal for protecting 20-30% of the world's oceans within representative Networks of MPAs by 2012 has been largely ignored and the Convention on Biological Diversity Meeting in Nagoya (2010) set the target to protect 10% of each coastal and marine ecoregion by 2020.

Fisheries management (no take areas, nursery areas, spawning areas, quotas)
Multiple management tools exist to meet combined fisheries and conservation objectives and reach consensus towards sustainable use of marine resources. Quota restrictions, gear modifications, temporal and spatial area closures, no take areas, community management, creation of economic incentives are all examples of traditional management tools that work towards restoring depleted populations, ultimately protecting them from local or global extinctions. Experience has shown that combining diverse management actions can lead to successful management of marine resources, keeping in mind that the best combination of management actions depends on the resource and on the local context.

Large shark monitoring in the Adriatic started in late 1990s by collecting the data from marine police, harbor offices and fishermen. Later, by advertising the monitoring in marine journals and other media, the monitoring was enriched by data compiled by the broader interested public. Currently, it constantly provides data not only on large sharks, which remain the main goal of the monitoring, but also on other marine organisms, especially rare and new species for the Adriatic.

Remedial actions

Better use of fisheries statistics (data*)*
Collection of scientific data has a long history. Nowadays most of the data are stored electronically and can be easily available thru web-based datasets such as the Global Biodiversity Information Facility [GBIF, www.gbif.org]. Until recently most of the scientific data were stored in paper format, in local libraries, limiting their dissemination and accessibility. Given the increasing rates of loss in biodiversity and extinction risk globally, it is essential to design strategies to digitally recover historical datasets, particularly the recovery of long-term and large scale historical surveys. Historical data can provide valuable information to construct baselines of species distribution, abundance and biodiversity, which is critical to monitor the extinction rate of species. We recommend and encourage any efforts to recover and restore historical data sets and facilitate their accessibility. Successful projects have shown that the cost of recovering data is a small percentage of the initial project costs. In addition, there have been numerous global strategies to construct global datasets such as the GBIF to encourage free and open access to valuable scientific data. We believe that scientific data should always be easily available and accessible and that a standard practice of any scientific project should be to ensure that no data is lost to future generation of scientists.

Issue proper legislation and enforce it (no paper parks)
Marine Protected Areas (MPAs) have been set up to protect vulnerable species and ecosystems, to conserve biodiversity and minimize extinction risk, to re-establish ecosystem integrity, to segregate uses to avoid user conflicts and to enhance the productivity of fish and marine invertebrate populations around a reserve (Pauly *et al.*, 2002; Hooker and Gerber, 2004).

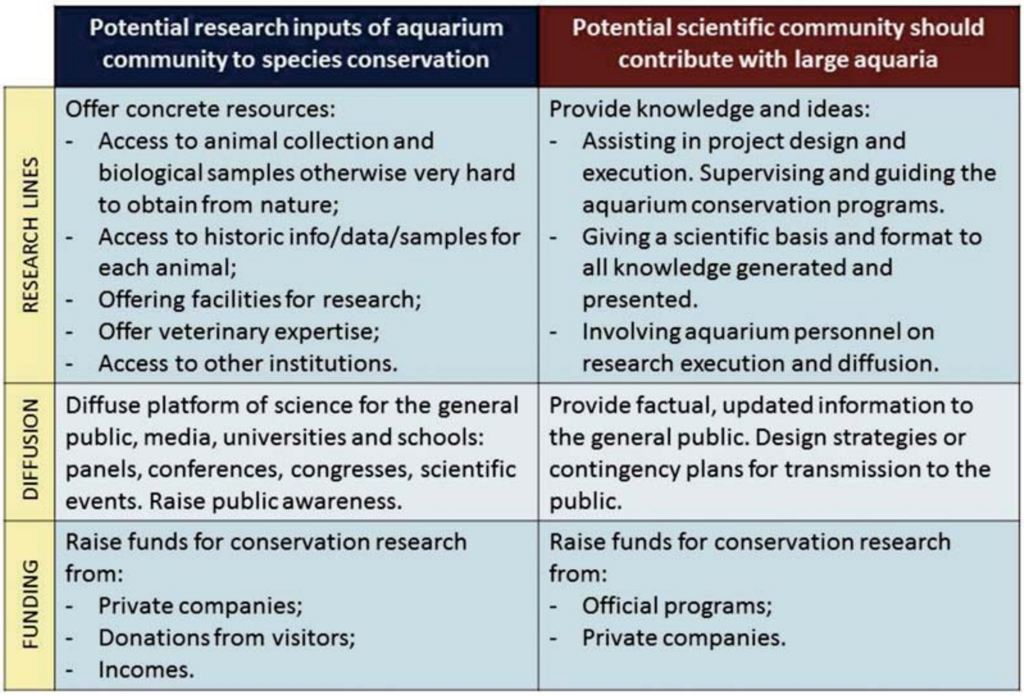
One of the crucial feature making a Marine Protected Area efficient is the establishment, maintenance and economical support of a proper management body. Without appropriate management plans, coupled with enforcement and compliance efforts to ensure that rules are respected and measures are correctly implemented, the risk that the MPA will be perceived only as a "paper park" is more than concrete (Notarbartolo di Sciara, 2008; Reeves, 2000).

Systematic monitoring programs, long-term goals, enforcement policy, public awareness efforts are among the tasks to include in a proper and effective management plan; these objectives should be assessed at regular intervals, to make sure the institutional aims of the Marine Protected Area are addressed and achieved.

Strengthen *ex situ* conservation
As shown in Box 2, much remains to be done to enhance useful synergies between the research community and large public aquaria. While these offer an unequalled showcase for displaying

recent scientific findings to a large audience, they also allow easy access to the animals for non-invasive research, for the study of aging, behaviour, lymphocytes, etc.

Box 2. The potential role of public aquaria for *ex situ* conservation by Daniel Garcia Parraga



	Potential research inputs of aquarium community to species conservation	Potential scientific community should contribute with large aquaria
RESEARCH LINES	Offer concrete resources: - Access to animal collection and biological samples otherwise very hard to obtain from nature; - Access to historic info/data/samples for each animal; - Offering facilities for research; - Offer veterinary expertise; - Access to other institutions.	Provide knowledge and ideas: - Assisting in project design and execution. Supervising and guiding the aquarium conservation programs. - Giving a scientific basis and format to all knowledge generated and presented. - Involving aquarium personnel on research execution and diffusion.
DIFFUSION	Diffuse platform of science for the general public, media, universities and schools: panels, conferences, congresses, scientific events. Raise public awareness.	Provide factual, updated information to the general public. Design strategies or contingency plans for transmission to the public.
FUNDING	Raise funds for conservation research from: - Private companies; - Donations from visitors; - Incomes.	Raise funds for conservation research from: - Official programs; - Private companies.

Some success stories

Marine turtles

The present status of the Mediterranean population of the loggerhead marine turtle *Caretta caretta*, an endangered species under strict protection (e.g. Barcelona and Bern Conventions, CITES), can serve as an example of effective monitoring and conservation efforts. Extensive research, including beach monitoring, tagging, and public awareness for more than 20 years in the main Mediterranean nesting areas (i.e. the western coast of Greece and Cyprus), has been carried out mostly by environmental organizations (Margaritoulis, 2005). In spite of difficulties due to ineffective enforcement of the legislation and incidental capture of turtles in fishing gear, encouraging trends of populations recovery have been observed in areas where conservation measures are applied (for details see Voultsiadou *et al.,* this volume). Stabilization of population numbers and increase of annual birth rate have been also recorded for the monk seal *Monachus monachus* in the Northern Sporades, Aegean Sea, since monitoring efforts started in the area (see Dendrinos *et al.*, 2007).

Sharks in Croatia

Chondrichthyans, especially sharks, have suffered huge declines in the Adriatic, as well as in whole Mediterranean area. In the absence of usually required stock assessment data, chondrichthyans were simply not managed. Now, Croatia has chosen to apply the precautionary approach to chondrichthyan management, based on existing available data (see Soldo, this volume). As a result, 23 chondrichthyan species (16 of them large sharks, mainly highly migratory species) have been granted strict protected status by Croatia in past five years, the highest level of protection in the country.

Rebuilding stocks of East Atlantic and Mediterranean bluefin tuna?

The overexploitation of East Atlantic and Mediterranean bluefin tuna is well documented, reflecting many problems found in the world fisheries, i.e. severe overexploitation driven by high market value, an open access in international waters where in the absence of control, regulations are easy to ignore. Recent indications of improvement in Atlantic bluefin tuna stock status (Porch and Fromentin, 2013) due to the imposition of strict fishery regulations, following intense mediatic pressure by concerned NGOs, illustrates that despite many sources of uncertainty in the projections of future trends, the management of a heavily exploited fish stock can still show hopes for recovery when there is a strong political will.

Global marine extinctions in historical time: what we know and why we don't know (a lot) more

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INTRODUCTION

Only a small handful of marine animals and plants are regarded as having become globally extinct since 1500 (a coarse temporal boundary before which reliable data are very scarce). Although few in number (Table 1), these species continue to attract interest relative to global extinction patterns, statistical methods for inferring extinction, and modern-day extinction risk (Collen *et al.*, 2012; Smith and Solow, 2012; Harnik *et al.*, 2012a; Glynn, 2012; Halpern and Kappel, 2012).

The small number of extinctions believed to have occurred over the past 500 years has led to two hypotheses: (1) extinctions in the sea are relatively rare, and, thus, marine species are less susceptible to global extinction than species in freshwater or terrestrial habitats (Dulvy *et al.*, 2003; Regnier *et al.*, 2009; Harnik *et al.*, 2012a; but see Myers and Ottensmeyer, 2005), or (2) extinctions in the sea are under-reported: the actual scale of marine extinction is thus poorly known, and thus a lower susceptibility of marine organisms to extinction cannot be presumed (Carlton, 2013). I examine both of these hypotheses here and also ask why it would be important to know the extent of historical extinctions ("neoextinctions" as compared to "paleoextinctions"; Carlton, 1993).

Table 1. Marine plants and animals extinct in historical time.

Taxon	Historical Range	Last Collection or Sighting of Living Individuals[1]	Probable Cause of Extinction	Reference
RHODOPHYTA				
Vanvoorstsia bennettiana (red seaweed)	Sydney Harbour, Australia	1886 (not 1916 as in Dulvy *et al.*, 2009)	Habitat destruction	Millar, 2003; Brodie *et al.,* 2009
MOLLUSCA Gastropoda				
Lottia alveus (eelgrass limpet)	Labrador to New York (last known population in Maine)	1929	Demise of host plant due to pathogenic disease	Carlton *et al.*, 1991
Lottia edmitchelli (rocky shore limpet)	Southern California (San Nicolas Island to mainland [Los Angeles region])	1861	Habitat destruction	Carlton, 1993
Cerithidea fuscata (salt marsh horn snail)	San Diego Bay, California	1935	Habitat destruction	Carlton, 1993
Littoraria flammea (mangrove periwinkle)	China	1840s	Habitat destruction?	Carlton, 1993

ARTHROPODA **Insecta**				
Saemundssonia jamaicensis (bird louse, on the extinct Jamaican petrel)	Western Atlantic Ocean (Jamaica)	1879	Extinction of host	Mey, 2005
MAMMALIA				
Neovison macrodon (sea mink) (= *Mustela macrodon*)	Northwest Atlantic Ocean (last known in Maine)	1880	Hunting	Carlton *et al.*, 1999; Sealfon, 2007
Zalophus japonicus (Japanese sea lion)	Hokkaido to Kyushu (last known on Liancourt Rocks, Sea of Japan)	1951	Hunting	Rice, 1998
Monachus tropicalis (West Indian monk seal)	Caribbean and Gulf of Mexico	1952	Hunting	Carlton *et al.*, 1999
Hydrodamalis gigas (**Steller's** sea cow)	Northwest Pacific Ocean (last known on Commander Islands)	1768	Hunting	Carlton *et al.*, 1999
AVES				
Phalacrocorax perspicillatus (Pallas's cormorant)	Northwest Pacific Ocean	*ca.* 1850	Hunting	Carlton *et al.*, 1999
Mergus australis (Auckland Islands Merganser)	Southwest Pacific Ocean	1902	Hunting	Carlton *et al.*, 1999
Camptorhynchus labradorius (Labrador duck)	Northwest Atlantic Ocean	1875	Hunting	Carlton *et al.*, 1999
Pinguinus impennis (Great auk)	North Atlantic Ocean (last known in Iceland)	1844 (with a possible last sighting in 1852)	Hunting	Carlton *et al.*, 1999
Haematopus meadewaldoi (Canary Islands oystercatcher)	Northeast Atlantic Ocean	*ca.* 1940? (last collected specimen, 1913)	Hunting	Carlton *et al.*, 1999
Pterodroma caribbaea Jamaican petrel	Western Atlantic Ocean (Jamaica)	1879	Hunting	Szabo *et al.*, 2012 (but here considered extinct, rather than "possibly extinct")
Oceanodroma macrodactyla Guadalupe storm petrel	Eastern Pacific Ocean (Guadalupe Island, Baja California, Mexico)	1912	Hunting	Szabo *et al.*, 2012 (but here considered extinct, rather than "possibly extinct"); R. Pitman, personal communication, 2012
Pterodroma rupinarum (Large St. Helena petrel)	South Atlantic Ocean: St. Helena Island	1500s	Hunting	Olson, 1975
Bulweria bifax (Small St. Helena petrel)	South Atlantic Ocean: St. Helena Island	1500s	Hunting	Olson, 1975
PISCES				
Anampses viridis (green wrasse)	Mauritius (Indian Ocean)	1839	Habitat destruction?	Hawkins *et al.*, 2000

[1] The last collection or sighting of living individuals is not necessarily (and often unlikely) to be when the species went extinct. In almost all cases, it is probable that individuals of a given species lingered on for years after the date shown.

Geographic-sale extinction can potentially escalate from a ***local*** scale (within a prescribed site or habitat) to ***regional*** or ***provincial*** (within a biogeographic province) to ***global*** (all populations are believed to have disappeared). The first two geographic scales may or may not parallel the categories of ***threatened*** and ***endangered***, depending upon the species in question. Additional extinction categories include ecological-scale ***functional*** extinction (the demise of an ecological engineer, for example) or economic-scale ***commercial*** extinction (the cessation of a fishery when the cost of the effort to seek out the last individuals makes the enterprise no longer viable).

For *global* extinctions, there is no consensus as to the length of time over which a species remains undiscovered, or the required intensity of search effort, after which a species is declared to have vanished. This is, in part, due to the HOSPET (hope springs eternal) belief that species which have not been detected for decades (or even centuries) may yet be re-discovered, a belief re-enforced on regular occasion by the discovery of modern "Lazarus" species long thought to be extinct (for example, Dell'Angelo and Van Belle, 1990; Glynn and Feingold, 1992; Florens and Baider, 2007). Thus the Galapagos damsel fish *Azurina eupalama*, last seen about 1982 (Roberts and Hawkins, 1999; Hawkins *et al.*, 2000; McCosker and Rosenblatt, 2010) and the Galapagos seastar *Heliaster solaris*, last seen in 1977 (Edgar *et al.*, 2009), remain absent from our current inventory of global extinctions, despite assiduous searches in their shallow water habitats and known locations, awaiting perhaps another 25 or 50 years before being declared probably extinct.

WHY WE SHOULD CARE

It is reasonable to ask why knowing which (and thus how many) species have gone extinct in the ocean is of interest and concern. At least five reasons can be offered in support of investing research effort in the depth and breadth of historical marine extinctions:

(1) There is fundamental scientific interest in the loss of distinct lineages. We rely on living species within a clade to assist us in understanding evolutionary biology, phylogeny, biogeography (historical and modern) and adaptations. Global extinction of species eliminates from these considerations potentially key links and nodes – essentially robbing us of a deeper appreciation of how, when, why, and where species groups came to be as they are.

(2) A robust understanding of the diversity of extinctions will permit insight into the types of *species* (such as trophic guilds, reproductive strategies, or the breadth (or lack thereof) of physiological plasticity) that are resistant or vulnerable to extinction. Our very limited understanding of which species have gone globally extinct in the sea inhibits our ability to make robust predictions as to extinction susceptibility of marine organisms.

(3) A robust understanding of extinctions may permit insight into the types of *habitats, communities and ecosystems* that are vulnerable to extinction.

(4) It is important to understand if modern-day studies of communities and ecosystems are undertaken without the knowledge that formerly common or abundant predators, competitors, or other potential ecological engineers, have, in fact, disappeared, such that extant species have been released from the predatory or competitive networks within which they evolved (this thought applies of course not only to extinctions but to fisheries as well, particularly where prominent species were reduced long before modern studies were undertaken). That species removals dramatically alter community structure through cascade effects is well known. How, for example, have marine communities in the Aleutian Islands responded in the short time (approximately 300 years) since a massive herbivore species, the stellar sea cow, was extirpated?

(5) There is, of course, fundamental cultural and aesthetic concern over the loss of species, concern which is not any less important than the other reasons identified here. Extinct species, for example, may have been significant in the history and culture of native societies. The loss of species lessens the natural world around us, a world with which we ask society – including the public, the press, and the political world – to engage in order to appreciate and support preservation, conservation, and restoration efforts.

WHAT WE KNOW

While Dulvy *et al.* (2003) listed 113 *local and regional* extinctions, the actual number of extinct *populations* (and thus the actual scale of genetic diversity loss) of thousands, if not tens of thousands of species, is not known, but likely approaches several orders of magnitude higher than 100-or-so records. Rather, we are concerned here with *global* extinctions. Carlton *et al.* (1999) identified 12 extinct species of marine invertebrates (4), birds (5) and mammals (3). Dulvy *et al.* (2003) recognized 20 extinctions: marine invertebrates (8), algae (2), fish (2), birds (5) and mammals (3); their list was critiqued by Monte-Luna *et al.* (2007). Dulvy *et al.* (2009) similarly listed 20 extinctions (marine gastropod mollusks (4), algae (1), fish (3), birds (8) and mammals (4)), but not all the same species as in their 2003 work.

Recognized here (Table 1) are 20 historical marine extinctions: algae (1 species), gastropod mollusks (4), insects (1), mammals (4), birds (9) and fish (1). The present list deletes three species recognized by Dulvy *et al.* (2009): the Tasman booby (*Sula tasmani*), now regarded to be the same species as the extant masked booby (*Sula dactylatra*); the Galapagos damselfish (*Azurina eupalama*), discussed above, and the New Zealand grayling (*Prototroctes oxyrhinchus*), a primarily freshwater species. In turn, I add here three species – two petrels and 1 marine insect.

There has been little advance in our knowledge of marine extinctions since the review by Carlton *et al.* (1999). Recognized by Vermeij (1993), then set aside by Carlton *et al.* (1999) as of uncertain status, but now restored here and recognized as globally extinct are the Jamaican petrel and the Guadalupe storm petrel. Not appearing in Carlton *et al.* (1999) are three species: one alga, one insect (a bird louse, a parasite apparently unique to the Jamaican petrel), and one fish, the Mauritian green wrasse.

Marine invertebrates, algae, and fish are too few in number to permit either geographic or temporal analysis. Two marine mammal extinctions occurred in the North Atlantic Ocean and two in the North Pacific Ocean; there are no marine mammal extinctions known in the southern hemisphere. Amongst the nine species of marine birds recognized here as extinct, three occurred in the Pacific Ocean (two in the North Pacific, and one in the South Pacific), and six occurred in the Atlantic (two in the South Atlantic, and the rest in the North Atlantic).

All of the marine mammals and birds were rendered extinct by hunting. The Mauritian wrasse, the Australian red algae (described from what was to become a highly urbanized harbor), and several of the marine snails likely disappeared due to wholesale habitat destruction. One marine snail, a limpet restricted to a seagrass, went extinct when the host plant suffered vast population declines in the 1930s due to a fungal disease. Finally, a bird louse ectoparasitic on the extinct Jamaican petrel went the way of the petrel as well. Unique symbiotic, endoparasitic, and ectoparasitic species likely occurred with many of the extinctions shown in Table 1, and thus this list may easily double were museum specimens examined and explored for associated species.

Although our time line for the present purposes was set at extinctions occurring since 1500, at least two marine birds that may have disappeared at the hands of prehistoric human hunters should be noted. These were an Hawaiian petrel (*Pterodroma jugabilis* [not *jugularis*, as in Vermeij, 1993 and Carlton *et al.*, 1999]), and a Californian flightless duck (*Chendytes lawi*) (Vermeij, 1993; Jones *et al.*, 2008), both apparently hunted to extinction by Polynesians and Native Americans, respectively.

WHY WE DO NOT KNOW A LOT MORE

Our limited understanding of the depth and breadth of marine extinctions in historical times arises from several sources. These include a lack of historical research, perhaps abetted by the enduring assumption that had extinctions occurred they would have been noticed. We start with the last.

Missing species would be noticed

Implied in recent accounts of marine extinctions (Dulvy *et al.*, 2003; Dulvy *et al.*, 2009; Collen *et al.*, 2012; Smith and Solow, 2012; Harnik *et al.*, 2012a; Glynn, 2012; Halpern and Kappel, 2012) is that if conspicuous and abundant marine species disappeared, a body of scientists (often referred to in the vernacular as “they”) would have noticed. “They” is a vague if not often imaginary group of scholars (natural historians, systematists, and biogeographers) who are presumed to have their finger on the pulse of intertidal and near-shore marine biodiversity. That obvious, common species can in fact disappear without their absence being remarked upon speaks to the opposite situation – that our ability to monitor the demise of coastal biodiversity is highly circumscribed, the more so if we ask about the extent of our knowledge and understanding of marine biodiversity prior to the 1900s. The fact that the following three examples all come to us from the 20th century only serves to underscore this conclusion.

Eelgrass limpet *Lottia alveus* (Mollusca: Gastropoda)

In one of the more spectacular cases of an abundant species disappearing and passing without notice, this 1 cm long (and thus not tiny!) snail lived and fed on the blades of the eelgrass (*Zostera marina*) in the northwestern Atlantic Ocean from Labrador to New York. It was collected alive by the thousands on the coast of Maine in 1929. Its presence and abundance on the Atlantic coast of North America remained commonly cited in faunal guides and seashells books into the 1990s, although it went globally extinct about 1930, due to a pathogenic marine fungus that caused a "wasting disease" which killed more than 90% of the host plant (Carlton *et al.*, 1991).

Blue mud shrimp *Upogebia pugettensis* (Crustacea: Decapoda: Thalassinidea)

This 15 cm long burrowing shrimp was one of the most conspicuous intertidal mudflat engineers of the Pacific coast, building deep burrows and hosting a large number of specialized commensals and symbionts (Kuris *et al.*, 2007). It was a staple of invertebrate zoology classes from British Columbia to California as well as mudflat field trips, where generations of students digging *Upogebia* to depths of 90 cm and more was a rite of passage as a fledgling marine biologist. In the 1990s and 2000s *Upogebia* disappeared from many bays and estuaries on the Oregon and California coast (Chapman *et al.*, 2012), without, apparently, any invertebrate zoologist commenting, at least publicly or in writing, on the lack of material for teaching or field demonstration. While *Upogebia pugettensis* is not extinct, it remains absent or rare from many sites where it was formerly abundant, a phenomenon that appears to have occurred in the short span of about 20 years. *Upogebia* is believed to have undergone a dramatic decline to the introduction of a non-native parasitic isopod, *Orthione griffenis*, from Japan (Chapman *et al.*, 2012).

Californian sea slug *Hyposelodoris californiensis* (Mollusca: Gastropoda: Nudibranchia)

This relatively large (4 cm long) spectacularly-colored sea slug, with a dark blue ground color and rows of bright yellow spots, was common to abundant in the early 20th century along the southern California coast, where it fed on several species of sponges, particularly *Dysidea amblia*. This range is still recorded in the most recent Pacific coast invertebrate guides (for example, McDonald, 2007), despite the fact that *H. californiensis* has not been sighted on the mainland coast for more than 30 years, a phenomenon that no one appeared to have noticed until announcement of its regional extinction (Goddard *et al.*, 2013). While the species still exists on offshore islands and in Mexico, it was last sighted on the California mainland coast in 1977, and its absence appears to have passed without widespread comment until now.

All three of these examples are characterized by being in regions densely populated, both historically and now, with a wealth of active marine biologists. As many of the coasts of the world are not so blessed, although still subjected to the pressures of human activity, it seems likely that many species – large and small – could decline (or go extinct) without record.

Lack of research on modern-day extinctions

The primary cause of our lack of knowledge of modern-day marine extinctions is that there are few (if any) workers actively engaged in research on historical extinctions, although this is not for a lack of rich resources or modern tools to do so. These assets include the ***archeological record,*** the ***written record***, and ***museum collections***; modern tools include molecular techniques to ferret out cryptic extinctions.

Archeological records are a potentially important but under-utilized resource for understanding the distribution and abundance of shallow-water species. Zooarcheological data may derive, for example, from shell middens (Rick and Erlandson, 2008) and artwork (Guidetti and Micheli, 2011). While such data are often utilized to understand the historic or prehistoric distribution and relative abundance of marine vertebrates (such as fish and mammal), far less has been done to expand our knowledge of early invertebrate populations. Particularly rich to mine in the archeological record would be the calcareous epibiota (such as barnacles, bryozoans, and serpulid polychaete tubes) on shellfish found in ancient middens.

The written record consists of hundreds of papers (often in extinct journals) from the 1600s, 1700s, and 1800s, with descriptions and drawings of many species that are often difficult to match to descriptions of known living species. Carlton (2013) has noted that a typical assumption in interpreting historical descriptions of species that cannot be clearly recognized is that such accounts must represent poor or partial accounts of still living species. An alternative hypothesis is that some of these early descriptions represent the only known records of species that became extinct long ago. No data base or synthesis exists of these many descriptions that are often listed at the end of taxonomic monographs under categories such as *species inquirendae* or *nomina dubia*. A thorough review of these lists would likely reveal taxa which were sufficiently described to permit us to conclude that they do not in fact match any known living taxa. Those taxa that occurred in intertidal or shallow, coastal habitats would be compelling extinction candidates.

The most important, richest, and untapped resources for discovering historical extinctions in the sea are museum collections. "Lower hanging fruit," without doubt, would be the discovery of species that simply ceased being collected long ago, similar to the eelgrass limpet *Lottia alveus*, followed by rapid reassessment of whether the animal or plant can still be found. Requiring more work would be the molecular resurrection of taxa that are in fact extinct, but buried in synonymies of living species. Many "older" species names from the 1700s and 1800s have been relegated to the synonymy of living taxa, on the assumption that these 18th and 19th century "species" represented mere phenotypes or clinal variants. (This is distinct from the above category, wherein older names cannot be matched to extant taxa).

To the extent that the type specimens, or other material, of such synonymized taxa are in museums collections – and to the extent that dried or wet tissue is available – selected examples (particularly from habitats or locations susceptible to human disturbances, such as lagoons, salt marshes, estuaries, and the supralittoral maritime zone) could be subjected to molecular genetic studies. Such studies could verify conspecificity (or the lack thereof) – and if nothing else, would almost certainly reveal the presence of extinct haplotypes (from what are likely long-gone metapopulations) no longer present in modern populations (see, for example, Hoos *et al.*, 2010, relative to the historical "haplotype T" in the Atlantic marine bivalve *Gemma gemma*).

CONCLUSIONS

The evidence at hand – the lack of historical research combined with assumptions that relatively recent disappearances of at least common and larger species would be noticed – suggests that we cannot conclude that extinctions in the sea are rare, but, rather, that we have no good working estimate or understanding of the scale of such extinctions.

Lacking a robust record, we cannot therefore conclude that marine species are less susceptible to global extinction than terrestrial or freshwater species. In this regard, the thoughts of Myers and Ottensmeyer (2005) are of interest, relative to their arguments that there are reasons to think that extinction in the sea may be "more of a problem" than on land. The first considers reproductive strategies in the sea, with the enhanced potential for Allee effects (positive density-dependent mortality – that is, a disproportionately lower recruitment rate when population densities are low) for many sessile species, because for fertilization to occur, individuals would have to be relatively close together. The second way in which extinction may be distinct in the ocean considers the larval behavior of many species, wherein larvae preferentially seek out and settle with conspecific adults. If species are reduced to low levels or local populations extirpated all together, recolonization and dispersal to new areas could thus be significantly hindered. Third, citing Steele (1985), Myers and Ottensmeyer compare the "red noise" of the sea (environmental variance increases over longer time scales) with the "white noise" of the land (where variability tends to be more constant over time) and the potential impact of this differential environmental stability on, for example, the long-term predictability of recruitment.

A WAY FORWARD

It may be noted that what little work there is on marine extinctions is scattered in a number of journals (see references herein). An important unifying force in science can be the evolution of dedicated societies, conferences, and journals that promote a field of endeavor, bringing together practioners and attracting students to investigate a nascent science. Thus, for example, there are now at least seven journals devoted to biological invasions, all appearing over the past 10 to 15 years (*Biological Invasions* [1999], *Aquatic Invasions* [2006], *Invasive Plant Science and Management* [2008], *Neobiota* [2010], *Management of Biological Invasions* [2010], *Russian*

Journal of Biological Invasions [2010], and *Bioinvasions Records* [2012]). There are no journals devoted solely to *Extinctions*, despite the fact that the literature on threatened and endangered species is increasing steadily (and perhaps inexorably). The time may be at hand to support such an outlet, and to encourage workers from across the freshwater, marine, and terrestrial realms to bring their work together, to seek the threads that bind.

EPILOGUE: THE SCALE OF EXTINCTIONS ANALOGIZED WITH THE HISTORY OF UNDERSTANDING OF MARINE INVASIONS

Fifty years ago little was known about the scale of marine bioinvasions in coastal environments. In the Hawaiian Islands, for example, about 35 non-native marine species were recognized in the 1960s while the number of invasions actually present exceeded 140 species (Carlton and Eldredge, 2009). In San Francisco Bay, perhaps 50 species were recognized as non-native in the 1960s; the actual number present in the Bay by that time exceeded 150 species (Cohen and Carlton, 1995). In South Africa in the 1960s, no marine invasions were recognized, but we now know that more than 50 non-native species were already present (Mead *et al.*, 2011).

The formal study of marine biological invasions had not yet begun in the 1960s. Arguments that discouraged if not impeded the development of the field in that era included the belief that the historical record was simply too limited to ever know whether a species was exotic or not, and that even “newly-discovered” species might in fact turn out to be endemic or indigenous species, simply overlooked in the past, due to biases in sampling techniques or habitat exploration. The latter, in particular, was often invoked to explain the novel “appearance” of phytoplankton species (dinoflagellates and diatoms) historically unknown in a region. We now recognize that many of these are probable ballast water introductions (CIESM, 2002).

It is thus interesting to observe that arguments that are similar to the ones above – relative to likelihood of being able to resolve the history of invasions – are frequently tabled today concerning the potential to recognize marine extinctions: that is, the record is simply too limited and sparse to know if a species is really extinct, and that even presumptive extinctions may be re-discovered. Rather, it appears that our understanding of extinctions in the sea at the beginning of the 21st century may be comparable to our understanding of invasions in the 1960s. Fifty years later, intensive paleontological, archeological, historical, biogeographic, and genetic work have all begun to reveal the actual scale of historical (and modern) invasions. Carlton (2013) has suggested that *nearly 200 species* of marine protists, invertebrates, algae, and fish may have gone extinct in the past several hundred years, an estimate based on assumptions of the minimum number of protist, invertebrate, fish, and algal species that may have gone extinct globally in highly vulnerable habitats – estuarine benthic and intertidal environments, supralittoral shores, and lagoons, all of which have succumbed extensively to coastal urbanization and industrialization. It will require the intensive effort similar to that mustered to understand invasion in the sea to ferret out those species that have been lost – at what may be a surprising scale.

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Marine mass extinctions and ecosystem crises in deep time

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ABSTRACT

The fossil record offers invaluable data to understand diversity dynamics at multiple temporal and spatial scales. Especially valuable are the data on ancient extinction rates that can be directly read from the marine geological record. These rates are traditionally assessed with large data compilations, which provided the backbone for the detection of mass extinctions in the past. The datasets evolved in the last ten years from simple compendia recording the times of origination and extinction of marine taxa to specimen-based relational web databases that allow for a compensation of sampling biases and an exploration of species-level traits such as geographic range. Small geographic range and preferences for tropical, shallow water calcium carbonate environments are among the most prominent actors enhancing extinction risk during times of background extinction but rules change partially during episodes of mass extinction. Because we are already approaching a time of mass extinction, attributes such as geographic range are likely to become irrelevant for species survival in the near future. Other lessons to be learnt from the fossil record are (a) that warming episodes were much more likely to cause mass extinctions than times of cooling, (b) that the adaptability to global change is limited and (c) that ecological changes are not necessarily linked to extinction toll.

INTRODUCTION

By far the most quantitative data on ancient biodiversity dynamics stem from the marine fossil record in shelf habitats. This delivered the data to define the ‘Big Five’ mass extinctions of the last 500 Ma (Raup and Sepkoski, 1982) and the values of extinction rates that are so often reported in the media. This is so because the completeness of the fossil record in shallow marine environments is much greater and reaches further back in time than that on land or in the deep ocean. The shallow seas also provide us with a wealth of data on marine ecosystems, which permits an assessment of the coupling of ecological and evolutionary change. Although deep time paleontological data are extremely valuable because they inform us about natural baselines of biodiversity change and extinctions, they cannot be taken at face value because the fossil record is far from being complete as it is, temporally coarsely resolved and selective in mostly preserving well skeletonized species. Hence several methodological issues and biases have to be considered when assessing ancient extinctions and their causes.

Paleontologists have been successful in developing methods to correct for many biases and in collecting their data in a way that allows for applying those methods. The next logical step is to use the fossil record more explicitly to predict the future. Attempts in this direction are becoming more and more common (Dietl and Flessa, 2011; Harnik *et al.*, 2012a; Louys, 2012) but a roadmap for developing the links further has yet to be developed. Here I provide the background that is required for marine biologists to evaluate and use results from paleobiology. Some perspectives are then provided on how the integration of fossil and recent occurrence databases may lead to mutual benefit.

METHODOLOGICAL ISSUES

Marine biodiversity through geological time is usually assessed at the genus level. The original paper defining the Big Five mass extinctions of the Phanerozoic eon even used the temporal ranges (durations) of marine families (Raup and Sepkoski, 1982). The higher taxon approach and its use to estimate species-level extinctions (Raup, 1979) are constantly being criticized by biologists who argue that everything above the species level is an artificial construct. However, species-level data can rarely be used directly for deep-time assessments of extinction rates:

First, the rates of extinction need to be assessed within discrete time intervals and at global scales. The best resolved time intervals, especially in ancient periods, are geological stages. These have an average duration of roughly 7 million years (myr) which is longer than the duration of the majority of marine species. Second, fossil species concepts often follow political borders rather than reflecting true biogeographic distributions. At regional levels, where a finer temporal subdivision is possible and consistent taxonomic concepts can be applied, trajectories of species and genus diversity are almost parallel and extinction pulses of genera match those of species (Crampton *et al.*, 2006). Although we are safe using genus-level approaches for assessing marine extinctions in deep time we should attempt a species-level approach if at all possible.

Another major issue is preservation. Under this term we subsume preservation quality and sampling completeness. Both are driven by a suite of factors such as diagenesis (the fossilization process), tectonics, weathering, and sampling effort. Although the factors driving preservation and those determining extinction might be tightly linked (Peters, 2008), we need to reduce the bias introduced by a heterogeneous fossil record with sampling standardization (Alroy *et al.*, 2001; Alroy, 2008; Alroy *et al.*, 2008; Alroy, 2010). Subsampling is at the core of all standardizations, that is, biodiversity and extinction rates are assessed based on random subsets of the original data. In other words, we degrade an already degraded dataset further to achieve homogeneous sampling. That paleobiologists are now able to compensate sampling bias is not only due to the development of methods but also owing to the data being compiled in a format that permit sampling-standardization in the first place. This has been achieved by the collaborative initiative of the Paleobiology Database (PaleoDB, http://paleodb.org), which has now compiled well over one million taxonomic occurrences of roughly 250,000 fossil taxa. Previous compendia (Benton, 1993; Sepkoski, 2002) recorded only the first and last appearances of higher taxa, whereas the PaleoDB records species occurrences in their geological context. Besides enabling rigorous sampling standardization of biodiversity and extinction rates, the PaleoDB also allows new approaches to assess extinction risk (e.g., the role of abundance and geographic range) and analyses of geographic subsets (e.g., the Mediterranean region, see below).

MASS EXTINCTIONS VERSUS BACKGROUND EXTINCTIONS

Species fade out all the time but there were episodes when the rate of extinction was significantly above background. These are the mass extinction episodes, which are distinguished from background extinctions by exactly this statistical condition: a significant elevation of extinction rates over background rates (Raup and Sepkoski, 1982). Therefore, some artificial number of diversity loss or extinction rate is not suitable for defining a mass extinction, especially because the background itself declined over time (Raup and Sepkoski, 1982; Alroy, 2008). A failure to consider background rates led to the erroneous assumption that a continuum of diversity losses, when those are ordered by magnitude, would imply that the term “mass extinction” was arbitrary. One can argue about the significance level of a mass extinction and how the data should be analyzed (Quinn, 1983). The outliers in boxplot statistics of logged diversity changes (log returns) over the last 490 million years match the classical definition of the Big Five mass extinctions very well (Kiessling, 2011) and confirm that the term mass extinction is not arbitrary but a true outstanding phenomenon.

Due to the great differences in time scales, the question of whether we are approaching or are already in the midst of a mass extinction is difficult to answer (Regan *et al.*, 2001). New approaches combine fossil extinction data and risk assessments based on IUCN (International Union for Conservation of Nature) Red List criteria. One recent comprehensive assessment came to the conclusion that current extinction rates are higher than those that caused the Big Five mass extinctions and the benchmark for a Big Five magnitude could be reached in 300 years from now (Barnosky *et al.*, 2011). However, great uncertainties remain, not only due to issues discussed by Barnosky and co-authors but also because the comparison was largely drawn between terrestrial vertebrates now and marine invertebrates then. It has long been known that marine invertebrates have, on average, longer durations than vertebrates (Stanley, 1979), which can represent a severe bias in past-present comparisons. The only marine invertebrates that have been fully assessed by IUCN are the scleractinian reef corals and here a large discrepancy exists between the numbers of historically extinct species (0) and those listed as threatened (33% of species: Carpenter *et al.*, 2008).

CAUSES OF EXTINCTIONS

Environmental change is almost universally seen as a trigger of mass extinction events. Although extinctions of all magnitudes can theoretically occur without extrinsic forcing (Maynard Smith, 1989; Newman and Palmer, 2003), the paleontological community traditionally evokes a suite of abiotic drivers to explore the causes of mass extinctions. The factors that paleontologists have identified as being important causes of mass extinctions are quite similar to those discussed by marine biologists as increasing recent extinction risk (Harnik *et al.*, 2012a). However, their relative importance does not match (Fig. 1). Today, overexploitation and habitat degradation are seen as the dominant drivers of current extinction risk, whereas rapid climate change, probably associated with ocean acidification, and the spread of anoxia are usually identified as proximate triggers of fossil extinctions (Kiessling and Simpson, 2011; Harnik *et al.*, 2012a). The ultimate causes are even more different, entirely anthropogenic today, but driven by volcanism and meteorite impacts in the past.

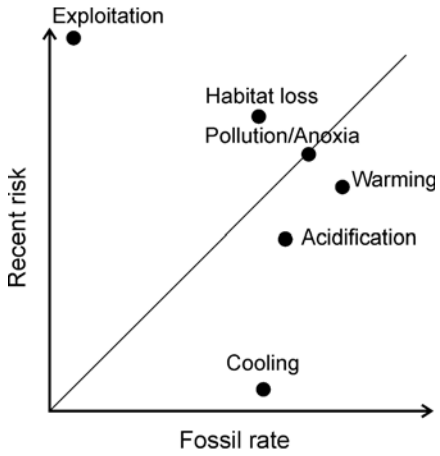

Figure 1. A scatter plot of factors thought to be relevant in marine species extinctions. The x-axis provides extinction rates during mass extinction episodes, whereas the y-axis estimates extinction risk today. Dots above the one-to-one line indicate that the factors are more relevant today than in the past, whereas the opposite holds true for values below. The rates and risks represent an educated guess based on multiple sources.

In terms of climate change, the available evidence has shifted substantially over the last 25 years. While Stanley (1987) devoted a whole book to the proposal that global cooling was a universal trigger of ancient mass extinctions, we now identify two of the Big Five mass extinctions to be associated with and probably caused by massive global warming: the end-Permian (ca. 250 million years ago, Ma) and the end-Triassic (ca. 200 Ma) mass extinctions (Kiessling *et al.*, 2007; Joachimski *et al.*, 2012; Sun *et al.*, 2012). The other mass extinctions are associated with a cooling /warming duo where cooling may precede the warming by almost two million years (end-Ordovician extinction, ca. 445 Ma) or decades as in the case of the impact winter at the Cretaceous-Paleogene boundary (65 Ma). We are still uncertain to what degree climate warming caused the extinctions by mechanisms that are relevant today (Pearson, 2011) or rather by associated factors such as, the spread of anoxia sea-level rise, and ocean acidification (Kiessling and Simpson, 2011). Just as in today's biodiversity crisis, multiple stressors are thought to have acted synergistically in most mass extinctions. Except for the end-Cretaceous, it is noteworthy however that all mass extinctions and several elevated background extinctions in the last 250 million years happened during times of global warming.

The ecological correlates of fossil extinction magnitudes provide a powerful tool not only to assess the proximate causes of extinctions but can also add to the assessment of current extinction risk. At the level of organismic traits, the concept of ecological buffering has proven to be especially useful (Knoll *et al.*, 2007; Kiessling and Simpson, 2011). This concept infers for high-ranked taxa the capacity with which they are likely to respond to chemical stress such as hypercapnia. Strongly calcifying organisms are considered to be unbuffered and thus should be strongly affected by extinction events involving ocean acidification. Three of the Big Five and several episodes of elevated background extinction show significantly higher rates for unbuffered than for buffered genera (Fig. 2), suggesting that ocean acidification might have played a substantial role. On the other hand, the two mass extinction episodes where there is evidence for cooling show either no selectivity (end-Ordovician) or a selective extinction of buffered organisms (end-Cretaceous), which are thought to be metabolically more active and hence are more prone to starvation (Kiessling and Simpson, 2011) a likely proximate cause of the end-Cretaceous mass extinction (Aberhan *et al.*, 2007).

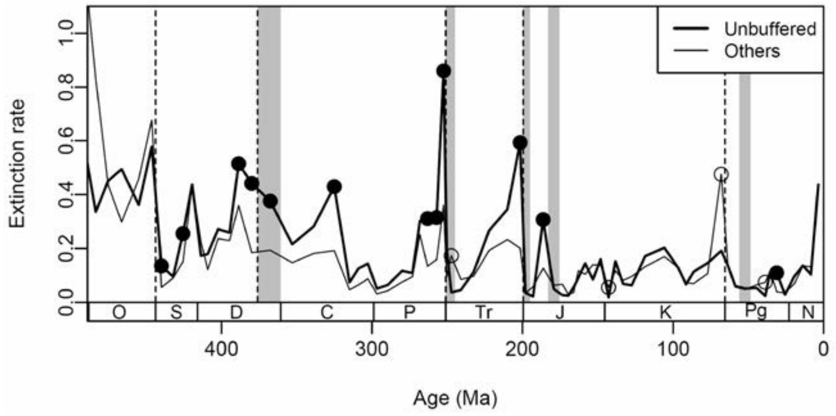

Figure 2. Raw extinction rates of marine animal genera in the PaleoDB over the entire Phanerozoic, grouped by inferred physiological buffering capacity. Rates are $-\ln(N_{bt}/N_b)$, where N_{bt}/N_b describes the ratio of species observed at the base and top of an interval relative to those seen only at the base (Foote, 2000). Because extinctions occur in pulses (Foote, 2005) rates were not normalized for interval duration. Thick lines indicate extinction rates in the unbuffered groups. Solid circles delineate times when extinction in unbuffered groups is significantly higher than in others, and open circles designate times when buffered groups were more affected. Dashed vertical lines demarcate the traditional Big Five mass extinctions and grey bars designate the time intervals of metazoan reef crises (from Kiessling *et al.*, 2011).

Geographic range is one prominent example of a species-level trait that can only be assessed with occurrence database such as the PaleoDB. Although geographic range (but not abundance) is considered as the most important factor governing extinction risk during background extinctions (Harnik, 2011), its role is greatly diminished or absent during mass extinctions (Kiessling and Aberhan, 2007b; Payne and Finnegan, 2007), which highlights the global scale of mass extinctions.

Habitats vary significantly in extinction risk. This has been demonstrated by contrasting extinction rates of genera with preferences for particular habitat types (Kiessling and Aberhan, 2007b). The marine habitats most prone to extinction are in shallow water, reef ecosystems and generally in the tropics. They are the same habitats that also facilitate speciation (Kiessling *et al.*, 2010). The rule of balance applies as well to species level traits such as geographic range and abundance. Small population sizes and geographic ranges increase extinction risk but also enhance the likelihood of speciation. One important exception is very large population size, which has been shown to enhance extinction risk in marine bivalves (Simpson and Harnik, 2009) but there is no evidence for an increase in chance of speciation.

Tempo of past extinctions

The pace of ancient mass extinctions is hard to constrain, largely due to uncertainties of geological dating. The most ancient mass extinctions probably happened over time scales of tens to hundreds of thousands of years. However, the impact scenario for the end-Cretaceous mass extinction implies a tempo of extinctions that is even greater than today. An important lesson to be learnt from this pattern is that extinctions can be similarly severe on short and long time scales. The mass extinctions occurring over long time scales should attract special attention because they demonstrate that the potential for adaptation may be limited in the face of severe environmental turmoil as we experience today.

Ecosystem crises and mass extinctions

The catastrophic nature of mass extinction events renders it likely that evolutionary and ecological changes are coupled. However, empirical evidence suggests that this is not the case (Droser *et al.*, 2000; McGhee *et al.*, 2004). Mass extinctions with a large extinction toll may show little evidence of ecological change (e.g., the end-Ordovician extinction, ca. 444 Ma), whereas the Late Devonian extinctions were modest in terms of species loss but accompanied by profound ecological changes especially in reefal ecosystems (Copper, 2002).

The response of reefs is often taken as an indicator of ecological changes but rarely in a quantitative way. Using changes in the calcium carbonate production of reefs per unit time, we can discern five metazoan reef crises (Kiessling, 2011; Kiessling and Simpson, 2011), three of which coincide with mass extinctions (Fig. 2), but all are linked to times of rapid global warming. Reef corals were only moderately affected by the end-Cretaceous mass extinction (Kiessling and Baron-Szabo, 2004), although the rudist bivalves that built reefal structures in the Late Cretaceous vanished. There was a major turnover in the ecological structure of reefs but reefal carbonate production and reef diversity were higher than before.

Phanerozoic-scale ecological changes of reef ecosystems must be assessed using general criteria such as the dominant reef building groups, the proportions of constructing and binding organisms and biodiversity. A multivariate analysis of eight such attributes led me to define seven Reef Evolutionary Units (Kiessling, 2001). An important conclusion from this exercise was that large-scale ecological changes within reefs are rarely associated with mass extinctions. The most prominent example is the end-Permian mass extinction. Metazoan reefs vanished completely for millions of years but the emerging reef systems in the Triassic were in many ways similar to their Permian counterparts (Weidlich *et al.*, 2003; Brayard *et al.*, 2011).

A focus on the Cenozoic and the Mediterranean region

The Cenozoic era (65 – 0 Ma) experienced substantial climatic fluctuations overlying a long-term cooling trend (Zachos *et al.*, 2001). The most prominent global events were the transient Paleocene-Eocene Thermal Maximum (PETM, Zachos *et al.*, 2005), the end-Eocene cooling (Wade *et al.*, 2012), and the Pleistocene glaciations. At the regional scale, the most profound event affecting the Mediterranean was certainly the Messinian salinity crisis (Krijgsman *et al.*, 1999; CIESM, 2007) that led to nearly complete desiccation of the Mediterranean sea. These events caused little extinction at the genus level, but there are distinct peaks at the species level (Fig. 3). The trajectories of extinction rates are well correlated between global and Mediterranean data (including the Paratethys) (first differences: $R = 0.77$, $p = 0.002$) but appear to be decoupled from the Miocene onwards. At global scales the most important extinction occurred near the end-Eocene (ca. 34 Ma), whereas a substantial extinction was associated with the Messinian salinity crisis in the Mediterranean. This kind of comparison helps distinguishing global and regional triggers of extinctions.

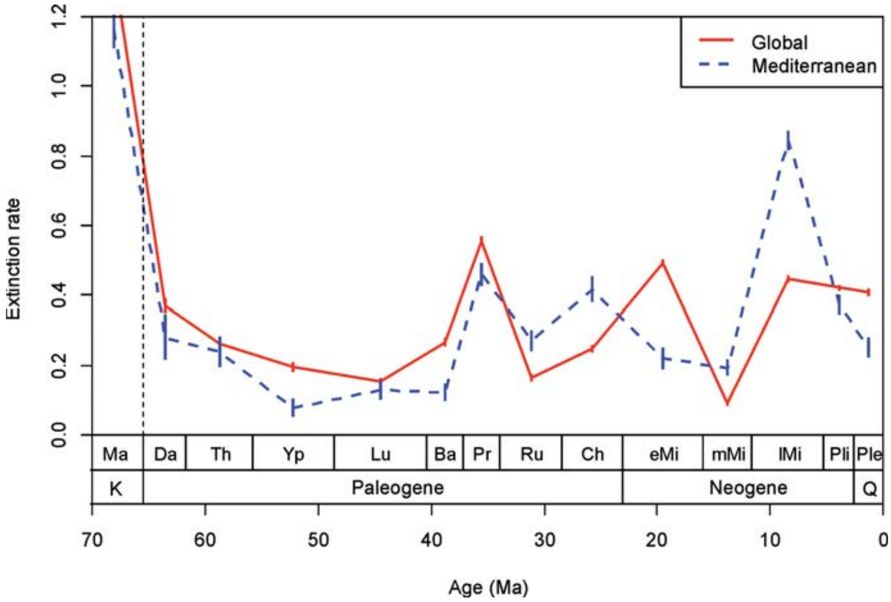

Figure 3. Raw extinction rates of marine invertebrate species of the last 70 million years, globally (red, solid line) and in the Mediterranean region (blue, dashed line). Extinction rates were calculated based on raw ranges extracted from fossil occurrences in the PaleoDB supplemented by recent species listed in the Ocean Biogeographic Information System (OBIS). The large peak at the beginning of the time series marks the end-Cretaceous mass extinction. Abbreviations: K – Cretaceous; Q – Quaternary, Ma – Maastriachtian; Da – Danian, Th – Selandian-Thanetian, Yp – Ypresian, Lu – Lutetian, Ba – Bartonian, Pr – Priabonian, Ru – Rupelian, Ch – Chattian, eMi – early Miocene, mMi – middle Miocene, lMi – late Miocene, Pli – Pliocene, Ple – Pleistocene.

BRIDGING THE GAP BETWEEN TIME SCALES

The fossil record demonstrates the potential of observations in deep time to put in context assessments of current extinction risk and ecological impact. With a more concerted effort, explicitly targeting on bridging the gap between fossil and recent time scales, the young field of conservation paleobiology will be able to provide more direct input to predict the future. Holocene and Pleistocene fossils offer an invaluable tool to validate the invasive nature of species, evaluate the natural variations of population densities of extant species, and the response of species to massive climatic fluctuations experienced during the Pleistocene glacial-interglacial cycles (Dietl and Flessa, 2011). Because the marine fossil record is so rich whereas modern assessments of extinction risk are heavily biased towards terrestrial organisms, marine systems are the ideal playground to achieve a shared benefit for paleontologists and biologists. One way forward is in a further development of large databases listing species occurrences (or observations) in an explicit spatio-temporal framework and stored with physico-chemical measurements or proxy data. Combining the power of the PaleoDB Database for fossils and information systems such as OBIS for the modern marine life can help marine ecologists overcome a major shortcoming: the scarcity, geographic patchiness, and short duration of their time series (CIESM, 2003; Richardson *et al.*, 2012).

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Patterns of ecosystem collapse and extinction during the Late Permian extinction event

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ABSTRACT

The late Permian extinction event is the largest biotic crisis of the past 500 million years and occurred during a time of global warming. Environmental changes that affected marine ecosystems are similar to those predicted for the near future. Collapse of complex marine ecosystems in most marine habitats was rapid and occurred during the time of rising temperature and atmospheric CO_2 levels. Key ecological changes include significant reductions in the body sizes of marine organisms; the disappearance of deeper infaunal animals including crustaceans; a reduction in burrowing depths and intensity; a loss of high tier epifaunal suspension feeders; and a change to communities of low diversity and evenness. These changes would have impacted a number of ecosystem processes, including nutrient cycling and secondary production. Post-extinction, hothouse communities in most shelf settings were controlled by physical factors such as fluctuating hypoxia and elevated sedimentation rates. Further detailed studies are needed to determine whether this event really is a useful analogue for predicted future changes, given the differences in geography, biota and initial starting conditions, although preliminary analyses are encouraging.

The biological consequences of present day global warming are likely to include major ecosystem disruption and potentially widespread extinction (Diaz and Rosenberg, 2008). Environmental changes, such as the expansion of hypoxia, can occur at a variety of temporal and spatial scales, but only the smallest temporal and spatial scales may be readily observed or recreated experimentally (e.g. Stachowitsch *et al.*, 2007). It is unclear whether the data from small-scale studies, and the models that are derived from them (e.g. Solan *et al.*, 2004), are applicable at larger scales, especially if, as predicted, climate changes move outside the realm experienced by modern ecosystems and into regimes known only from the deeper geological record (Belanger, 2012). Data from the largest temporal, spatial and ecological scales can, however, be sourced from the fossil record, which provides an archive of natural experimental data from a number of past episodes of climatic and environmental change (e.g. Jablonski, 2004).

The most significant extinction event of the past 500 million years occurred towards the end of the Permian Period, approximately 252 million years ago (Ma). Estimates vary, but approximately 90% of species, 80% of genera and 50% of families appear to have become extinct globally (e.g. Benton and Twitchett, 2003; Payne and Clapham, 2012). In the oceans, global diversity apparently fell to levels not recorded since the Late Cambrian. The groups that suffered most at this time were members of the so-called ‘Palaeozoic Fauna’ of Sepkoski (1984), characterized by sessile, epifaunal filter feeders such as articulate brachiopods, rugose and tabulate corals and crinoids (Payne and Clapham, 2012). This event marks a major shift in the ecology, evolution and composition of marine ecosystems (McGhee *et al.*, 2004), and is intimately associated with an episode of global warming (Benton and Twitchett, 2003; Kidder and Worsley, 2004; Kearsey *et al.*, 2009).

While the Late Permian event might provide a possible narrative for the future (Payne and Clapham, 2012), a key criticism of this simplistic approach is that obvious differences in the Earth's geography and biota, as well as the magnitude and rates of environmental change and the initial starting conditions, may render applicability to the present somewhat limited. Nevertheless, this event provides one end-member in the spectrum of possible extinction scenarios. This paper describes the patterns and possible causes of ecological changes in marine ecosystems during this event, based largely on field data collected over the past two decades.

Late Permian environmental changes

The environmental changes associated with the Late Permian extinction event are similar to those changes predicted for the near future by general circulation models (Twitchett, 2007a). The trigger for the onset of global warming appears to be volcanic activity related to emplacement and eruption of the Siberian Traps large igneous province (Saunders and Reichow, 2009), which released enormous amounts of CO_2 over a relatively short time interval. Geological evidence demonstrates that elevated CO_2 led to global warming; changes in rainfall patterns and run-off; accelerated continental weathering; sea-level rise; ocean stratification and a slowdown in circulation; and the expansion of hypoxia and anoxia on the shelves and in the oceans (e.g. Kidder and Worsley, 2004; Grice *et al.*, 2005; Twitchett, 2007a; Algeo and Twitchett, 2010; Fig. 1). These recorded changes are similar to those predicted for the near future (e.g. Diaz and Rosenberg, 2008). Weathering of silicate rocks would have eventually led to a reduction and drawdown in atmospheric CO_2, but volcanic eruptions continued, at least sporadically, for 10^5 to 10^6 years after the extinction event (Saunders and Reichow, 2009). It appears that elevated seawater temperatures (Kearsey *et al.*, 2009; Sun *et al.*, 2012; Joachimski *et al.*, 2012), weathering rates (Algeo and Twitchett, 2010) and widespread hypoxia (e.g. Wignall and Twitchett, 1996; 2002) were commonplace in most shelf settings, especially in the tropics, for at least several hundred thousand years after the extinction event.

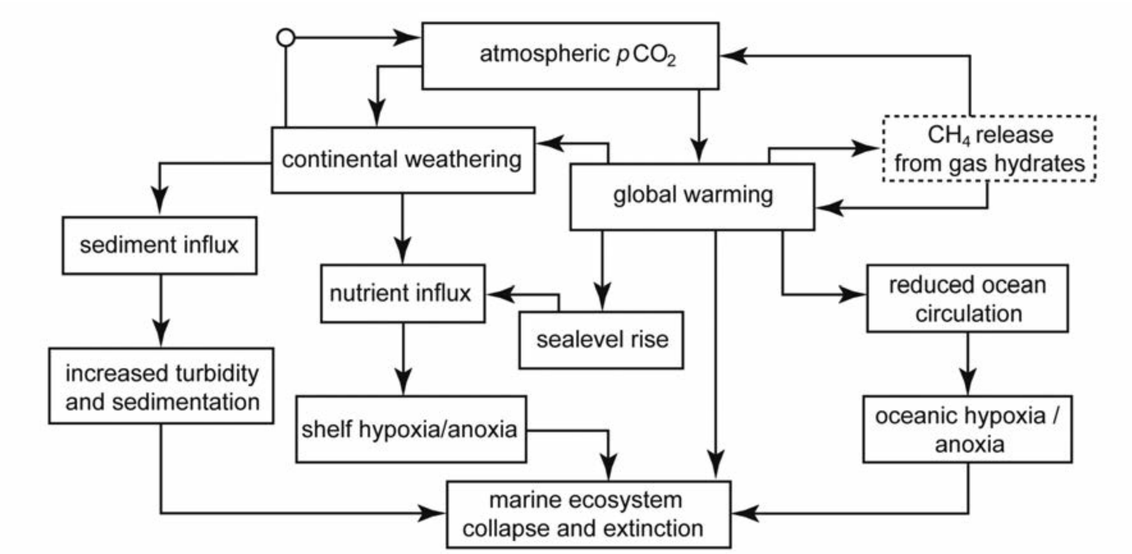

Figure 1. Schematic systems analysis of the effects of Late Permian CO_2 rise on marine ecosystems. The dashed box indicates that supporting geological evidence is weak; all other boxes are supported by good geological evidence. Bullseye indicates a negative relationship. Based on Kidder and Worsley (2004), Twitchett (2007a), Algeo and Twitchett (2010) and references therein.

PATTERNS OF ECOSYSTEM COLLAPSE AND EXTINCTION

The late Permian pre-event assemblages in most sampled shallow marine ecosystems from the low and mid palaeolatitudes represent typical climax communities living in well oxygenated, optimal environments and sharing a number of common characteristics. Taxonomic and ecological diversity are both high, with numerous taxa recording a range of life habits although assemblages are often dominated, especially in the tropics, by sessile epifaunal, low tier suspension feeders such as brachiopods. A diverse epifauna of erect, suspension feeders such as bryozoans, crinoids and sponges comprise the ‘high tier’ in most shallow, soft-bottom habitats (Bottjer and Ausich, 1986).

Despite the dominance of epifauna in these latest Palaeozoic communities, the substrate was nevertheless relatively well burrowed, in terms of both the amount and depth of bioturbation, by a diverse infaunal community. This is particularly evident in the temperate regions. Of particular note are the relatively high abundances of crustaceans (as evidenced from trace fossils such as *Rhizocorallium* and *Thalassinoides*) and the presence of deeper infaunal suspension feeders (including those that produced trace fossils such as *Skolithos*, and *Arenicolites*). Similar fossil assemblages characterise ‘normal’ background times throughout the Mesozoic and Cenozoic in most shallow marine tropical and temperate settings.

Collapse of shallow marine ecosystems (i.e. disappearance of these climax marine communities) is relatively rapid, and, as far as can be determined from current data, appears to have taken place during the time that temperature and CO_2 were both increasing and prior to maximum temperatures being reached (Sun *et al.*, 2012; Joachimski *et al.*, 2012). The rapidity of the extinction event in many invertebrate groups has been shown, for South China at least, by using statistical analyses of the fossil ranges of species (Jin *et al.*, 2000). Calculation of average sedimentation rates suggests that in East Greenland, collapse of Late Permian ecosystems took no longer than 10,000 to 30,000 years (Twitchett *et al.*, 2001). It is difficult to determine which of the associated environmental changes (Fig. 1) were responsible for the collapse in any particular local ecosystem. A number of ecological changes occurred, apart from loss of taxonomic diversity, as evidenced by the nature of the marine fossil assemblages from the immediate aftermath of the event, during peak global warming. The key changes are in relative abundance, body size, burrow diameter, depth and amount of bioturbation, tiering and occupied ecospace. Each of these factors has important implications for ecosystem structure and function and can be measured, or inferred, from fossil evidence, albeit with reference to the potential preservational and other biases that affect all fossil data.

Body Size: a significant reduction in body size is recorded, or has been inferred, in the immediate aftermath of the Late Permian mass extinction event in many marine taxa, including macroinvertebrates (e.g. Metcalfe *et al.*, 2011), foraminifera (Song *et al.*, 2011) and fish (Mutter and Neuman, 2009). The ‘Lilliput effect’ is a term coined by Urbanek (1993) to describe the temporary reduction in body size of animals that survive extinction events in the fossil record. This Lilliput effect lasts for perhaps a few hundred thousand years at most, and has been recorded after many different extinction events. In the aftermath of the Late Permian extinction event, the Lilliput effect, lasting on the order of 10^5 years, is recorded in several surviving invertebrate taxa (Twitchett, 2007b; Metcalfe *et al.*, 2011). In addition, the sizes of many marine animal taxa remain smaller than expected throughout much of the Early Triassic; a longer duration phenomenon that has confusingly and erroneously been termed the Lilliput effect by some authors. A number of environmental changes could be responsible for the size reduction, such as increased temperature, hypoxia, hypercapnia, reduced food supply and increased turbidity (Twitchett, 2007b; Algeo and Twitchett, 2010). In single-locality studies, body size reduction may simply reflect rising sea-level and sampling of a deeper habitat in the extinction aftermath; this, and other potential biases, such as hydrodynamic sorting, need to be properly assessed in interpreting size changes in fossil communities. Body size has a key role ecosystem function, including nutrient cycling (e.g. Woodward *et al.*, 2005), and size reduction would have led to important changes in these parameters. Size reduction appears to have affected both tropical and temperate ecosystems, although as expected, individual taxa are larger at higher (cooler) latitudes (Twitchett, 2007b).

Size reduction in marine vertebrates is also a predicted consequence of current global warming (Cheung *et al.*, 2012).

Burrow diameters: an equally significant reduction in burrow diameters is also recorded in the extinction aftermath and affects all burrow types (ichnogenera) to some degree (Twitchett, 1999; 2007; Fig. 2). Given that burrow diameter is a proxy for body size, and provides a maximum constraint on two of the tracemaking animal's linear dimensions, a reduction in burrow diameter implies a reduction in size of the trace maker and indicates that similar size changes affected all of the benthic infauna, not just those with mineralized skeletons. Burrow diameters have been shown to correlate with a range of environmental parameters, such as oxygen and water depth (e.g. Savrda and Bottjer, 1991). The size of the infauna is an important parameter in assessing the bioturbation potential of a benthic community, which in turn affects several key ecosystem functions (Solan *et al.*, 2004). Open burrow networks constructed by macroinvertebrates such as *Callianassa* and *Upogebia* have also been shown to significantly enhance nitrogen cycling due to their positive impact on the microbial communities (Laverock *et al.*, 2011). The reduction in size of these types of burrows (e.g. the ichnogenus *Thalassinoides*) through the Late Permian extinction event (Fig. 2) therefore presumably had a significant negative impact on nitrogen cycling.

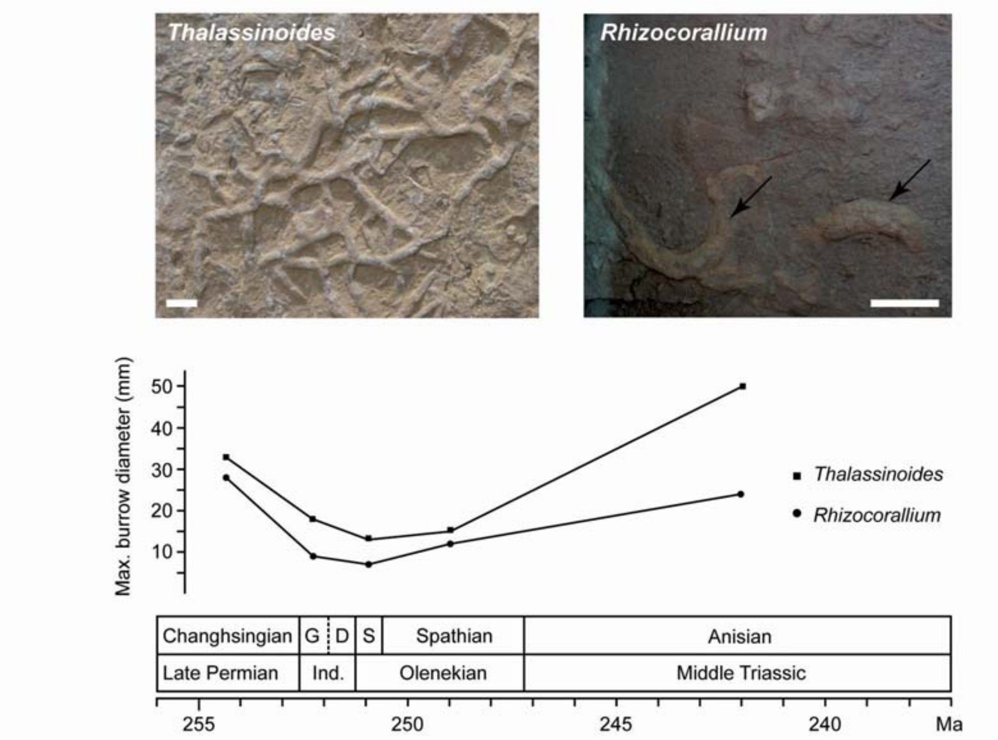

Figure 2. Maximum burrow diameters and images of the trace fossil ichnogenera *Thalassinoides* and *Rhizocorallium* through the Late Permian extinction event and recovery. Values are the maximum recorded globally for each stage or substage, and are plotted in the midpoint of their respective stage/substage. Data are from field sampling and literature survey. Timescale from Algeo and Twitchett (2010). Image of *Thalassinoides* is from the upper Griesbachian of northern Italy. Image of *Rhizocorallium* from the Spathian of northern Italy. Scale bars are 20mm. G = Griesbachian; D = Dienerian; S = Smithian; Ind = Induan.

Burrow depth: absolute burrow depths can be measured in some instances, but usually only when sediment accumulation is episodic or at sedimentary hiatuses (i.e. breaks in sedimentation) when the original sediment-water interface is preserved, and when the amount of sediment compaction is known. At other times, direct measurement provides a minimum estimate of burrow depth and relative burrow depths can be estimated from cross cutting relationships. Burrow depths significantly declined through the Late Permian extinction event, globally and locally, and in the immediate aftermath, the entire infauna appears to have been restricted to the upper 5-6cm of the sediment at most. Given the strong relationship between depth of bioturbation and oxygenation, it is likely that expanding hypoxia was the main reason for this.

Amount of bioturbation: organisms that interact directly with the substrate leave records of their activities that may be preserved. These may comprise discrete trace fossils (i.e. discrete burrows, tracks, trails, borings or other traces) or simply a disturbance or homogenization of the primary sedimentary laminae (i.e. an ichnofabric). Several different ichnofabric indices have been formulated to provide a measure of the amount of bioturbation and to enable (semi)quantitative data to be collected in the absence of discrete trace fossils. Locally, the amount of bioturbation decreases dramatically through the extinction event and most sedimentary rocks in the immediate aftermath are laminated, unbioturbated or poorly bioturbated (e.g. Barras and Twitchett, 2004). Erwin (1993) suggested that the lack of bioturbation was due to the severity of the extinction event and the widespread loss of bioturbating macro-invertebrates. In fact, in most locations, bioturbating organisms were not completely exterminated and bioturbated horizons are present, but these are thin, rare and are usually separated by a considerable thickness of unbioturbated sediment. A better explanation is that fluctuating anoxia is controlling bioturbation: when conditions were suitable, a small-sized, shallow-burrowing infauna was able to briefly colonize the substrate, but the local return of severe hypoxia/anoxia exterminated these pioneers. High sedimentation rates, and episodic sediment influx, may also have suppressed bioturbation in the extinction aftermath (Algeo and Twitchett, 2010).

Tiering and occupied ecospace: the vertical stratification of marine organisms above and below the sediment-water interface in soft-bottom shelf settings has been termed ‘tiering’ (Bottjer and Ausich, 1986). As discussed above, evidence from burrow depth measurements demonstrates that infaunal tiering was dramatically reduced through the extinction event, due to the disappearance of deeper burrows. Evidence from organisms with a mineralized skeleton shows that globally, the shallow infaunal and semi-infaunal organisms most affected were facultatively motile, attached suspension feeders. An additional ecological effect of the Late Permian extinction was the elimination of the high tier suspension-feeding epifauna from most habitats, for example sponges and crinoids (Bottjer and Ausich, 1986). The disappearance of these organisms may have been a consequence of changes in food supply and/or the postulated increases in turbidity of shallow marine ecosystems (Algeo and Twitchett, 2010). The earliest post-extinction assemblages that record abundant crinoids are those from offshore seamounts and structural highs (Twitchett *et al.*, 2004), which were situated away from sediment-laden rivers and where local topography may have induced upwelling and production.

Relative abundance: although absolute abundance is a crucial parameter for estimating biomass, counting individuals in fossil assemblages is not straightforward. Although fragmentation is low in Permian-Triassic fossil assemblages, due to the relative lack of durophagous predators at that time, multi element skeletons are typically disarticulated and incomplete following soft tissue decay. Furthermore, the rate of decay increases with increased temperature (typically doubling for every 10°C rise in temperature), which is a challenge when investigating changes through past global warming events. Fossil assemblages may also be the product of winnowing or hydrodynamic sorting which may affect relative abundance. Often, counts of individual fossilized skeletal elements (i.e. bioclasts) are used in local studies as measures of relative abundance (e.g. Jacobsen *et al.*, 2011), although estimates of the minimum number of individuals that could have produced the recorded bioclasts can also be made. Globally, the number of occurrences has been used as a proxy of abundance. Despite these issues, it appears that relative abundances changed dramatically through the extinction event, with ecosystems in the immediate aftermath being dominated by one or two relatively abundant taxa, and being of much lower evenness than the pre-extinction communities.

Thus, in most tropical and temperate marine habitats, fossil assemblages of marine communities in the immediate aftermath of the Late Permian extinction event comprise low diversity, high dominance assemblages of small sized, often thin-shelled animals (e.g. the bivalves *Promyalina* and *Claraia*, inarticulate brachiopods and rarer microgastropods). These taxa are considered to be pioneering, *r*-selected opportunists (Rodland and Bottjer, 2001; Fraiser and Bottjer, 2004). Occasional horizons of small diameter *Planolites* burrows indicate temporary colonisation events by a scarce soft-bodied infauna of small, deposit feeders living just a few centimetres below the sediment surface (Twitchett, 1999). Equally, most epifaunal organisms would have been restricted to the substrate surface and few would have extended more than ~5 cm up into the water column. Locally, stromatolites, and other evidence of microbial mats, may be encountered (e.g. Schubert and Bottjer, 1995). In the temperate regions, a fairly diverse, but small-sized, nekton of fish and ammonoids is recorded.

The sediments supporting these assemblages are mostly laminated and were deposited under fluctuating anoxic or euxinic conditions (Wignall and Twitchett, 1996; 2002), with biomarker evidence indicating that at times euxinic conditions extended from the seafloor to the photic zone (Grice *et al.*, 2005). For most of the ocean floor, benthic colonization would only have been possible during brief oxygenation episodes. During the most severe euxinic intervals, the benthos would have been eliminated and pelagic organisms would have been restricted to the upper metres of the photic zone. Continental weathering rates, rainfall and run off would have been high, and sediment influx would also have had a severe impact on shelf settings (Algeo and Twitchett, 2010). Globally, the highest diversity and most productive marine ecosystems in the immediate aftermath of the extinction would be likely to be found in shallow, extra tropical seamounts or offshore highs. On the shelves, the shallowest, wave- and wind-mixed zone has been hypothesized as a potential refuge (Beatty *et al.*, 2008), but in the tropics such settings were probably too hot and saline for most organisms. Thus, it is likely that only cooler, higher latitude settings, away from significant river input, would have offered a refuge on the shelf in the immediate wake of the Late Permian extinction.

ECOSYSTEM RECOVERY

It has been frequently stated that the post-Permian recovery was 'delayed' and that recovery is proportionally longer than would be expected for the magnitude of the diversity loss (Erwin, 1993 p. 263). Recent advances in radiometric dating have reduced the apparent duration of the Early Triassic (Ovtcharova *et al.*, 2006), so the lag between extinction and recovery has been somewhat shortened. From the perspective of global biodiversity, however, it still took some 100 million years for family-level marine diversity to return to pre-extinction levels, and from an ecological view, complex structures, such as metazoan reefs, did not reappear for at least 5 million years (Benton and Twitchett, 2003).

Rates of ecological recovery in marine settings can be compared between locations, regions or indeed extinction events, using a simple four-stage recovery model based on the ecological parameters discussed above and taking into account trace fossil as well as body fossil evidence (Twitchett *et al.*, 2004; Twitchett, 2006; Fig. 3). Recovery stage 1 concerns the grossly disturbed communities in the immediate aftermath of the extinction as described above. The next stage involves the reappearance of more complex infaunal communities and in particular of deeper infaunal suspension feeders (e.g. *Arenicolites* and *Diplocraterion*). Stage 3 is defined by the reappearance of epifaunal, erect and higher tier suspension feeders, such as crinoids. Finally, Stage 4 records a return to the levels of ecological complexity, diversity and body size approaching that of pre-event communities and in particular the reappearance of larger (burrow diameters commonly in excess of 20 mm) crustacean burrow networks such as *Thalassinoides*. Using this model, higher latitude shelf ecosystems recovered faster than those from the tropics (Twitchett and Barras, 2004), especially in shallow water settings within wave base (Beatty *et al.*, 2008), and seamounts recovered faster than shelf settings (Twitchett *et al.*, 2004). Pockets of rapid recovery have been described from rare localities within the tropics (e.g. Hoffman *et al.*, 2011) but these do not appear to have led to sustained regional recovery. It took until the Anisian, some 6-7 million years after the event, for final recovery and common, large *Thalassinoides* to be widely recorded (Fig. 2). The lengthy recovery is partly due to rock record biases, and partly due to further episodes of climatic change that had a negative impact on local, regional and global recovery.

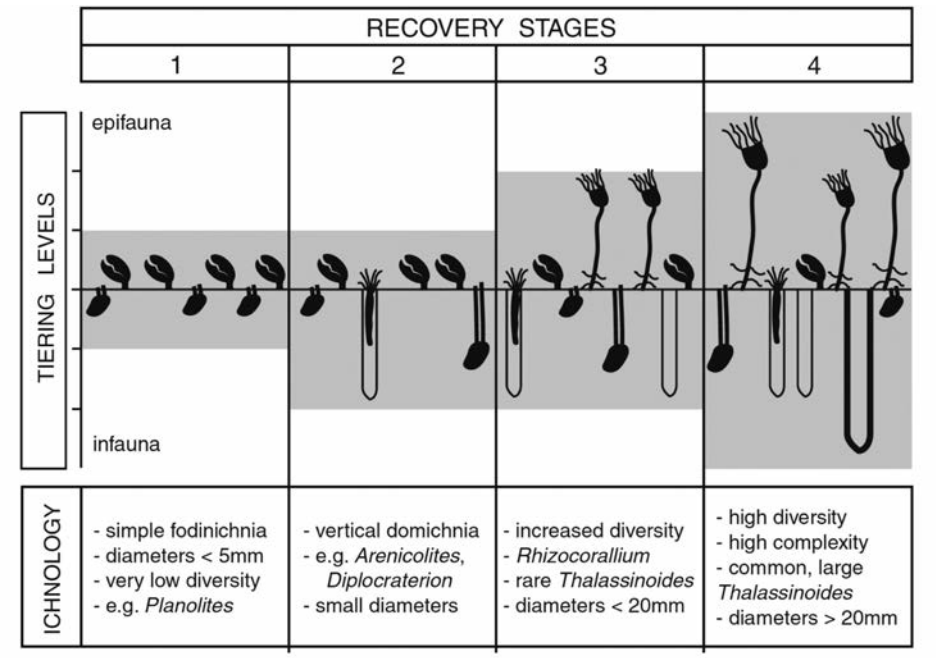

Figure 3. Four stage model for quantifying ecosystem recovery after the Late Permian extinction event, based primarily on tiering and ichnology. Figure from Twitchett (2006).

IS THE LATE PERMIAN EVENT AN ANALOGUE FOR THE FUTURE?

Despite being associated with similar environmental changes as those modelled for the near future, problems with using the Late Permian as an analogue for the future are the differences in the Earth's geography and biota, as well as the magnitude and rates of environmental change and the initial starting conditions. One way to address such obvious concerns is to compare this event with other, more recent, warming-related extinction episodes (e.g. the Late Triassic and Early Toarcian events of the Mesozoic) and to compare and potentially integrate Late Permian data with those from modern experiments, small scale studies and models. If similar patterns are recorded in the fossil data despite the differences in geography, biota and environmental conditions, it would imply that scale-invariant processes are operating which would both strengthen the use of the fossil record in predictions of future change as well as strengthen our confidence in global predictions based on modern, small scale studies. The challenge is to determine which (palaeo)ecological data are most useful, and how the two datasets, modern and fossil, are best integrated in a biologically meaningful way. Integrating data from trace fossils provides one way of adding information from the non-mineralized fossil infauna; alternatively, stripping out the non-mineralized taxa from modern datasets, and re-running the analyses, would provide a better comparison to the past.

Preliminary comparisons of the fossil data from different extinction events do show striking similarities in patterns of ecosystem response, despite differences in initial starting conditions, as well as measureable differences in magnitudes and rates (e.g. Barras and Twitchett, 2007). Equally, some outcomes predicted from modern experiments are apparently recorded in the fossil data (Findlay *et al.*, 2011). Thus, the palaeoecological changes recorded through past episodes of global warming, such as the Late Permian, Late Triassic and early Toarcian intervals, in parameters such as diversity, dominance, bioturbation, body size and ecosystem function are all changes that may occur in the near future under continued global warming.

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Population genetics and the sixth extinction threat on marine species

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INTRODUCTION

Although Mediterranean marine species remained relatively under-studied by population genetics for a while, a very rapid increase in the quantity and quality of publications recently occurred. Even more recently, technological progress revolutionized the way sequence data and polymorphism data can be scored from non-model organisms. We are still on the steep part of the slope of this progress and it is difficult to decide which technology will be the most relevant in a few months to achieve a given goal. What must be known before reading this contribution is that the cost and the complexity of such tools may no longer be considered as limiting factors for biodiversity studies, when genetic data are of use. I will attempt to survey the role that population genetics and phylogeography had or may have in documenting how marine species are threatened by extinction and in helping us to set up management strategies and marine protected areas. First I review theoretical notions and some difficulties or misconceptions; then, I briefly mention certain case studies and draw lines of a (not yet exhaustive) review of Mediterranean marine phylogeography, and finally I suggest how population genetics may provide innovative management tools.

1. THEORETICAL RELATIONSHIPS BETWEEN POPULATION GENETICS, SUSTAINABILITY AND CONNECTIVITY

Divergence time estimations

Population genetics, phylogeography and molecular genetics use the same data sets. One of the uses of genetic data in populations is to allow dating divergences resulting from vicariance, as well as dating of population expansions which often occurred after colonization (or recolonization) of a basin, for instance after glaciations or low sea levels. This is relevant with respect to the study of marine extinctions since this field has much to learn from paleontological and paleo-environmental data (see Kiessling, this volume). Such methods were recently improved (using the BEAST software in particular (Drummond and Rambaut, 2007) and are now reliable enough. The progress in marker development and in sequencing technology (Chenuil, 2012; Chenuil *et al.*, 2010; Gérard *et al.*, 2013) will allow using several markers to improve the reliability and precision of such estimations, so that the limiting factor will often be fossil data : these should ideally be from closely related taxa, not too recent (Ho *et al.*, 2005), not too ancient.

Effective sizes and genetic diversity

We have known for long that the effective size of a population at a given time (i.e. the number of individuals which effectively participate in reproduction) is a much better predictor of its capacity to resist perturbations than census size (e.g. Franklin and Frankham, 1998; Luikart *et al.,* 2010). In addition, census size may be very difficult to assess in the marine environment. Population genetics is of great help since simple mathematical relationships exist between genetic diversity and effective sizes for "neutral" genetic markers (i.e. precisely, markers for which the distinct alleles at non negligible frequencies confer the same selective value, even though some very rare deleterious mutants may arise once upon a time but are rapidly eliminated by natural selection). Although such equations depend on simplifying assumptions (for instance equilibrium may not be reached due to a population size bottleneck, a population size increase, or an admixture event) and their interpretation depends on the underlying model, the genetic diversity as measured at a given time is more relevant than population census size estimates, and also more relevant than effective size to estimate the capacity of a population to survive perturbations since adaptation is directly related to genetic diversity. Adaptation consists in gene frequency changes as a result of natural selection, leading to higher fitness of a population, and is the process by which a population (or a species) changes by selecting adapted genes. The efficiency of this process directly depends on the amount of genetic variation available in the population (see Fig. 1). Genetic diversity as evaluated by genetic markers is supposed to be well correlated with genetic diversity at adaptive loci.

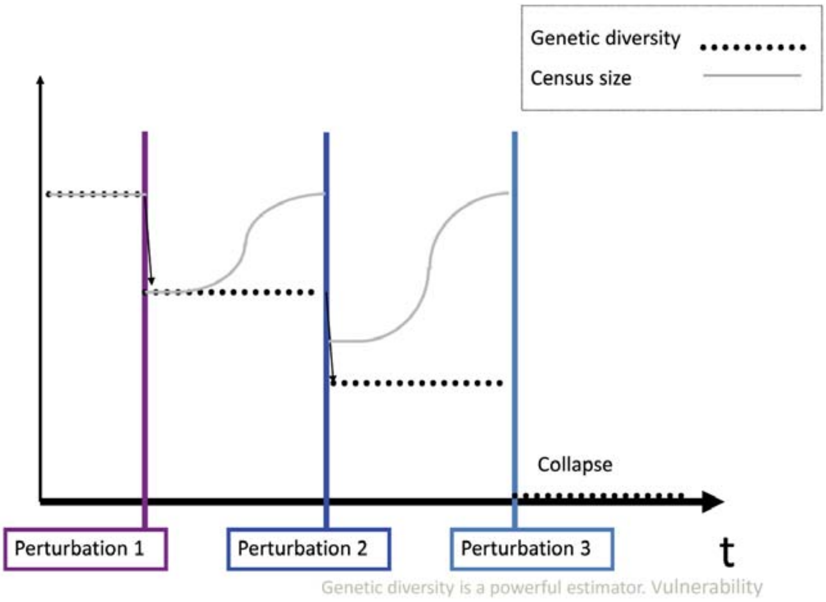


Figure 1. Schematic scenario of changes in census size and genetic diversity after three perturbation events. Census size may totally recover its original value but genetic diversity cannot recover (or would recover at much larger time scales) since new mutants need to arise or migrants need to bring new genes in the population. Thus in this example, the 3rd perturbations lead to population collapse since no variant, adapted to the perturbation, remains. This and other reasons make it preferable to monitor genetic diversity rather than census size. Monitoring census sizes may lead to overlooking the decrease in genetic diversity and increasing threat, until it is too late.

Connectivity

It is well recognized that population genetics allows inferring connectivity among populations and thus helps to define management units. In effect, studies of genetic structure can reveal isolation among populations: if, in a given species, individuals from population A never reproduce with those from population B (due to absence of migration, mortality of migrants, or prezygotic barriers), then protecting population A will have no effect on population B (although from the population dynamics point of view, one may imagine a temporary positive effect on B if for instance predators can move from A to B for feeding on preys). On the other hand, if one of these populations is genetically impoverished, individual transplantations from the "good" population to the impoverished one may bring new alleles and improve genetic diversity. However, if the level of genetic differentiation exceeds a given level, genomic incompatibilities among populations can result in a lower fitness of the individuals resulting from crosses between A and B, independently of any consideration of local adaptation that may have arisen in A and B (Orr and Turelli, 2001). Two classes of methods can be distinguished to assess connectivity using genetic tools. The direct approach –consists in a kind of genetic fingerprinting and allows detecting individual migrants when they are rare and when a sufficient number of individuals are genotyped from the possible source and destination populations. This approach was relatively rarely applicable in marine species, but technological progress, allowing a considerable increase in the number of genetic markers, render it possible in more and more cases. When genotypic data sets obtained by this approach do not appear powerful enough for tracking individual migrants, the data obtained can be used by the indirect approach. Indirect approaches, more widely applicable, assess the circulation of genes among populations by comparing allele frequency distributions between populations which are a consequence of individual migrations (the most ancient approach – still very useful and widely used – consists in computing F_{ST} statistics among populations, and their significance levels, or more generally, in testing the null hypothesis that populations have identical allele frequencies (at the inferred marker loci). The advantage of the direct approach relies in the precise identification of individual migrants and of their population of origin, and when such genetic data are available one can always use them with the indirect approach methods. Increasingly, such approaches are using a large (or very large) number of molecular markers, and are used to detect local adaptation (often named "genome scan"). They can identify outlier populations and outlier genes or detect Genome Environment Associations (GEAs) (e.g. Hohenlohe *et al.,* 2010; Schoville *et al.,* 2012). Most of the studies using such approaches concentrate on the identification of local adaptation genes (outlier genes displaying higher F_{ST} values), although theoretical data predict that such outlier genes may not be local adaptation genes and may not even be physically linked in the genome with such genes (Bierne *et al.,* 2011). However, outlier populations identified by such approaches, paradoxically, may allow the identification of environmental discontinuities since genetic clines tend to be trapped either by areas of low gene flow, which can be created by both ecotones or low quality environments. These results are thus useful for conservation purposes.

Invasive species

Population genetics provides important results to the study of alien species. Genetic diversity and comparisons among geographical areas not only helped to deduce the origin of aliens, but often evidenced the multiplicity of introduction events, and contradicted the widespread idea that invasive species suffered bottlenecks and were genetically impoverished though successful (Martel *et al.,* 2004; Roman and Darling, 2007).

Cryptic species

Numerous cryptic (or "sibling") species were evidenced by genetic tools (Knowlton, 1993; Boissin *et al.*, 2008). These are important results to properly estimate not only biodiversity levels, but also biodiversity dynamics: often the cryptic species are sympatric and appear ecologically equivalent (although the similarity of the ecological niches is nearly impossible to strictly establish). This suggests that cryptic (or sibling) species may replace each other (functional redundancy) but also that they may collapse at the same time under environmental change. Such species can also be considered to provide "replicates" and may provide interesting monitoring targets using this property (c.f. section 3).

2. MAIN PHYLOGEOGRAPHIC PATTERNS DISPLAYED BY MEDITERRANEAN MARINE SPECIES

In this part I will very briefly present some population genetics studies of endangered species, and a preliminary review of Mediterranean marine "invertebrate" phylogeography.

Examples of case studies on endangered or fished species

Studies of population genetics are now available for nearly all endangered or managed species but in numerous cases these studies are extremely partial and poorly informative, generally because a single or few genetic markers were used. In general, Fishes were studied more thoroughly than invertebrates and non-animal taxa, both because of their commercial interest and the least difficulty in finding or setting up molecular markers for their study.

Davies *et al.* (2011) found in the albacore tuna, that the South West Pacific, North East Atlantic and Mediterranean stocks were significantly distinct from one another, corroborating previous studies based on mitochondrial DNA, nuclear DNA (other than microsatellites) and allozyme analyses. They detect the potential presence of three populations across the NEA and two separate populations in the Mediterranean Sea.

Qiu and Miyamoto (2011) report for the pacific bluefin tuna that “Bayesian estimates of effective population size are exceeded by those of census population size (as obtained from fisheries catch data) by a factor of >500” confirming that census sizes give a much too optimistic view of population sustainability and supporting the view that genetic diversity is an interesting monitoring tool.

The dusky grouper (*Epinephelus marginatus)* provides an example of another application of genetic tools for protection, which is potentially easy to develop in any species: PCR tests to identify, from a minute piece of tissue, the species (or in certain cases the geographical origin) of fish in restaurant industry (Asensio *et al.,* 2009). On the same species, Schunter *et al.* (2011) made a genetic structure study using 12 microsatellites markers and found three main zones among which there was significant differentiation: Senegal, Algeria and the rest of the Mediterranean. Previous studies were more partial but compatible with this one (some used mitochondrial DNA).

Rabaoui *et al.* (2011) used mitochondrial COI sequence and found an absence of differentiation in Tunisia, whereas Katsares *et al.* (2008) with the same marker revealed differentiation among populations in Greece for the fan mussel *Pinna nobilis*, the largest endemic bivalve of the Mediterranean Sea. Genetic diversity appears very low with two close haplotypes relatively frequent and few other rare ones. Sanna *et al.* (2013) added a third set of localities and another marker (still from the mitochondrial genome) and concluded that three management units, corresponding to regions, should be considered. Defining management units from population genetic data is not straightforward. In this case, there is allele frequency differentiation among regions, but there are no very divergent groups of alleles, and many alleles are shared among regions. Thus, to establish whether the different entities exchange genes presently, at least an independent (thus nuclear) marker is requested. On the other hand, even within regions, there is significant differentiation among populations, which should be taken into account by managers: genetically differentiated populations may not be connected enough to support each other when one undergoes bottlenecks. Still no reliable and independent molecular marker is published for this species despite its conservation importance and its threatened status due to overexploitation, although nuclear markers are now easy to find for any marine metazoan (e.g. Gérard *et al.,* 2013). Casu *et al.* (2011) evidenced complex patterns of genetic structure in the limpet *Patella ferruginea* using ISSR markers although mitochondrial DNA did not present enough diversity to be informative. ISSR markers potentially allow finding codominant (rarely) or dominant markers rapidly in species for which absolutely no sequence data are available. They are not very widely used in animals. Despite the fact that the information they provide makes their interpretation a little trickier than haploid sequence data or diploid codominant genotypes, such population structure information is crucial for non-model species when no other molecular markers are available. However, microsatellites had been developed on *P. ferruginea* by Machordom *et al.* (2010) and should provide a richer and more reliable genetic information than ISSR, allowing to infer inbreeding as well as population differentiation. Schultz (2011) reviewed genetic diversity of monk seals and found it was extremely reduced for all markers in the Mediterranean stock, as well as other species, as expected knowing how observed population sizes collapsed. Pastor *et al.* (2007) compared the Greek remnant population with the west African coast one and found a very high F_{ST} value between them (0.56). Surprisingly enough, they concluded that the African population could thus be used to reintroduce variation in the Greek one although such values rather suggest that genetic incompatibilities may exist and that their admixture could lead to hybridization and hybrid dysgenesis (low survival and fertility, see Orr and Turelli, 2001).

Galov *et al.* (2011) used microsatellite markers on the bottlenose dolphin *Tursiops truncatus* and characterized 220 individuals from the Adriatic Sea. Fernandez *et al.* (2011) with the same markers plus mitochondrial sequences revealed a fine structure of the species in Atlantic Iberian waters. No published analysis combined both studies to compare Adriatic and Atlantic samples. Contrary to sequence data, which can be retrieved from nucleotide databases, microsatellite genotypes are not straightforward to compare among assays, and at least a few individuals need to be genotyped by two different labs (or "runs" within a laboratory) to be able to combine data sets from both laboratories.

There are many more examples. Although those species have been subject of a population genetic approach, few of them provided estimates of effective size and most were restricted to a relatively small number of populations and markers (though in general nuclear markers and also mitochondrial sequences were available, which is a good point. Data sets from different teams are not always analysed jointly, and collaborations should be encouraged to achieve progress in characterizing those endangered species. None of them benefited of a genome scan approach (e.g. Roesti *et al.,* 2012) or a seascape genetics approach (Schoville *et al.,* 2012) which may allow the identification of influential genes or environmental factors, probably because of their cost. In some cases, few individuals are left alive and accessible for sampling, although non-invasive sampling is often possible. With new genomic technologies, and decreasing prices, it is likely and desirable that such studies are undertaken in a near future, so as to reveal the relevant environmental discrepancy in the distribution of genetic variability within these species.

A remark naturally arises after reading this section: how can such studies be useful for biodiversity management and prevention/prediction of extinction of the marine species? Although simple theoretical bases were discussed above, no clear recommendations were given. For instance one should be willing to ask: is there a minimum value of effective size under which we should take protection measures? Clearly, it may be difficult to give universal threshold values of genetic diversity (or minimum number of living individuals, or critical sizes, as were once used for emblematic mammals) and the most powerful application of genetic tools to estimate population sustainability probably relies on monitoring approaches: by repeating each year (or more or less frequently) one can relatively easily detect a sudden or progressive drop in genetic diversity. Independently, when populations are relatively isolated, temporal sampling of a given population allows to estimate its effective size (Waples, 2005), assuming it did not vary among dates.

General phylogeography and population genetics patterns in the Mediterranean: a preliminary survey

A research in bibliographic databases of papers related to population genetic structure of marine species in the Mediterranean Sea or some of its basins resulted in about 700 papers. Because time was limiting, I only examined those containing the keyword "phylogeography", which led to losing some relatively thorough studies that did not use this keyword (e.g. Boissin *et al.,* 2011). Still for time reasons, I surveyed only those which dealt with metazoans except vertebrates (about a hundred studies). I considered the following basins: Alboran Sea, western Mediterranean (north and south), Central basin (without Ionian Sea), Adriatic, Ionian Sea, Aegean Sea, Levantine Basin, Black Sea, Caspian Sea. None of the study displayed samples in each basin for a given species, even excluding the Caspian and the Black Seas.

The Adriatic was relatively well studied with at least 12 distinct species (Aurelle *et al.,* 2011; Peijnenburg *et al.,* 2004; 2006; Triantafyllidis *et al.,* 2005; Perez-Losada *et al.,* 2007; Iannotta *et al.,* 2007; Luttikhuizen *et al.,* 2008; Derycke *et al.,* 2008; Virgilio *et al.,* 2009; Reuschel *et al.,* 2010; Maltagliati *et al.,* 2010; Yebra *et al.,* 2011; Pavesi *et al.,* 2012; 2013; Sanna *et al.,* 2013; Penant *et al.,* 2013). I also noticed very numerous studies in Tunisia, which allowed comparing both sides of the Siculo-Tunisian sill, but in general, the species had not been sampled elsewhere. For the 12 species sampled in the Adriatic, a large majority (i.e. eight of them) displayed clearcut genetic differentiation between the Adriatic and the other basins where they had been characterized, and in general the Adriatic was the most divergent basin; for one species, a jellyfish (*Pelagia* *noctiluca*) there was no differentiation of the Adriatic, as for none of the basins sampled but this species is a highly dispersive pelagic one, which presence in the Adriatic is well known as a result of outbreaks and not permanent. One species, the cuttlefish *Sepia officinalis*) displayed no differentiation of the Adriatic although some comparisons among other basins displayed differentiations. For two species (*Lysidice ninetta* and *Palaemon elegans)* we could not answer this question (cryptic species were evidenced and present in the Adriatic and elsewhere but genetic structure within species could not be investigated). Clearly this confirms the general isolation of the Adriatic Sea. This basin was recently colonized due to low depths when the sea level increased (about 8,000 years ago) and is presently relatively isolated by gyres (opposing the movements of individuals in or out this sea) or by distinct environment conditions such as low winter temperatures (opposing the survival of potential migrants in or out of the Adriatic which may not be adapted). Contemporary processes thus appear as better explanations than past vicariance to explain this general isolation of Adriatic populations.

Among the 12 invertebrate studies made in Tunisia and encompassing the Siculo-Tunisian sill (Perez-Losada *et al.,* 2007; Zitari-Chatti *et al.,* 2007; 2009; Dridi *et al.,* 2008; Fassatoui *et al.,* 2009; 2012; ben Faleh *et al.,* 2009; Gharbi *et al.,* 2010; 2011; Bottari *et al.,* 2011; Rabaoui *et al.,* 2011; Casu *et al.,* 2011; Hmida *et al.,* 2012; Chatti *et al.,* 2012), six displayed differentiation at the Siculo-Tunisian sill location precisely, three cases display differentiation but the location did not correspond to the STS (*Pagellus erythrinus, Pinna nobilis* and a gastropod currently under study by Marzouk *et al.* (submitted), and three cases did not display differentiation (the jellyfish *Aurelia aurita*, the cuttlefish *Sepia officinalis*, and *Echinaster sepositus* (but sample sizes for this species may not be sufficient).

The well-known distinction between the Alboran Sea and the rest of the Mediterranean basin is also well supported, though less conspicuously than the Adriatic one (e.g. Patarnello *et al.,* 2007).

The eastern Mediterranean basin deserves more scrutiny. Although rarely presented as hosting major phylogeographical breaks, it seems to display genetic discontinuities in a number of species (some still not published), more marked than the Siculo-Tunisian sill. Thus the sea urchin *Paracentrotus lividus* displays a larger differentiation between Crete and Lebanon than across the STS (Penant *et al.*, 2013), the cockle *Cerastoderma glaucum* (Tarnowska *et al.,* 2010), *Ophioderma longicauda* (Boissin *et al.,* 2011; Weber and Chenuil, 2013), the damselfish *Chromis chromis* (Domingues *et al.,* 2005) and the sea bass (Bahri-Sfar *et al.,* 2000) also display genetic discontinuities within the eastern Mediterranean which are important relative to their overall population structure. In particular, some of these species do not even display a phylogeographic break between the Atlantic and western Mediterranean. Biogeography and oceanography support the view of a discontinuity within the Eastern Mediterranean, the Levant being rather distinct of the Aegean Sea in particular.

A review of phylogeographic studies may allow finding very common phylogeographical breaks that tend to be shared among species. However, such breaks may be due to two main different causes: the presence of barriers to dispersal or a survival differential across the barrier (when local adaptation led to differentiation of adaptive genes across the barrier). Disentangling between the two causes is crucial for biodiversity conservation but this requires studies with more fine grained population sampling than currently done: this will not be solved by new technology tools only, but requires field sampling and basic environmental data also (see section 3).

Misconceptions found in published studies

A substantial number of Mediterranean marine population genetics or phylogeography studies conclude more or less the same thing: “as expected for a marine species dispersing via planktonic larvae, there is no gene flow restriction among basins”. However, I identified two important misleading factors: for a number of them, mostly the oldest ones, sample sizes were very low and one cannot rule out that non-significant genetic differentiation is only due to low statistical power. I therefore recommend to investigate the power of the data set, a practice which is still uncommon but now made possible with recently available softwares: Powsim (Ryman and Palm, 2006) allows to investigate the effect of sample size and allele frequency distributions under some assumptions, while SPADE or SMOGD (Crawford, 2010) provide confidence intervals on between-differentiation estimators such as the D of Jost, an analogous to the F_{ST}. In addition, most studies used the Phi_{ST} statistics instead of the F_{ST} when they have sequence data (most of the marine phylogeography studies have COI sequence data) and most authors (and reviewers) are convinced that this statistics, since it takes into account the relatedness among haplotypes (F_{ST} is only based on frequency distributions) is more powerful. But the reverse is much more generally true (e.g. Penant *et al.*, 2013) and simulations (Chenuil and Aurelle, unpub.). Thus published studies globally underestimate genetic differentiation among basins or among populations within basin. Other kinds of misconceptions are also commonly found (Karl *et al.*, 2012).

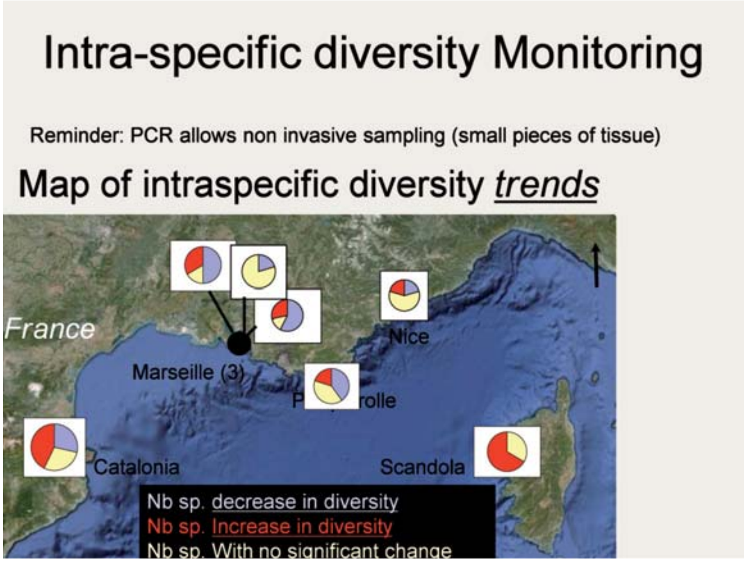
3. INNOVATIVE MANAGEMENT TOOLS FROM POPULATION GENETICS

It is recognized that fauna and flora inventories on a repeated temporal basis are crucially needed, even with large temporal steps, at least for the baseline).

- Genetic monitoring is recognized as a promising tool for conservation and management (Schwartz *et al.,* 2007) but remains very rarely undertaken.

- Sampling of tissue, frozen or in alcohol (for DNA) but also eventually in RNA-later for expression analyses should systematically be done in parallel with taxonomic biodiversity inventories. This would naturally result in common sampling location sets across species studied in phylogeography and represent a progress (commonly population genetic researchers study a single species and sample in few scattered locations thus no common sampling sets of locations are available among species for efficient meta-analyses).

- Such locations should encompass zones of barriers to movements of animals and zones of variable environment characteristics on a relatively fine grained scale, to allow distinguishing hydrological barriers from ecotones.



Intra-specific diversity Monitoring

Reminder: PCR allows non invasive sampling (small pieces of tissue)

Map of intraspecific diversity *trends*

Figure 2. Mapping the trends in genetic diversity for a given species can reveal general or local loss or improvement in sustainability. When correlating to changes in environmental factors this allows identifying influencial factors.

- Thus, I suggest that a new index of ecosystem sustainability could be provided to monitor localities: a multispecific index of within species genetic diversity. Such parameters, associated with ecological studies, are of primary importance to detect when a population is endangered, and to predict the influence of environmental change on individual species. Indeed, intra-specific genetic biodiversity monitoring can display early alarm signs much before studies of inter-specific diversity (i.e. typical biodiversity studies). For a common set of localities combining as in Fig. 2, data on intraspecific genetic diversity for a set of taxonomically and ecologically diverse species potentially provides a powerful ecosystem monitoring index.

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Radiations, collapse and recovery of biodiversity

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ABSTRACT

Explosive radiations of diversity in aquatic ecosystems are pervasive in the history of life. They encompass broad-scale radiations like the diversification in body plans in Cambrian phyla, to recent, rapid radiations like the cichlids in Eastern Africa. Adaptive and non-adaptive processes promoting fast diversification range from niche specialization to sexual selection, respectively. Yet how disturbance regimes differentially collapse or recover entire communities generated throughout these processes remains largely unexplored. The aim of this contribution is twofold. First, I present some of the eco-evolutionary models with explicit demography of populations and speciation dynamics to illustrate the idea of a radiation and their connection to the formation of biodiversity patterns. Second, I briefly summarize recent work showing patterns of collapse of entire communities in aquatic systems. I finally discuss some of the open challenges to combine the adaptive and non-adaptive processes predicting radiations with the observed collapse and recovery of entire communities in aquatic ecosystems.

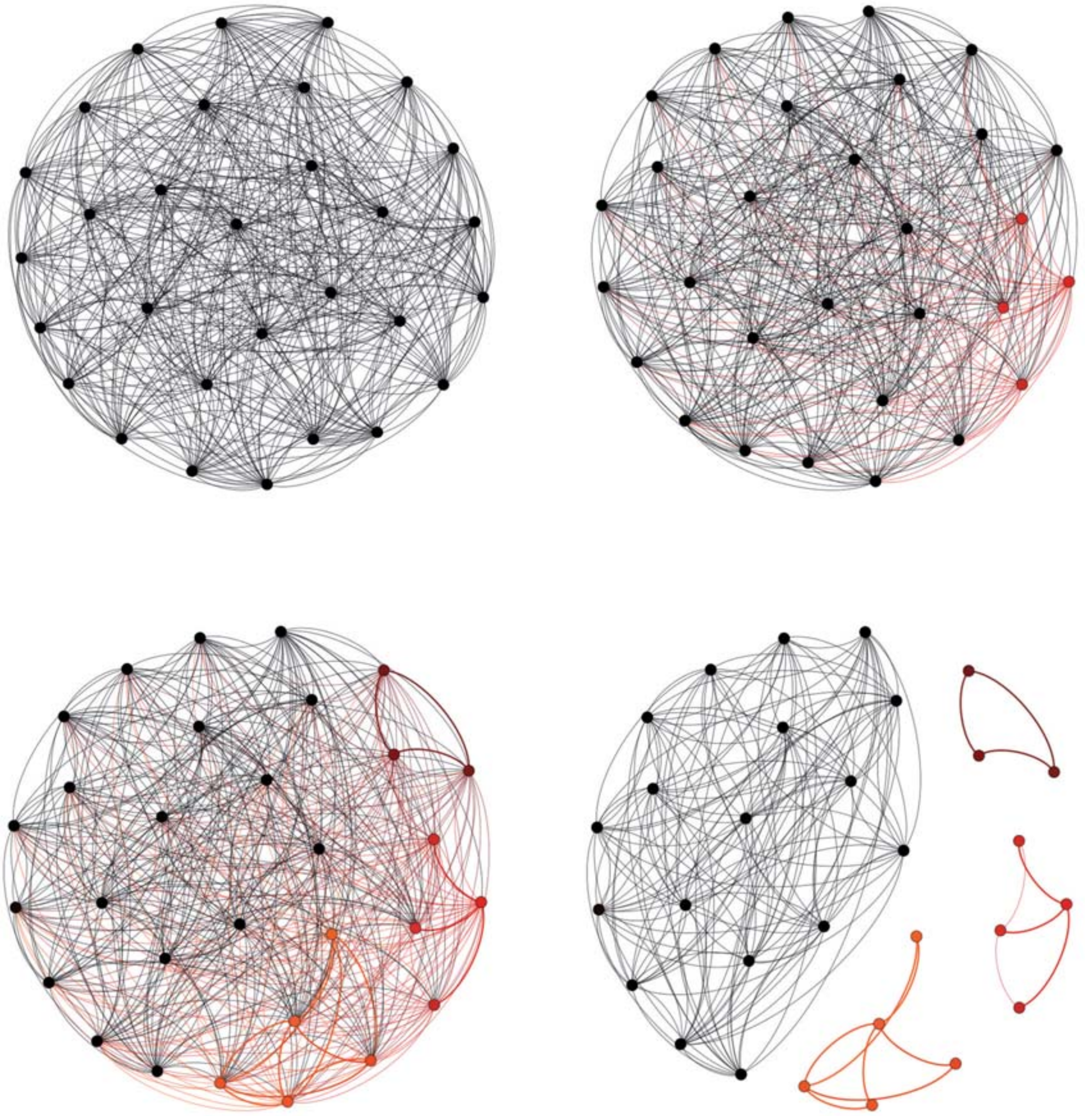
RADIATIONS

Some 20,000 species of fish are currently known but diversity in fish is still severely under-documented. Although biological radiations are pervasive in the history of life (Marshall, 2006; Davidson and Erwin, 2006), the number of species formed throughout adaptive and non-adaptive radiations is currently unknown (Schluter, 2000; Kocher, 2004; Seehausen, 2006; Gavrilets and Losos, 2009), and several questions remain open. What are the mechanisms driving biological radiations? Are there unifying principles underlying the patterns of radiations? How do patterns of biological radiations relate with biodiversity patterns? Does the type of radiation (adaptive or non-adaptive) influence the rate of species loss under different disturbance regimes and environmental fluctuations? How does the type of radiation influence the rate of recovery in natural ecosystems?

Several theoretical and empirical studies suggest that radiations driven by niche diversification (adaptive radiations) shape patterns of evolution mainly as a consequence of local adaptations to environmental factors and ecological interactions (Seehausen, 2006; Schluter, 2009; Butlin *et al.*, 2009; Gavrilets and Losos, 2009), but explanations accounting for a burst of biodiversity in the absence of ecological mechanisms (non-adaptive radiations) also exist (Ritchie, 2007; Rundell and Price, 2009; De Aguiar *et al.*, 2009; Morlon *et al.*, 2010; Venditti *et al.*, 2010; Melián *et al.*, 2010; Davies *et al.*, 2011). Recent studies have shown that a combination of adaptive and non-adaptive mechanisms can predict a radiation (Wagner *et al.*, 2012), yet a framework to infer the adaptive and non-adaptive mechanisms from data is lacking.

Fortunately, the last decade has seen the rise of datasets with genetic, morphological and ecological information for a large number of individuals. One of the main surprises in analysing such data has been the discovery of large genetic, phenotypic, behavioural and metabolic variations among individuals within many natural populations (Lloyd-Smith, 2005; Glazier, 2005; Mitchell-Olds *et al.*, 2007; Biro and Stamps, 2010; Bolnick *et al.*, 2011; Melián *et al.*, 2011). A parallel discovery from theory and experiments has shown a strong temporal convergence between evolutionary and ecological dynamics (Yoshida *et al.*, 2003; Hairston *et al.*, 2005; Hendry *et al.*, 2007; Schoener, 2011). These results suggest the absence of a framework to infer mechanisms to study radiations; their connection to biodiversity patterns presents new computational and analytical challenges.

I shall illustrate with a graph an example of the gaps to connect theory and data and the challenges we face if we attempt to fill those gaps with a modelling exercise (Box 1). Say we have genotypic, phenotypic and ecological data on a large number of individuals and sites belonging to several species. The data have sufficient level of resolution within each species, and the number of species and sites to permit inference not only at individual and population level, but also at community and metacommunity level. How many mechanisms do we need to take into account in a model to predict a radiation? Box 1 (below) attempts to answer this question under the simplest scenario.



Box 1. Radiations in spatial networks: I here present an eco-evolutionary toy model that, in its simplest form, aims to infer a set of mechanisms whose expectations can be tested using individual-population-metacommunity level data (top left). As the ideal data come at individual level with explicit sampling locations, the model should take into account individuals located in spatial landscapes. Top left represents the initial stage with each individual represented as a black node in a given spatial location. If we want to infer the observed genetic and phenotypic divergence within and between populations, within and between sites, we would like to start by assuming that all the individuals are reproductively compatible corresponding to a completely connected graph. This is like going backwards in time and as if there was a founder effect with little standing genetic variation. At this stage, distance edges, represented by the geographic distance matrix D, containing all the dij values, capture both geographical separation of each pair of individuals and viable edges. Viable edges mean that two connected individuals can produce viable offspring if they are sufficiently similar at genetic level. Let me assume the classical Mayr species concept based on reproductive isolation. Because we define the genome for all individuals, we know the pairwise genetic similarity matrix Q that defines all the qij values for individuals i and j. A species is defined as a population whose genetic similarity of each pair of individuals within the population is above a minimum genetic similarity threshold, qmin. For example, the genetic similarity between each pair of individuals i and j, qij, within the population in red (top right) satisfies qij > qmin. Let me assume at each time step that an individual die and the offspring of two randomly selected parents within maximum distance for mating dmax reproduce, and the offspring fill the empty spot. After some generations, all the individuals in the network are still reproductively compatible, but divergence has started to occur in the periphery of the graph (top right). How many mechanisms can predict the divergence at genetic and phenotypic level given the observed data? This is a quite challenging question, but the simplest scenario is ready to be tested. Under the simple rules specified above, species formation start in some geographical locations (red circles, top right and dark red, red and orange, bottom left). In the last stage, individuals within each species are reproductively isolated to all other individuals in the population. For example, each pair of individuals i and j within the species in red now satisfies qij > qmin and qik ≤ qmin for all the individuals k outside the red population. Formed species have different abundance (i.e., dark red (3), red (4) and orange (5). Modified from (Melián *et al.*, 2012).

Fig. 1 presents some of the outputs from the simple model described in Box 1. Despite its simplicity the model is rich in expectations, and small additions like negative frequency-dependent sexual selection alter completely the patterns observed in the simulations. The model with negative frequency-dependent sexual selection is like the model explained in Box 1, but now rare genotypes reproduce at higher rates than common genotypes. The metaphor here is that rare types increase the probability to escape from virus or parasites attacking reproductive proteins and thus increase the probability to have more offspring during their adult stage. Again we can ask, what are the mechanisms driving biological radiations? Well, as we can see in Fig. 1, neutral dynamics predicts speciation events occurring at a nearly constant rate and the addition of negative frequency-dependent sexual selection dramatically alters this pattern. Specifically, the advantage of the rare shows a rapid series of speciation events followed by a plateau with very low speciation and extinction events (black *vs.* red in Fig. 1a).

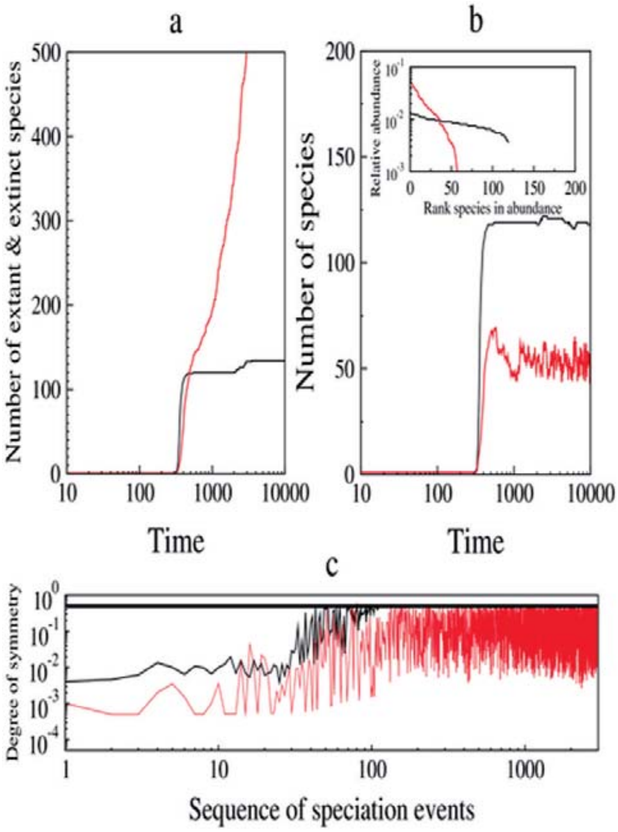


Figure 1. Radiations, number of species, and diversity. (a) Simulated total number of species (both extant and extinct) as a function of time for the model with (black, also used for b and c) and without (red) frequency-dependent sexual selection. Time measured in generations where one generation is J time steps and J is the total number of individuals in the graph. After a transient phase, speciation events occur at a nearly constant rate in the model without frequency-dependent sexual selection. In contrast, the frequency-dependent sexual selection scenario shows a rapid series of speciation events followed by a plateau with very low speciation and extinctions events. (b) Simulated number of extant species as a function of time for the model with and without frequency-dependent sexual selection. Insets represent the species abundance distribution at stationarity; x and y-axis represent the rank in species abundance from the most common to the most rare and the relative abundance of each species in the community, respectively. Frequency-dependent sexual selection produces more extant species and higher diversity (black line inset in b). (c) Simulated abundance symmetry of the new species after each speciation event. We measured the degree of symmetry in each speciation event as S=(S/M), where S and M are the size of the smallest new species and the mother species, respectively. Perfect symmetry means that the new species abundance is identical to the mother species abundance; low value means that the new species abundance is much smaller than that of the mother species. Thick line represents perfect symmetry. Modified from (Melián *et al.*, 2010).

How do patterns of biological radiations relate to biodiversity patterns?

The number of species present at steady state changes substantially between the radiation scenario, with the advantage of rarity, and the nearly constant rate of speciation in the neutral scenario, where there is not advantage of being rare. Under most parameter combinations explored, the number of species under negative frequency-dependent sexual selection doubles the number of species under the neutral scenario (black vs. red in Fig. 1b). In addition to these predictions, both scenarios also differ in the patterns of diversity. In contrast to the neutral scenario, where most species are rare and only a few species are common, most species in the advantage of the rare scenario have similar abundance (Inset Fig. 1b). Finally, these models generate some expectations that may be useful to understand speciation and extinction dynamics. The advantage of the rare predicts larger incipient species abundance than the neutral scenario which suggests that demographic stochasticity is a main driver of extinction and operates mostly under the neutral dynamics (Fig. 1c).

COLLAPSE AND RECOVERY OF BIODIVERSITY

A theoretical framework to infer the mechanisms driving a radiation and its connection to biodiversity patterns is still at its incipient stage, yet there is a larger gap in how disturbance regimes differentially collapse or recover entire communities generated throughout adaptive or non-adaptive radiations. Questions like "does the type of radiation (adaptive or non-adaptive) influence the rate of species loss under different disturbance regimes and environmental fluctuations?" or "how does the type of radiation influence the rate of recovery in natural ecosystems?" are still far from being answered. Here, I briefly summarize recent work showing the collapse of entire communities in aquatic systems and discuss the connection which this collapse may have with an adaptive or a non-adaptive radiation.

Local extinctions of genotypes are expected to occur quickly if most individuals within any given genotype in a given population or metapopulation are highly specialized to a few resources or dimensions within a niche. This expectation to extinction may even be faster after some disturbance regime (i.e., environmental fluctuations, fisheries, habitat loss, toxicants, etc.) that may erode reproductive isolation among differentiated populations (or species), leading to drastic changes in genetic, developmental and ecological differentiation. This is the concept of speciation reversal (Vonlanthen *et al.*, 2012). As populations, or stocks, decline through demographic processes, the genetic diversity within these populations may collapse irreversibly through evolutionary processes coupled with the demographics.

More than 30% of the 20th century diversity of European lake whitefish has been lost irreversibly between the 1920s and now (Vonlanthen *et al.*, 2012), and more than 50% of the endemic species of cichlid fish in Africa's Lake Victoria between 1980 and now (Seehausen, 2006). With some 200 species extinct in just 30 years the latter case entered textbooks as the largest mass extinction of animal species witnessed by scientists. Pollutants, eutrophication and fisheries – related species introductions are among the most important events that drive such a massive event of speciation reversal. Given these numbers can also be applied to several taxa, let us consider the speciation reversal of entire communities under the adaptive and non-adaptive radiation scenarios presented in the previous section. Which of the two scenarios will drive higher rate of speciation reversal and extinctions? How does speciation reversal connect to local and regional extinction dynamics of several species? Under the neutral scenario, adaptive mechanisms are not necessary to have a speciation event and only dispersal limitation and restrictions to mate drive divergent populations and speciation in space. Fluctuating environments in the landscape may have an impact on the dynamics of these divergent populations as the volume of the habitats may be reduced but, since selection on traits is weak, populations under neutral dynamics may quickly expand their distributions after a disturbance, especially if dispersal constraints are released.

A more realistic scenario can be the one that considers negative-frequency dependent sexual selection as in the previous example. This scenario can occur at least under two different mechanisms. A niche-driven scenario and a negative frequency-dependent sexual selection scenario. Let us say we have a niche-driven scenario with just one niche dimension, for example depth, as the main driver to predict a radiation of species in a given aquatic ecosystem. Colonization of a depth gradient may imply the advantage of the rare: some individuals colonizing deeper zones may increase their chances to have offspring, and assuming there is not an excessive accumulation of deleterious mutations in the front of the population, new types may adapt to those environments after several generations. Traits adapted to deeper zones may also drive sexual differentiation and other ecological processes in those populations but these processes are assumed to be a by-product of natural selection. If selection on traits is strong with depth, then species can be formed and richness increase, but unfortunately reduction of habitats as a consequence of overload of nutrients or other disturbances can drive speciation reversal in a few generations like in the example of the European lake whitefish (Vonlanthen *et al.*, 2012).

Let us imagine now the scenario with sexual selection as the main driver of divergence. Will the reduction of habitats as a consequence of nutrients overload have the same impact? The spatial structure is not as important as in the niche-driven scenario in the sense that the one dimensional gradient is no longer the main force driving divergence and speciation. Selection is now driven by the advantage of the rare regardless where they are in space and one may think that recovery can be faster after nutrient reduction because individuals can escape from the one-dimensional constraint towards new dimensions in the niche space. Unfortunately a big gap between these intuitions, theory predictions and data constrain our understanding of biodiversity dynamics under these scenarios.

CONCLUSIONS

I briefly summarize some of the open challenges to connect the mechanisms driving biological radiations with the formation of biodiversity patterns. This connection is still at an incipient stage both from a modelling and an experimental perspectives. I also have tried to show the large gap between models and data. This is to understand how disturbance regimes differentially collapse or recover entire communities generated throughout adaptive or non-adaptive radiations. I illustrate how neutral dynamics or the advantage of the rare dynamics differ in the probability to predict a radiation, in the number of species and diversity and in the probability of extinction. Finally, I have presented how a niche-driven community may collapse and how radiations driven by neutral dynamics may be expected to delay the probability to collapse and recover sooner than niche-driven radiations. At present, these expectations are highly speculative and they all deserve further theoretical explorations and comparison with data and specific experiments.

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Extinction trends of marine species and populations in the Aegean Sea and adjacent ecoregions

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ABSTRACT

Despite its relative oligotrophy, the eastern Mediterranean – and particularly the Aegean and Ionian ecoregions – supports a great marine wealth with considerable populations of endangered species. Available historical and current data indicate severe declining trends reaching sometimes local depletion and extinction of several populations such as the Mediterranean monk seal, loggerhead turtle, bath sponges, red coral, elasmobranchs, cetaceans, and edible bivalves. Intensive exploitation, prey depletion, accidental catches, habitat degradation, pollution and climate change are the major threats, having severely impacted the physiognomy of local marine ecosystems, although monitoring and conservation efforts, focused on *Monachus monachus* and *Caretta caretta* over the last 20 years, have led to a relative stabilization of certain local populations.

1. INTRODUCTION

1.1 Regional characteristics

The Aegean Sea represents a distinct Mediterranean ecoregion characterized by extremely complex morphology, with more than 3,000 islands and islets. It comprises wide plateaus and deep canyons and exhibits great habitat diversity alternating rocky coasts, sandy shores, sea-grass meadows algae-dominated bottoms, coralligenous formations and marine caves. This habitat variability, along with its specific temperature, salinity and water circulation profile is reflected in its biota, which is rich and comparable to the other northern Mediterranean subareas, namely the Gulf of Lion and the Adriatic (Coll *et al.*, 2010). As part of the eastern Mediterranean basin, the Aegean Sea is subject to the so-called “tropicalization” or “meridionalisation” process (see Bianchi, 2007; CIESM, 2008; Lejeusne *et al.*, 2010) of the Mediterranean. The warmer water of the Aegean Sea (Skliris *et al.*, 2011), favor the northwards expansion of the biota at the detriment of the native species.

The Aegean is connected with the Black Sea, from which it constantly receives brackish and colder waters. This influence and the higher river runoff are determinant for its northern sector, which is distinct by higher productivity and diversity from the southern (Lykousis *et al.*, 2002). On the other hand, the influence of the saline and warm waters flowing northwards from the Levantine enables the settlement of Lessepsian migrants in the southeastern Aegean and their further dispersal to the rest of the Mediterranean (CIESM, 2013; Zenetos *et al*., 2009).

Beyond the differences between north and south sectors, the Aegean ecosystem as a whole is of great interest for research and conservation purposes. Its rich waters host extensive and healthy *Posidonia oceanica* meadows, shallow reefs covered with *Cystoseira* assemblages, the largest population of monk seals in the Mediterranean, high benthic diversity on soft sediments (especially in lagoonal and estuarine habitats), rich benthic communities on coralligenous and cave habitats, including rare and endemic species, valued commercial invertebrates such as bath sponges and precious corals, and dense populations of small cetaceans.

Yet little of this biodiversity has been adequately studied and evaluated – a lack of knowledge particularly crucial since these areas have suffered centuries of exploitation. Evidence of interaction between humans and the marine fauna dates back to the Paleolithic period and continues through the Greek antiquity, the Roman, and Byzantine periods: fishes, crustaceans, mollusks, sponges, corals, even the monk seal have been harvested or hunted leading to conspicuous local depletions and extirpations (see Coll *et al.*, 2010).

At present, most of the Greek coasts are affected by multiple high-impact anthropogenic activities; tourism and human recreational settlement are fairly widespread, while urbanization, industry, agriculture, aquaculture and waste disposal also impact the natural marine ecosystem (Anagnostou *et al.*, 2005). These factors, along with an ongoing intensive exploitation of fishery resources and the added effects of climate change and biological invasions, especially in the southern Aegean, currently constitute the main threats for marine biodiversity.

Despite the high value and significance of Aegean biodiversity, only one Marine protected area (MPA) has been established to date in the Greek territorial waters, the “National Marine Park of Alonissos Northern Sporades” (NMPANS), which is the second largest Mediterranean MPA, covering approximately 2,260 km^2. Furthermore, there are more than one hundred ”Sites of Community Importance” of the Greek NATURA 2000 Network (92/43/EEC) encompassing marine areas (Thessalou-Legaki and Legakis, 2005) for which management measures have not yet been implemented.

1.2 Estimating patterns and processes of local extinction

Under the scope of the extinction threat in the Aegean and adjacent ecoregions, we surveyed: i) the status of Mediterranean species that have been recently assigned as (critically) endangered in this region and ii) certain species, which, mostly due to overexploitation, present a conspicuous decline of their populations, but are still not included in Red Lists. We focused further on two case studies, one for each of the above issues in order to investigate and elucidate the patterns and processes potentially leading to extinction: i) the monk seal, an emblematic, critically endangered species and ii) the bath sponges, a marine resource appreciated worldwide, harvested in this area for centuries. In each case we went through the historical background of the species interaction with humans, their past distribution and abundance, the causes of population depletion and/or distribution shrinkage, and we present the current status of their populations, threats and conservation measures (if any).

2. MEGAFAUNAL SPECIES UNDER THREAT

2.1 Case study: the monk seal *Monachus monachus*

Since 1996 this species is critically endangered (IUCN and Greek Red Data Book category: CR) on the basis of its very small, heavily fragmented population structure and declining numbers.

2.1.1 Historical data on population and distribution

The monk seal has been interacting with man for centuries, being now very close to extinction. While originally it had a wide distribution across the entire Mediterranean basin and the Macaronesian region, through time this has been increasingly limited to certain areas, specifically the Aegean Sea (Figure 1). Historical evidence from Antiquity concerning its habitat indicates that it was living along all the Mediterranean mainland coasts in addition to the island populations; it inhabited sandy beaches in large herds, as vividly described by Homer in *Odyssey*, sometimes reaching up to thousands of individuals, not only the rocky coasts of remote islands (see Johnson and Lavigne, 1999 for a detailed review). As Johnson (2004) analytically described, the distribution shrinkage and population depletion of the species, which resulted in the virtually exclusive use of isolated caves, were actually triggered by human disturbance. The shift in habitat might explain the change in monk seal's character traits and behaviour, driven either by survival instinct and natural selection or by individual learning experience: from a gregarious and docile animal it gradually became solitary, retiring, and shy (Johnson and Lavigne, 1999). Moreover, this prolonged decline has produced a severe bottleneck that significantly reduced genetic variability, while at the same time a substantial genetic divergence has been observed between the extant populations (see Aguilar and Lowry, 2008).

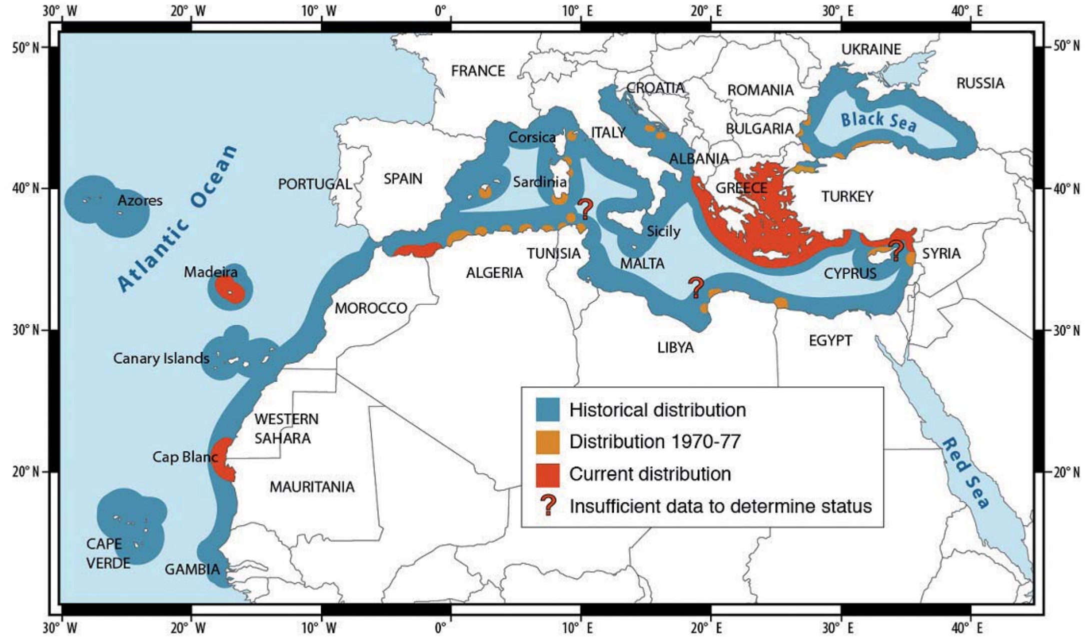

Figure 1. General distribution of the monk seal, modified from Johnson *et al.* (2011); distribution in 1970-77 (depicting only sites additional to the current distribution) was plotted according to Sergeant *et al.* (1978).

2.1.2 Causes of decline

Two main factors caused the historical decline of *M. monachus*:

i) Its intensive exploitation over the Mediterranean during the past two millenniums, particularly during the Roman period. Seals were massively hunted for leather, oil, medicines, and zoo supply, and they continue to be killed by fishermen for damaging their equipment and competing for fish resources. Their commercial exploitation in the Black Sea up to the 1970s led to the species extinction from this area (Kirac, 2001 *in* Johnson, 2004).

ii) Deterioration of the species preferred habitat. This started in the Roman Era as well, with the intensive deforestation and consequent destruction of coastal vegetation, which gave the seals shelter from the sun. The gradual occupation of sandy coastline by humans and the development of tourism in the past century led the species to an almost exclusive use of caves, limiting social interaction and reducing mating and breeding success (Johnson, 2004).

Due to the above reasons, the monk seal populations eventually disappeared through the past century from the western Mediterranean and Adriatic coasts. Furthermore, the species is considered regionally extinct in many areas of the eastern Mediterranean, while its populations suffered a 50% decline on the coasts of Turkey during the last twenty years (Güçlüsoy *et al.*, 2004).

2.1.3 Current population status

Globally

According to the most recent IUCN estimates (Aguilar and Lowry, 2008), the current global population size is 350-450 animals distributed as follows:

- 20-23 individuals in the archipelago of Madeira. The population is under protection, showing signs of recovery (Pires *et al.,* 2008).
- 130 individuals at Cabo Blanco Peninsula, Western Sahara. It is one large colony living in two caves on a 4 km long beach.
- 10 animals on the coast of Morocco and Algeria (Aguilar, 1999). Its survival is questionable.
- 250-300 individuals in the eastern Mediterranean Sea.

IUCN also reports the extinction of many small subpopulations during the last two decades. The estimated eastern Mediterranean population in the 1970s (Figure 1) was 350-390 individuals and the global species population counted around 625 individuals (Sergeant *et al*., 1978).

In the eastern Mediterranean

Out of the total estimated population size, approximately 200 individuals live in the Greek and 100 on the Turkish coasts. The minimum estimated population size for the Greek islands where the species is mainly distributed is 179 adult individuals, representing around 40-50% of the global population and giving annually an average offspring of 27 pups (Dendrinos *et al.*, 2009).

Estimates based on direct observations, remote sensing, mark-recapture methods, but mostly on the recording and monitoring of the suitable habitat and annual pup production (data from Güçlüsoy *et al.*, 2004; Gucu *et al.*, 2004; Mom, 2009), indicate that the largest and best studied sub-populations within this region (the minimum numbers of estimated individuals are given in parentheses) are located at the Northern Sporades Islands (52), the islands of Gyaros (55), Kimolos (49), and Karpathos (23) in Greece and at the Cilician Basin (25) in Turkey. The populations along the Aegean coasts of Turkey count approximately 63 individuals whereas on the rest of the Greek coasts around 46.

The major factor favouring the survival of the monk seal in the eastern Mediterranean and particularly the Aegean Sea is the presence of suitable habitat both for resting and pupping, due to the specific geomorphology of the area. During the last 20 years of research, a large number of monk seal sightings (Figure 2a) and more than 560 suitable monk seal shelters (Figure 2b) have been identified throughout Greece (Mom, 2009). However, IUCN points out the small number of mature individuals in the eastern Mediterranean population, the loss of the original colony structure of the species and the abnormal reproductive rate. It is worth mentioning that recent monitoring of monk seal population on the uninhabited island of Gyaros (southwest Aegean) revealed a colonial population structure of the species on open beaches, unique in the Mediterranean Sea (Karamanlidis *et al.*, 2012).

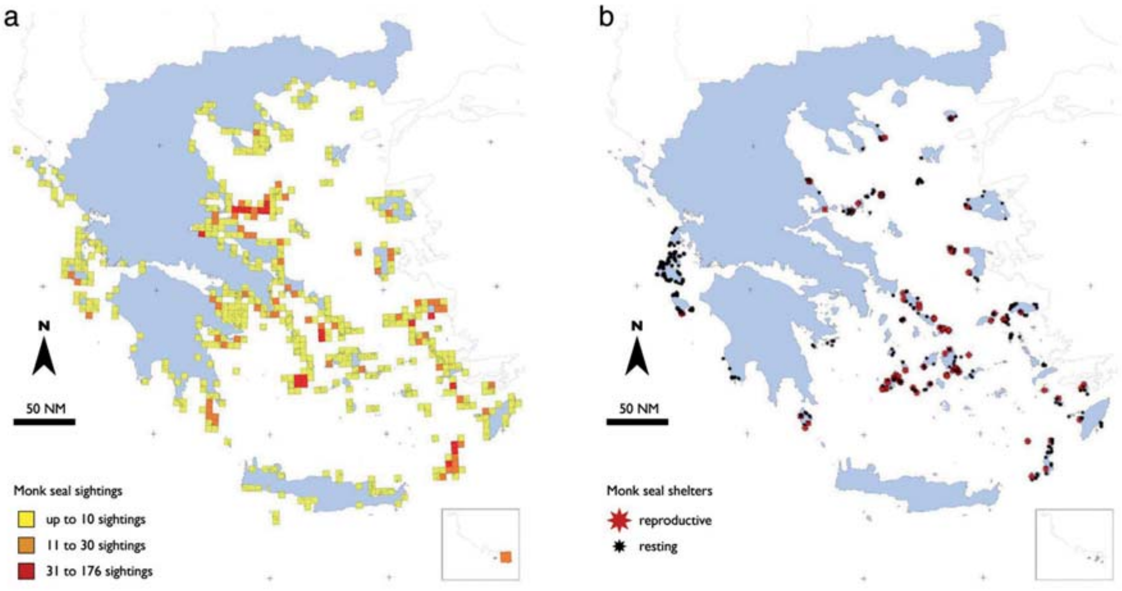

Figure 2. Mediterranean monk seal sightings (A) and locations of suitable shelter (B) recorded through the operation of the Rescue and Information Network in Greece from 1996 to 2009 (from Mom, 2009).

2.1.4 Current threats

Investigations (mostly necropsies of stranded animals) both in Greece and Turkey (Güçlüsoy *et al.*, 2004; Androukaki *et al.*, 2006) suggest that the main current threats to *M. monachus* are habitat destruction through tourism, increased mortality through deliberate killing (by artisanal fishermen, who generally remain hostile towards the seal) or accidental entanglement in fishing gear, as well as the depletion of food sources due to pollution, overfishing and illegal fishing. Susceptibility to diseases should be also taken into account, since small populations have lower resistance due to loss of genetic variability through genetic drift and inbreeding. Nowadays random misfortunes on a relatively small scale can have a dramatic impact on seal populations; as in the case of the Cabo Blanco population which suffered a 66% reduction in only two months in 1996 as a consequence of exposure to toxins through fish consumption (Forcada *et al.*, 1999).

2.1.5 Protection

The species is strictly protected under the Greek law (Presidential Decree 67/1981), European Directives, and International Conventions (Table 1). The NMPANS is the main region assigned specifically to the protection of the monk seal. Moreover, the area of northern Karpathos (since 2002) in Greece, along with several sites on the Aegean and Mediterranean coasts of Turkey, is also under protection, mostly regarding local seal populations.

Because of the limited methodology, it is still very difficult to answer questions about the exact current population size, make comparisons with past times, and evaluate the conservation measures taken (Gucu, 2010). The only area exhibiting stabilization of its population numbers in the past twenty years is the Northern Sporades (along with Desertas in Madeira), but this area only shelters 10% of the global population of the species (Aguilar and Lowry, 2008); the annual birth rate has increased since monitoring efforts started in the area (see Dendrinos *et al.*, 2007). Moreover, individuals recently recorded after more than 50 years on the coasts of Israel (Scheinin *et al.*, 2010) and Italy (Bundone, 2010) are believed to originate from the area of Cilicia in Turkey and the Greek seas, respectively.

IUCN foresees an overall declining trend of the species, mostly due to absence of effective conservation efforts in the field and a high extinction risk of the species unless there is urgent

Table 1. Species reported in the present study and their international and Greek protection status.

SPECIES	1	2	3	4	5	6	7	8	9	10	11
PORIFERA											
Hippospongia communis (Lamarck, 1814) †		III				III					
Spongia (Spongia) lamella (Schulze, 1879) †		III				III					
Spongia (Spongia) officinalis Linnaeus, 1759 †		III				III					
Spongia (Spongia) zimocca Schmidt, 1862 †		III				III					
ANTHOZOA											
Corallium rubrum (Linnaeus, 1758) †	+	III			V	III					
CRUSTACEA											
Melicertus kerathurus (Forskål, 1775) †											
BIVALVIA											
Flexopecten glaber (Linnaeus, 1758) †											
Ostrea edulis Linnaeus, 1758 †											
ELASMOBRANCHII											
Alopias vulpinus (Bonnaterre, 1788)				I					DD	VU	VU
Carcharias taurus Rafinesque, 1810									VU	CR	CR
Carcharhinus plumbeus (Nardo, 1827)				I					NT	EN	EN
Carcharodon carcharias (Linnaeus, 1758)		II	I/II	I		II		II/B	VU	EN	EN
Dipturus batis (Linnaeus, 1758)									CR	CR	CR
Isurus oxyrinchus Rafinesque, 1810		III	II	I		II/III			VU	CR	CR
Lamna nasus (Bonnaterre, 1788)		III	II	I		II/III			VU	CR	CR
Oxynotus centrina (Linnaeus, 1758)									VU	CR	CR
Prionace glauca (Linnaeus, 1758)		III		I		III			NT	VU	VU
REPTILIA											
Caretta caretta (Linnaeus, 1758)	+	II	I/II		*II/ IV	II		I/A	EN	EN	EN
Chelonia mydas (Linnaeus, 1758)	+	II	I/II		II/ IV	II		I/A	EN	EN	EN
Dermochelys coriacea (Vandelli, 1761)	+	II	I/II		IV	II		I/A	CR	CR	CR
MAMMALIA											
Delphinus delphis Linnaeus, 1758	+	II	I/II	I	IV	II	I	II/A	LC	EN	EN
Monachus monachus (Hermann, 1779)	+	II	I/II		*II/IV	II		I/A	CR	CR	CR
Phocoena phocoena relicta Abel, 1905 ‡	+	II	II		II/IV	II	I	II/A	LC	EN	EN
Physeter macrocephalus Linnaeus, 1758		II	I/II	I	IV	II	I	I/A	VU	EN	EN

1, Presidential Decree 67/1981; 2, Council of Europe, 1979 – Convention on the conservation of European wildlife and natural habitats (Bern Convention); 3, Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention, 1979); 4, United Nations Convention on the Law of the Sea (UNCLOS); 5, Habitats Directive 92/43/EEC; 6, Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean (Protocol of Barcelona Convention), 1995; 7, ACCOBAMS - Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic Area (1996); 8, Convention on International Trade in Endangered Species of Wild fauna and flora (CITES, 1973) Council Regulation EC 338/97; 9, IUCN Red List of Threatened Species – International Level; 10, IUCN Red List of Threatened Species – Mediterranean Level; 11, Greek Red Data Book of Threatened Species (2009); I, II, III, IV, V, Appendix/Annex I, II, II, IV, V; A, B, Species of Appendix A and B of the regulation applying CITES in the EC; *, Priority species for the European Union / Priority habitat for *P. oceanica* meadows; †, Fisheries and exploitation of the species/animal group is regulated under relevant national legislation; ‡: Endemic Species or subspecies; DD, Data Deficient; LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered

action. Güçlüsoy *et al.* (2004) confirmed this opinion for the Turkish population. It is highly believed that a well developed MPA network is the most realistic solution for maximizing the survival chances of the species (Panou *et al.*, 1993) through the protection of important pupping sites from accidental entanglement and other threats (Karamanlidis *et al.*, 2008).

2.2 Sea turtles

Three species of marine turtles inhabit the Aegean and Ionian Seas, the loggerhead *Caretta caretta,* the green turtle *Chelonia mydas* and the leatherback *Dermochelys coriacea.*

The loggerhead is the only marine turtle nesting in the Greek seas. The island of Zakynthos in the Ionian Sea is the centre of its nesting activity, hosting about 26% of the documented total nesting effort and the highest total nesting density in the Mediterranean (Margaritoulis, 2005). *C. caretta* nests also in other Greek areas, mostly Peloponnesus and Crete. Overall the Greek coasts host about 60% of the total Mediterranean nests, 43% of which are located in Laganas Bay, Zakynthos and 19% in Kyparissia, Peloponnesus (Margaritoulis, 2009). A twenty year survey in Laganas Bay showed that turtle nesting is taking place in six discernible beaches, mainly in Sekania (54% of the total nests), which is the least disturbed area (Margaritoulis, 2005). Standardized beach monitoring in the main nesting areas in Greece was initiated in 1984 and continues until present; moreover, records of the frequency of stranding, incidental catches in fisheries and tag recoveries have revealed that turtles frequently visit many marine areas of the Ionian, south and north Aegean (including the Thracian Sea) as foraging or wintering grounds (Margaritoulis and Panagopoulou, 2010). However, the main areas of migration once they have completed nesting in Laganas Bay are the north Adriatic and the Gulf of Gabes in Tunisia (Zbinden *et al.*, 2008).

Main threats in Greece are: i) degradation of nesting areas due to coastal development and tourism, ii) incidental capture in fishing gear. According to a recent estimate of loggerhead bycatch (Lucchetti and Sala, 2010), the annual number of individuals caught in the Greek drifting longline and bottom trawl fishery range from 1,475 to 9,153 per year; no regional data on direct mortality exist and no mitigation measures have been tested, in contrast to other areas, such as the Italian Ionian Sea, Tunisia and Turkey. A long-term study (15 years) of nesting areas in Crete showed an alarming, highly significant, decreasing trend in nesting levels (Margaritoulis *et al.*, 2005). Although no apparent trend has been observed in the longest monitoring project in Greece, i.e. Laganas Bay (Margaritoulis, 2005), it is worth noting that the number of nests during 2009 represented the lowest number ever recorded (829) since 1984 (Venizelos *et al*., 2009). On the other hand, the population in Kyparissia seems to be increasing, likely due to conservation efforts during the last 15 years (Margaritoulis *et al*., 2012).

The species is listed as endangered (IUCN and Greek Red Data Book category: EN). Recent evaluations of the existing threats in the Mediterranean suggest that, given the lack of bycatch reduction in commercial and artisanal fisheries and the ineffective implementation of conservation measures, the Mediterranean *C. caretta* population is at immediate risk of extinction (Conant *et al.*, 2009).

C. caretta is a protected species in Greece, according to national and international legislation (Table 1). One of the two National Marine Parks (i.e. the NMPZ) is devoted to its protection, since 1999. The MPA comprises primarily the coastal and marine area of Laganas Bay in Zakynthos, which is subjected to a continuously expanding tourist development. Efforts and achievements of NGOs (in particular Archelon) and the Management Agency of the Park include nest management and predation control, public awareness, and beach management; however, there are still problems with the effective enforcement of the legislation because of local reaction and inadequate political will (Margaritoulis and Panagopoulou, 2010). The nesting areas in Kyparissia and Lakonikos Bay (Peloponnesus), as well as in Rethymno, Chania, and Messara (Crete) are under protection as sites of the Natura 2000 network.

The green turtle *Chelonia mydas* is an endangered species with no regular nesting areas in Greece. Its main Mediterranean nesting areas are in Turkey, Cyprus and Syria. It is regularly found in the Greek waters and Lakonikos Bay is considered a developmental habitat of the species, since many young individuals have been observed (Margaritoulis and Teneketzis, 2003). The leatherback *Dermochelys coriacea* is a critically endangered species only visiting the Mediterranean Sea and rarely found in Greek waters. Both these species suffer the same threats as *C. caretta* and are protected under a common legislative framework.

2.3 Cetaceans

The Aegean Sea along with the western Mediterranean is an area of concentration for marine mammals (Coll *et al.*, 2010; Panigada and Pierantonio, this volume). Seven cetacean species are commonly observed in the Aegean and Ionian ecoregions: the striped dolphin (*Stenella coeruleoalba*), common bottlenose dolphin (*Tursiops truncatus*), short-beaked common dolphin (*Delphinus delphis*), Cuvier's beaked whale (*Ziphius cavirostris*), sperm whale (*Physeter macrocephalus*), Risso's dolphin (*Grampus griseus*), and fin whale (*Balaenoptera physalus*); one more species, the Black Sea harbour porpoise (*Phocoena phocoena*) is restricted to a small area in the north Aegean (Frantzis *et al*., 2003).

Out of these, three species have been indicated as Endangered (EN) both in the IUCN Red List (at least their Mediterranean and Black Sea populations) and in the Greek Red Data Book of Threatened Species (Legakis and Maragou, 2009).

- *Phocoena phocoena relicta:* this subspecies (Viaud-Martinez *et al.*, 2007) occurs in the Black Sea, Marmara, and north Aegean, but not in the rest of the Mediterranean. Its Aegean subpopulation is roughly estimated to comprise between 30 and 450 individuals (Paksimadis and Frantzis, 2009), while a total population size of as much as 10,000-12,000 individuals is estimated in the Black Sea, despite a severe 70% decline experienced during the last thirty years; the latter was mainly a result of prolonged hunting for the cetacean-processing industry (up to the 1980s), supplemented by a mass mortality event after the explosion in 1982 at a gas-extraction platform in the Azov Sea (Reeves and Notarbartolo di Sciara, 2006). Among the three Black Sea cetacean species it makes the most significant proportion by far (95%) of the bycatch (Birkun and Frantzis, 2008). Main threats are accidental takes in fishery activities, contamination by xenobiotics, population disruption due to disturbance, and climate change (Reeves and Notarbartolo di Sciara, 2006; Paksimadis and Frantzis, 2009).
- *Delphinus delphis*: the species is found locally in the Aegean and Ionian Seas. The largest population seems to live in the Thracian Sea (north Aegean), while very small populations of few dozens of individuals appear in the eastern Ionian Sea and the Gulf of Corinth (Paksimadis and Frantzis, 2009). The well-studied eastern Ionian population suffered a decline from 150 individuals in 1996 to only 15 in 2007 (Bearzi *et al.*, 2008) due to an overall negative impact of local fisheries on the dolphin population (Pirodi *et al.*, 2011). The species is mainly threatened by prey depletion resulting from overfishing, and contamination by xenobiotics (Bearzi *et al.*, 2003).
- *Physeter macrocephalus*: The total number of individuals in the Aegean and Ionian Seas is estimated at 180-240, while 200 of them are living or visiting the Hellenic Trench, a key Mediterranean area for the species (Paksimadis and Frantzis, 2009). Main threats are accidental catches in fisheries (pelagic driftnets), along with collisions and accidents with vessels (Reeves and Notarbartolo di Sciara, 2006).

Despite the fact that most cetaceans are protected under international Conventions and Greek law (Presidential Decree 67/1981), practically no specific measures have been implemented. Several areas of the Aegean and Ionian Seas have been indicated by ACCOBAMS (Resolutions 3.22 and 4.15) for the establishment of MPAs in order to maintain a favorable conservation status of cetaceans in this area of special importance.

2.4 Elasmobranchs

Up to date, 63 elasmobranch species have been recorded in the Greek Seas; 13 of them are considered regionally threatened, while the others have not yet been evaluated according to the IUCN criteria (Megalophonou, 2009). Five of these species, namely the sand tiger shark (*Carcharias taurus*)*,* the shortfin mako (*Isurus oxyrinchus*)*,* the porbeagle shark (*Lamna nasus*)*,* the angular roughshark (*Oxynotus centrina*) and the common skate (*Dipturus batis*), are considered critically endangered as far as their Mediterranean (IUCN) and Greek populations are concerned. Although their population status remains uncertain, it is estimated that regional shark populations are lower in abundance than in the western Mediterranean basin due to accidental catches, habitat loss and degradation of coastal areas serving as nursery grounds, combined with intrinsic slow life history traits (Megalophonou, 2009).

Current studies on pelagic shark populations from the eastern Mediterranean reveal the presence of both large and juvenile individuals, with a larger mean size recorded from the Levantine Basin, that receives relatively lower fishing effort (Megalophonou *et al.*, 2005), possibly because of their low commercial value in this area (Golani, 2006). Furthermore, certain areas of the Aegean Sea have been reported as breeding or nursery grounds for particular shark species (*Carcharhinus plumbeus* – Musick *et al.*, 2009; *Carcharodon carcharias* – Kabasakal and Gedikoglu, 2008). Recent studies on the eastern Mediterranean blue sharks (*Prionace glauca*), caught as bycatch from swordfish fisheries, showed that local values of catch per unit effort (CPUE) were much lower compared to those recorded from the western basin (Megalophonou *et al.*, 2009a).

Additionally, the main bulk of shark catches from the Aegean (i.e. *Alopias vulpinus*, *I. oxyrinchus*, and *P. glauca*) is composed of immature and maturing specimens (Megalophonou *et al.*, 2009b). These findings are of great concern and highlight the need for further assessment studies and management actions in the area.

The above-mentioned elasmobranchs are not target species for the Aegean fisheries, yet they are accidentally caught quite often; such is the case for the critically endangered shortfin mako (Peristeraki and Megalofonou, 2007). Despite the fact that several elasmobranchs occurring in the Greek Seas are currently protected under European or International legislative frameworks (Table 1), in practice there is an apparent lack of protection and management. Extended monitoring of the existing stocks and strict enforcement of conservation measures are urgent priorities. Moreover, the protection of local populations, migratory paths and nursery grounds under national legislation or transnational cooperation (e.g. Marine Peace Parks) is critically needed.

3. Local depletions of commercially exploited species

3.1 Case study: the bath sponges

Four sponge species belonging to the family Spongiidae are commercially harvested in the Mediterranean as ‘bath sponges’: the iconic species *Spongia officinalis* – the nominal archetype of the poriferan phylum – and conspecifics *S. lamella* and *S. zimmocca* along with *Hippospongia communis*. Their exploitation has been extensive historically in the eastern basin of the Mediterranean, including the Aegean Sea, the Apulian coast in the Ionian Sea, and the coasts of Tunisia, Libya, Egypt, Lebanon and Syria (Milanese *et al.*, 2008; Pronzato and Manconi, 2008; Voultsiadou *et al.*, 2011). Harvesting in those regions has been predominantely performed by fleets and crews originating from the Aegean Islands, at least before the second half of the 20th century.

3.1.1 Tracing past and present abundance

An era of rich grounds and thriving production

Although sponge beds in the Mediterranean have purportedly been remarkably rich up till the turn of the 19th century, only scarce official data regarding catch numbers exist for this period, making the assessment of bath sponge abundance mostly a matter of speculation. Sparse bits of information, such as the annual tribute of 4,000 choice sponges routinely paid to the Sultan of the Ottoman Empire from 1522 to 1909 by the people of Syme, a small sponge-producing island of the Aegean (Kalafatas, 2003), give us a glimpse to the rich overall production of times past. References to the widespread use of a nowadays neglected harvesting practice, that of harpooning sponges from atop a boat assisted by a glass bottom bucket (Flegel, 1908), indicate that bath sponges were likely abundant at depths shallower than 10 m. The industrial revolution caused a boost to the worldwide demand for sponges (Bernard, 1987) and a sharp growth of the existing Aegean sponge-fishing fleet (Chadjidakis, 1999); consequently, in the second half of the 19th century, the overharvesting of the Aegean sponge grounds led to the expansion of sponge fishery to the northern African coast. The introduction of the scaphander in 1866 allowed exploitation of previously inaccessible sponge grounds. By the end of the century, annual production had reached 250-300 tons (Voultsiadou *et al.*, 2011). Sporadic references to the number of fishing boats and crews active in the sponge industry at that era let us assume a thriving industry that could only be based upon plentiful stocks. The production for the fleet of Kalymnos, a major sponge-producing island of the Dodecanese, was higher than 80 tons annually for the time span from 1910 to 1940 (Bernard, 1987). It should be noted that since weight estimates actually refer to treated, dried sponges, one kilogram can correspond to more than a hundred individuals, depending on their size.

Decline through the 20th century

A gradual decline of the Aegean sponge fisheries started after the heyday of sponge fishing in the 1910s and carried on towards the 1940s. During that time span, the Greek fleet shrank from somewhat 600 vessels in 1912, to 216 in 1948 (Bernard, 1976); this drop can be assumedly related to a continuous degradation of the exploited sponge banks. The ongoing reduction of sponge production in Greece since the 1950s can be observed from the relevant data (Figure 3), while a similar reduction is observed for the number of active vessels and men employed in the sponge fisheries. It is notable, however, that the yield per man increases despite the negative trend in production, indicating increased fishing effort and pressure to the stocks. During the decade after 1960, the synthetic sponge began to cut sharply into Kalymnian markets (Bernard, 1976), while African Mediterranean countries such as Libya, Egypt, and Tunisia successively nationalized their fishing grounds in the 1960s and 1970s prohibiting access to Greek divers (Kavalakis, 2001). Both factors further contributed to the decline of sponge production in Greece. A global shrinkage of sponge production followed during the course of the 20th century, with total annual output dropping from an average of 347.5 tons during the 1930s to 123.2 tons in the early 1980s (Josupeit, 1991).

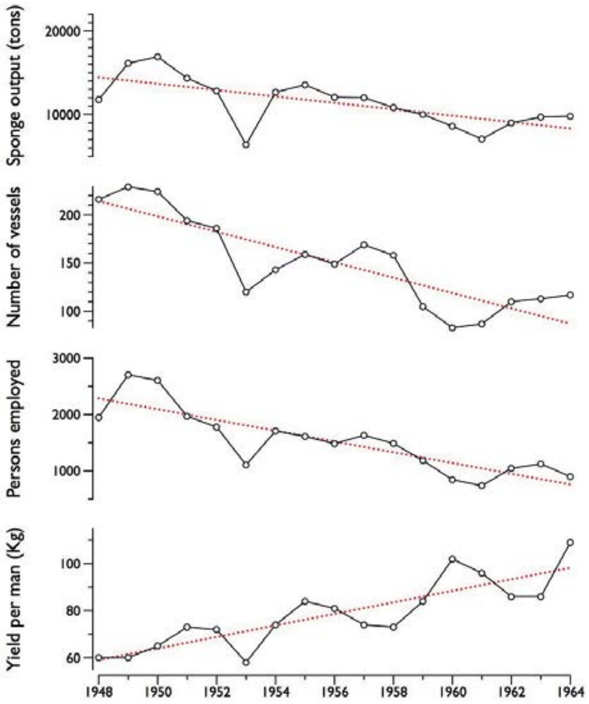

Figure 3. Sponge production, number of active vessels and total persons employed in sponge fishing (divers and crews), and yield per person in Greece from 1948 to 1964. Data from the National Statistical Service of Greece, as reported in Bernard (1987).

Disease and depletion

Through the years 1986 to 1990, a devastating disease spread mainly in the Aegean and the eastern Mediterranean, decimating the already declining populations (Vacelet *et al.*, 1994). Four consecutive years of exposure to the disease caused a rapid decline of the sponge-harvesting fleet and respective production of the Aegean, while also affecting the output of all major Mediterranean sponge-producing countries (Figure 4). As Voultsiadou *et al.* (2011) reported, during the combined fishing seasons of 1988-1989 a total of just 5.3 tons of bath sponges were harvested in the Aegean Sea. While a gradual recovery from the disease was observed in the Aegean and the Mediterranean coast of Egypt (Castritsi-Catharios *et al.*, 2005 and 2011, respectively), the assessed densities of bath sponges remained low. An additional field survey in Libya in 2005, almost twenty years after the first outbreak, reported the absence of *H. communis*, the main species harvested in the area before the disease, at least at the studied sites (Milanese *et al.*, 2008). An extensive survey in the Aegean Sea between 2004 and 2008 (Voultsiadou *et al.*, 2008; 2011) reported moderate to high densities of *S. officinalis* and *H. communis* in certain sites, but also low abundances or complete absence in locations acknowledged as rich sponge grounds before the disease.

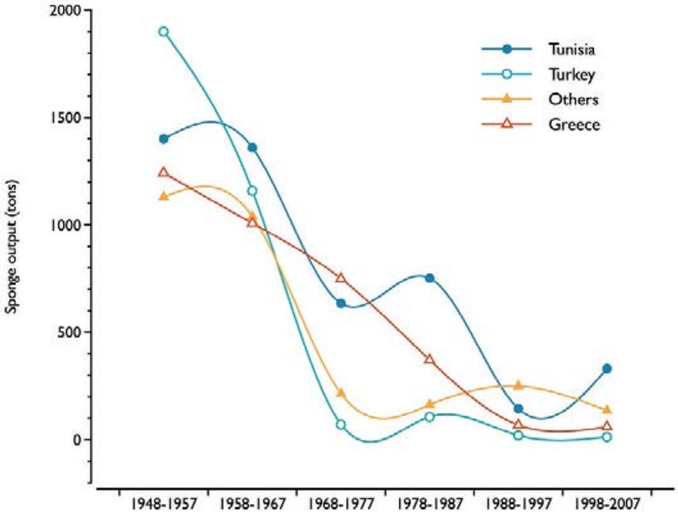

Figure 4. Sponge production decline during the last 60 years for the main Mediterranean producing countries according to the GFCM (General Fisheries Commission for the Mediterranean) database reports from FAO.

3.1.2 Present status and threats

At present, the populations of bath sponges in the Aegean Sea – concerning the most abundant species, *S. officinalis* and *H. communis* – appear fragmented and patchy at least regarding their shallow distribution down to 30 m depth (Voultsiadou *et al.*, 2008; 2011 and authors' unpublished observations). The Greek production originates mainly from sectors of the Aegean (the northern continental coastline, the Dodecanese and Cyclades archipelagos, as well as the islands of Crete and Karpathos) and, occasionally, from the southeast coast of Italy. The only sponge-fishing fleet remaining active is that of Kalymnos, counting 100-120 qualified divers working on 17 licensed boats and producing annually 4 tons of sponges approximately (Voultsiadou *et al.*, 2011).

Two main sources of pressure can be recognized regarding the remaining stocks in the Aegean Sea. (i) The harvesting pressure from the remaining Kalymnian fleet; at least five boats perform extensive fishing trips of variable route each year and exhaustively exploit every sponge bed that appears lucrative, excluding only the smallest cluster of individuals (< 5 cm diameter). Consequently, even though the fishing effort can be presumed low overall, the imposed pressure can be actually high on remaining populations. (ii) Mortality from disease is still an ongoing threat in the Mediterranean, since several severe incidents have been reported in different parts of the basin during the past decades (Webster, 2007; Garrabou *et al.*, 2009), affecting bath sponges and other sessile invertebrates. Mass mortality events have been associated to environmental temperature anomalies that promote stress and, consequently, chemical and microbial shifts in the affected organisms (Webster *et al.*, 2008; Lejeusne *et al.*, 2010), and thus are expected to be more intense and recurring within a reportedly increasing warming trend (Coma *et al.*, 2009).

3.1.3 Protection schemes and outlook

All commercial bath sponge species are included in the Annex III (requiring regulation) of the Barcelona Convention, and Annex III (protected species) of the Bern Convention (Table 1). Practically, however, little or no control is enforced by the Greek authorities over sponge fishers or merchants. Apart from specific locations where general prohibitions apply, such as MPAs or sites of archaeological importance, diving for sponges is practically allowed everywhere, presuming that the vessel is licensed for sponge fishing. The minimum size of harvested sponges is regulated by the Greek legislation (Fisheries Code, Decree 420/1970) and is confined to 5 or 10 cm, according to commercial quality.

Recent studies suggest that protection measures favor the viability of bath sponge populations, in contrast to unprotected sponge fishery areas of the Aegean (Voultsiadou *et al.*, 2011). Notably, high abundances of bath sponges have been reported during experimental surveys in the Aegean, where exploitation (including diving for sponge harvesting) is prohibited. Accordingly, high abundances of bath sponges were recorded at the islet of Koufonissi (southeast Crete), where archaeological regulations imposed restrictions to fishing and recreation activities (authors' unpublished data).

Despite centuries-long harvesting and recurrent massive mortality episodes affecting the species in broad geographic scales, high levels of genetic diversity in most populations of *S. officinalis* have been reported in the Mediterranean (Dailianis *et al.*, 2011). One of the putative reasons proposed is the existence of robust populations, scarcely influenced by fisheries and epidemics that could promote re-colonization of affected areas. Indeed, the occurrence of shallow populations that tolerated recent mortality events, probably due to a beneficial current flow regime, has been recently reported (Voultsiadou *et al.*, 2011). Moreover, the existence of robust populations in deep waters and sizes inaccessible to harvesting by diving should be explored. Although increased dimensions and abundances of bath sponges at depths greater than 30 m are reported (e.g. Castritsi-Catharios *et al.*, 2005; 2011), no systematic survey of the deeper zone of distribution of bath sponges in the Mediterranean has been implemented up to present.

3.2 The precious Mediterranean red coral *Corallium rubrum*

The red coral *Corallium rubrum* has been exploited in the Mediterranean Sea since ancient times (Tsounis *et al.*, 2010). Despite its economic value, the available stocks have never been evaluated, and little is known about its ecology, bathymetric and spatial distribution in the eastern Mediterranean. In Greece, the most abundant populations of red coral are found in the north Aegean Sea, as illustrated by the total landings from this area, which are twice as high as those recorded from the Cretan and Ionian Seas taken together (Dounas *et al*., 2010). However, total Aegean and Ionian Greek landings are extremely low compared to those of the western Mediterranean (Bruckner, 2010), confirming the ancient literature sources (e.g. Hesychius and Dioscorides), which indicated the Island of Sicily as its main fishing area.

According to the available Greek fisheries data, shallow water stocks (down to 60 m) are almost depleted, and so professional divers are forced to harvest at greater depths (all the way down to 130 m) by means of mixed gas diving techniques. Evidence for declining of stocks in areas only recently opened up to exploitation suggests that harvesting was carried out in these areas throughout the closed period, possibly by using illegal dragging gears (Dounas *et al*., 2010).

Since 1994 red coral stocks have been regulated in the Greek Seas on a 5-year rotational basis in five large geographic areas (Presidential Decree 174/1994; Ministry Decision 240102/1995). To date only three zones have been harvested (Crete, north Aegean and Ionian Sea). The south-eastern Aegean was recently opened to exploitation (2011-2015) with only four harvesting licenses granted for the current year. Harvesting is permitted only by means of scuba or hookah diving at depths not shallower than 50 m.

Recently, preliminary evidence of a significant decrease of Mediterranean red coral stocks, along with the slow potential for recovery, has generated a debate whether *C. rubrum* should be enlisted on Appendix-II of CITES (Bruckner, 2009). In Greece, additional management measures for the control and monitoring of red coral landings are urgently needed. The rotating harvesting system should be re-examined in order to assess the effectiveness and viability of the present scheme (Dounas *et al*., 2010; Tsounis *et al.*, 2010), especially in the light of recent findings regarding the species' genetic structure that indicate restricted dispersal range and low power of recolonization (Ledoux *et al*., 2010). Apart from management measures, there is a crucial need for scientific investigation of the ecology, size and structure of coral populations in Greek waters. Detailed mapping and effective protection of the coralligenous and cave habitats of the species is of great importance in order to safeguard its future potential exploitation and conservation.

3.3 Edible bivalves

Bivalves have been widely used as food and medicine sources since Greek Antiquity (Voultsiadou, 2010). Several areas of the Greek Seas, such as Thermaikos and Saronikos Gulf, have been overexploited during the past century for bivalves and decapod crustaceans. The existing legislation had a rather poor effect on the sustainability of mollusk natural populations and exploitation resulted in severe population decline and stock collapse (Koutsoubas *et al.*, 2007), even for well established species. Two well-known examples developed in Voultsiadou *et al.* (2010) are:

> i) the collapse of the scallop *Flexopecten (=Chlamys) glaber* population since 2003 in Kalloni Bay, Lesvos Island, one of the species' main fishing areas in the Aegean Sea, due to intensive harvesting and lack of rational management. Similar collapses were observed in the distant past, in this area. Aristotle, for example, reports that scallops had vanished from Kalloni Bay due to the fishing method, as fishermen used an instrument which scratched the sea bottom, quite similar to the dredge gear "arghalios" or "lagamna" which is still in used today.
>
> ii) the European flat oyster's (*Ostrea edulis*) populations have severely declined and finally collapsed in the late 1990s in Thermaikos Gulf, its main fishing area in Greece, due to overfishing and parasite infection. This species has been exploited as well, even cultivated in estuarine areas, since the time of Aristotle.

Evidence of local depletion, probably enhanced by mass mortality events, also exists for the edible European thorny oyster *Spondylus gaederopus* in areas of the south Aegean (C. Antoniadou, pers. com.). The decline of its populations, even its disappearance in some areas, for unknown reasons in the beginning of the 1980s, has been previously recorded (see Katsanevakis *et al.*, 2008). Local extinction from many sites has been reported also for the common piddock *Pholas dactylus*, a strictly protected species, due to collection for food and bait and as a result of pollution (Katsanevakis *et al.*, 2008).

4. Biological invasions – a cause for depletion of local species

Until today, a total of 237 alien species have been recorded in the Aegean (mostly the southern part) and Ionian ecoregions, which may function as a gateway for their dispersal to the rest of the Mediterranean (Zenetos *et al.*, 2011). Currently, the Suez Canal is the main vector for aliens of Indo-Pacific origin (around 80%), the Atlantic influx being limited (CIESM, 2001/2002; Corsini-Foca *et al.*, 2010). Most of these species are mollusks (~27%), fishes (~21%), and crustaceans (~20%). The Red Sea species influx is a continuously increasing phenomenon, intensified during the last decades (Raitsos *et al.*, 2010; Turan, 2010) and several species have established sustainable populations in the Levantine and the southeast Aegean (Turkish coasts and Dodecanese Islands). Raitsos *et al.* (2010) using long-term data showed that the mean annual introduction rate of warm and tropical alien species showed an increase of 150% after 1998 in response to an abrupt temperature rise in the Greek Seas, specifically the southern Aegean. As of 2010, their impact on fisheries was of local character and only nine species were regularly occurring in catches in the southernmost areas of the Greek waters (Lefkaditou *et al.*, 2010). Concerning mollusks and decapods, a statistically significant acceleration of the entrance rate of Lessepsian migrants in the Aegean has been recently assessed (Koukouras *et al.*, 2010; Tzomos *et al.*, 2012).

Many of the alien species exhibit invasive behaviour (see Streftaris and Zenetos, 2006), which could potentially cause severe alterations to the natural environment (e.g. replacement of native species, biodiversity loss, decrease of habitat cover, and cascade effects on trophic webs). Notable examples of species which seem or could potentially provoke such phenomena are the following:

- The highly invasive green alga *Caulerpa racemosa var. cylindracea* is established in all Greek seas, occupying diverse substrata, between 0 and 70m, in both polluted and clean areas, exhibiting high adaptability to physical stressors (Zenetos *et al.*, 2009). This species forms extensive mats altering the local vegetation and the composition of the macrofaunal assemblages in parts of the eastern Mediterranean basin (Cyprus – Argyrou *et al.*, 1999). The most vulnerable habitats to its expansion are 'matte morte' (zones of fibrous remnants of a former *Posidonia oceanica* bed), rocky bottoms, and the margins of *P. oceanica* meadows (Katsanevakis *et al.*, 2010).

- The Kuruma prawn *Marsupenaeus japonicus* appears to have evicted the overexploited native Caramote penaeid prawn *Melicertus kerathurus*, which has almost disappeared from the Levantine, its habitats having been overrun by the former (Galil, 2007). The situation is somewhat urgent since the *M. kerathurus* populations are declining due to intensive exploitation in the Greek Seas (Kevrekidis and Thessalou-Legaki, 2011).
- Two species of rabbitfish, *Siganus luridus* and *S. rivulatus*, which have established large populations in the eastern Mediterranean, were found to deplete erect algae (mainly *Cystoseira* spp.) on the Turkish coasts turning algal assemblages into ‘barrens’, and causing a dramatic reduction in biodiversity and biomass (Sala *et al*., 2011).
- The Indo-Pacific blue cornetfish (*Fistularia commersonii*), a highly invasive piscivore, has developed large populations along the Levantine, parts of the Aegean and Tyrrhenian Seas (Zenetos *et al.*, 2009). It reproduces and grows extremely rapidly, reaches a large size and preys on native fishes of economic value, as well as on small benthic and newly hatched fish (Kalogirou *et al.*, 2007). It has been classified among the top predators of the Greek seas along with *Dentex dentex*, *Epinephelus marginatus*, *Euthynnus alletteratus*, *Sarda sarda* and *Xiphias gladius* (Stergiou and Karpouzi, 2005).

If alien species in the eastern Mediterranean continue to increase, these newcomers could seriously threaten the equilibrium of the regional marine ecosystem.

5. DISCUSSION AND CONCLUSIONS

5.1 Unique biodiversity of the Aegean and adjacent ecoregions threatened with extinction

The Greek Seas (Aegean and Ionian) high biodiversity is under threat. As shown in the present review, a variety of marine taxa exhibit clear trends of decline: these include marine mammals, cetaceans, elasmobranchs and sea turtles, as well as invertebrate groups such as sponges, corals, and mollusks.

Subareas of the Aegean Sea exhibit different characteristics from a biodiversity and conservation point of view. The higher biodiversity of the north Aegean has been shown for different benthic invertebrates (e.g. Voultsiadou, 2005; Lampadariou and Tselepides, 2006), while the diversity characterizing the south Aegean is closer to that of the impoverished Levantine Basin. As shown here, the northern part of the Aegean is also characterized by the largest monk seal population in the Mediterranean, the only Mediterranean population of the Black Sea harbor porpoise, and the most abundant populations of red coral in the area. It also encompasses the most extensive fishing grounds in the Greek territory supporting around 70% of the total Greek fishing effort (Hellenic Statistical Authority, 2011).

The south Aegean, on the other hand, is influenced by an intense wave of biological invasions in the form of Lessepsian migrants, enhanced by climate warming. Evidence of alterations imposed on the local species composition (Streftaris and Zenetos, 2009; Raitsos *et al.*, 2010), as well as diseases and mass mortalities of benthic invertebrate populations in response to extreme temperature events (Voultsiadou *et al.*, 2011) is already available. The same authors suggest that sponge populations in this area are more susceptible to mass mortalities than those in the northern Aegean, where lower temperatures inhibit the rapid spread of diseases.

The Ionian Sea, finally, is the centre of nesting activity for the sea turtle *C. caretta* in the Mediterranean and constitutes remarkable feeding ground for cetacean populations.

Marine conservation practices in the eastern Mediterranean are inferior compared to those implemented in the northwestern basin, where well-enforced no-take reserves seem to have positively affected ecosystem health (Sala *et al*., 2012). Fortunately substantial populations of marine megafauna still exist in the Aegean and Ionian ecoregions (e.g. *C. caretta*, *M. monachus*, and cetaceans). Likely due to the geomorphological complexity of their marine environment. A general West to East gradient regarding the decline of certain marine taxa is apparent in the Mediterranean: the western basin has suffered much more severe population depletions, with the monk seal being the paramount example, followed by sea turtles, etc (see Coll *et al*., 2010). It has been even suggested that the progressively unsuitable conditions prevailing in the western basin make the eastern sector (Levantine and south Aegean) a "heaven" for some cetacean populations (Kerem *et al*., 2012), in spite of ineffective protection and impoverished biomass and primary production levels.

5.2 Local extinction characteristics

Exploitation is generally considered the main cause of marine extinctions (Dulvy *et al.*, 2003). Most of the species examined in this review have been subjected to human harvesting or hunting in the eastern Mediterranean since ancient times. Bath sponges, corals, mollusks, sharks, turtles and seals, have been used by humans since antiquity for food, medicines, crafts, and household purposes (e.g. Johnson and Lavigne, 1999; Voultsiadou 2008; 2010). Industrialization of fisheries during the past centuries combined with habitat degradation has led to severe population declines, even local extinctions. Moreover, the impact of exploiting marine ecosystem engineering species (Coleman and Williams, 2002) may be high for the marine biodiversity of the Aegean area since healthy sponges and corals have been shown to support rich benthic communities in the area (e.g. Koukouras *et al.*, 1998; Voultsiadou *et al.*, 1987). Another major problem with species like sponges and corals is that their economic value increases as they become less abundant, this leading to more intensive harvesting. Such species may not necessarily become "economically extinct" before their local or regional extinction, as is assumed for fish stocks (see Dulvy *et al*., 2003).

This review shows that historical information, though often fragmented and sometimes inconsistent, is sometimes the only source available to estimate long-term population trends, especially for species that are commercially exploited for centuries. Following historical data on coral, sponge and monk seal population status and distribution, for instance, we can reconstruct the condition of marine ecosystems in past times. Interestingly, if one could go back 2,000 years in time and dive in the Mediterranean waters, a rather different picture of the sea bottom and coastal zone would be witnessed: extended red forests of robust and tall *C. rubrum* colonies (especially in the western basin, see Tsounis *et al*., 2010), dense populations of black bath sponges in the eastern basin and large herds of seals lying fearless on sandy beaches. Thus, we could argue that the major extinction that has taken place in the Mediterranean is that of the physiognomy of the marine ecosystem as a whole.

5.3 Conservation preventing extinction

The eastern Mediterranean basin and most specifically the Aegean archipelago and its adjacent waters preserve important core zones which support specific Mediterranean features that have almost disappeared from other areas of this basin (e.g. *M. monachus*, *P. phocoena*). However, there is an obvious lack of adequate and efficient marine conservation in the Mediterranean, and particularly in the eastern and southern areas, possibly attributed to the lack of scientific spatial data in the region as well as to the socio-economic, political and cultural context (see Giakoumi *et al*., 2012 and references therein).

Over the last years, the urgency for the establishment of networks of marine reserves, high seas MPAs and 'Marine Peace Parks' in a pan-Mediterranean scale has been underlined by researchers (e.g. Coll *et al*., 2012), scientific commissions (e.g. CIESM, 2011), NGOs (e.g. Greenpeace, 2006; OCEANA, 2011), and Agreements (e.g. ACCOBAMS) (see Giakoumi *et al*., 2012). Several areas of the Greek seas have been included in such proposals (i.e. Thermaikos Gulf, Thracian Sea, Northern Sporades, Saronikos Gulf, Eastern Ionian and Gulf of Corinth, Southwest Crete/Hellenic Trench, Dodecanese) since they host important populations of marine mammals, sea turtles, large pelagic fish (including sharks), as well as unique environments and communities, e.g. upwelling areas, offshore banks, seamounts, coralligenous beds and deep sea corals, mud volcanoes, cold seeps and brine pools with interesting microbial communities (OCEANA, 2011 and references therein).

A major impediment to marine conservation is the ineffective management and surveillance of MPAs: several cases are tuning to be 'paper parks', where no management measures have yet been implemented (Abdulla *et al*., 2008). On the other hand, established MPAs have proved successful in recovering and preserving certain features of the Mediterranean marine environment and often benefit a broader geographic sector than the strict area of protection (PISCO, 2007). Such an example is the appearance of bath sponges in high abundances in areas associated with MPAs in the Aegean Sea, probably due to the protective measures facilitating colonization by larvae and growth of young sponges.

The absence of scientific data noted here should not be used as an excuse for no protection or management on a precautionary basis, particularly for marine species and habitats (Bussoletti *et al*., 2010). For instance, the lack of habitat maps in Greek waters has severely contributed to a consecutive ongoing degradation even of priority habitats (e.g. sea-grass meadows and coralligenous beds) and supporting diversity, in spite of the existing, relevant national legislation.

The lack of environmental awareness constitutes an added, a potential threat for vulnerable species. For example, despite the legislative framework for the commercial exploitation of threatened elasmobranch species, large sharks (e.g. *Cetorhinus maximus*) caught as bycatch have been reportedly sold in Greek fishmarkets (Megalophonou, 2009). Information campaigns could raise environmental awareness of fishermen, fish merchants, relevant authorities and consumers who should avoid further exploitation of threatened species. Both cases illustrate that the existence of legislative frameworks does not always guarantee protection of species/habitats and that further actions must be taken for regulation enforcement.

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The bio-ecology of marine extinctions, with a lesson from the Hydrozoa

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Abstract

Extinction is a natural phenomenon in the history of life. If past extinctions are easily detected through the analysis of the fossil record, recent extinctions are, instead, rather difficult to prove. Even though rarity is a precondition to extinction, it is incorrect to consider all rare species as being on the verge of extinction, especially the inconspicuous ones. The greatest majority of biodiversity, in fact, is made of rare species and if them all were in danger of extinction, a global biodiversity crisis would be imminent. It is clear that only a careful evaluation of the status of every species will allow the detection of extinction dangers. A key question might be: for how long a species has to be unrecorded to be considered as putatively extinct? The analysis of the records of the Hydrozoa of the Mediterranean, a rather well-known group in the basin, shows that 67 species have not been reported since at least 41 years. The same exercise can be carried out for all groups, with the production of complete lists of species that are unrecorded since a very long time. The hypothesis of their extinction can be tested through focused surveys. The presence of resting stages in many marine species, however, can lead to the sudden re-appearance of species that were previously absent. This is called the Lazarus effect and can be hypothesized for species with particular life cycles.

Introduction: what is extinction?

Species are like individuals, they are borne, they grow, they die. Individuals, at a certain stage of their development, can produce new individuals, through reproduction. Extinction is the death of a species. There are three main types of extinction (see Carlton *et al.*, 1999; Roberts and Hawkins, 1999; Dulvy *et al.*, 2003 for reviews):

- local extinction: when a species becomes extinct in a portion of its area of distribution, while remaining present in other portions;
- final extinction: when a species ceases to exist, due to the death of its last representative;
- extinction by speciation: when a species ceases to exist, evolving into another species through anagenesis.

Is rarity a precondition to extinction?

When the individuals representing a species decrease in number, lost individuals not being replaced with new ones, their fitness decreases and, at a certain moment, the number of representatives of that species is so scant that it can be perceived as rare (i.e. difficult to find due to its scarcity). If all extinct species were rare before their final extinction, is it reasonable then to sustain that all rare species are near to be extinct, especially those that were previously represented by abundant individuals? Any analysis of biodiversity at a given place will show that there are few species that are very abundant (i.e. represented by many individuals) whereas most species are represented by just a few individuals (Boero, 1996). Of course these individuals must still be able to meet each other and to contain a sufficiently varied genetic pool, so as to allow for the viability of their populations, avoiding Allee effects (Courchamp *et al.*, 1999). Obviously this is possible for most species, since they continue to persist in spite of being rare. Extinction risks, thus, are more reasonable if a trend towards rarity is perceived, rarity alone not being a reasonable precondition to extinction.

If rarity were a sufficient precondition to extinction, most biodiversity (in terms of species) would be on the verge of extinction: most species, in fact, are rare.

Is rarity a precondition to speciation?

Among the textbook models of speciation, quantum speciation is based on the arrival of a few individuals at a site that is usually disconnected from the main area of distribution of a given species (e.g. an island far away from a continent). The very small population goes through a genetic bottleneck, and is subjected to founder effect and genetic drift (Boero, 1994). Such circumstances might often lead to local extinction, but they are also conducive to speciation. It is well known, for instance, that the heavy use of pesticides caused mass mortalities in the target species, reducing their populations to almost extinction, triggering, however, the emergence of new populations, resistant to pesticided. The periods of success (flushes), for most species, are rather short, and are followed by periods of rarity (crashes). This is well described by the flush and crash model (Carson and Templeton, 1984) and might be the main motor of evolution: the crises are the “creative” periods of evolution. The same abundance patterns are described by Lotka and Volterra models, with periods of abundance and periods of rarity in a prey-predator landscape.

From the above, it can be inferred that rarity, alone, cannot be regarded as being conducive to the extinction of a species.

The ecology of rarity

Schoener (1987) distinguished suffusive from diffusive rarity, two concepts already introduced by Darwin in the “Origin of Species”. Suffusive rarity pertains to species that are rare throughout their distribution ranges, whereas diffusive rarity describes species that are rare at some portions of their distribution ranges, but are rather abundant at other portions. It is rather important to distinguish between the two, when labeling a species as “rare”, especially when conservation measures are to be designed.

Why aliens do not become extinct? (most probably do)

During biological invasions, a species reaches a site that is outside of own natural range of distribution and establishes there a viable population that, in the worst cases, can become a threat to local biodiversity and ecosystem functioning; it is often the case that invasions start with just a few individuals and that the invading species, at first, is rather rare and with a restricted distribution. Most of these species simply become extinct and it is probable that most “aliens” are not even detected. But, against all odds, an alien can become dominant in the face of genetic bottlenecks, founder effects, Allee effects, genetic drift, not to speak about the competition with (or the predation by) the indigenous species, that co-evolved with the “invaded” environment (Boero, 2002). The explanation is in the pre-adaptation of the previously rare “alien” since the populations of the invaders, at the beginning of the invasion, are just like those of any rare native species, at least from a quantitative point of view.

Modeling population advances and retreats

Darwin (1859) treated the issue of modeling population growth and decline in “The Origin of Species”: “*I have taken some pains to estimate the probable minimum rate of elephant’s natural* *increase...*" the way he describes the exercise (it costed him pain) shows that he did not like at all to use his brain for searching evidence in numbers written on paper. He thus liquidates the issue with: "*...but we have better evidence on this subject than mere theoretical calculations, namely, the numerous recorded cases of the astonishingly rapid increase of various animals in a state of nature, when circumstances have been favourable to them for two or three following seasons*".

Darwin very often refers to the fact that any species might occupy in a relatively short time the whole space where "the elements" (as he called abiotic factors) allow for its existence, if there were no checks from the rest of nature (i.e. biotic interactions) on its reproductive potentials. So, species are all potentially increasing and they alternate in having chances of doing so. What is abundant today was rare yesterday, and what is rare today might become abundant tomorrow. If this happens within the domain of ecology, there is just the alternation of periods of rarity and abundance of the very same species, when evolution enters the game, then there can be speciation, sparked by a period of rarity (Boero, 1994; 1996).

MEDITERRANEAN EXTINCTIONS

In a period of global change, the features of "the elements" change. If global warming occurs, for instance, air temperature is the first element to change, but this can trigger even counterintuitive effects. If artic ice suddenly melts at an unprecedented pace, a huge amount of cold water will spread in the boreal regions, eventually even stopping the Gulf Stream that mitigates the cold winters of the north-eastern Atlantic. Higher temperatures of the air, thus, might lead to lower temperatures of the water. In any case, if conditions change, the species that are adapted to a given environmental setting are in distress and run the risk of becoming extinct wherever the conditions for their existence are not met any more. This should lead to local extinctions, sometimes stemming from dramatic mass mortalities. It is to be expected that species with restricted distributions, and sensitive to changes in abiotic factors might easily suffer from global change, unless their populations have the potential of becoming adapted to the novel conditions, just as pests become adapted to cope with pesticides.

The Mediterranean Sea is one of the best candidates to local extinction at a basin level. It is almost closed, it has a high rate of endemism, it is much smaller than any ocean and so it responds more quickly to environmental change. Furthermore, the Mediterranean Sea does have a particular biota, made of highly seasonal species that are present either in the winter (boreal contingent) or in the summer (tropical contingent). It is to be expected that global warming will favor the tropical contingent, whereas the boreal one will be in distress (Boero *et al.*, 2008). The abiotic change, triggered by increasing temperatures, is followed by biotic change, with the arrival of aliens of tropical affinity, or the prevalence of the summer contingent that expands its potential for success, making competition harsher for the species of cold water affinity. If global warming can kill species, the potential victims are of cold water affinity.

LOOKING FOR PUTATIVE EXTINCTIONS

Many marine species have yet to be discovered. The still undiscovered species are probably rare, or are cryptic species that make up species complexes that are not recognized as being made of more than one species. Of course, it is very difficult to recognize a putative extinct if we do not even know that it exists! While considering only the already described species, it is possible, however, to build hypotheses about the possibility that they are extinct.

A GENERAL PROTOCOL TO DETECT PUTATIVE EXTINCTIONS

Every known species has been described by a taxonomic paper (the original description) and the date of its first finding is the beginning of the history of its knowledge. After the original description, species are usually recorded again in other taxonomic papers or in faunistic and ecological ones. The knowledge about each species is stored in the scientific literature. Analyzing the temporal and spatial distribution of species, as recorded by the scientific literature, we can reconstruct maps of their recorded presence in space and time. Such maps can be compiled for every known species, but they are to be carefully compiled by experts who can recognize synonyms and doubtful records due to lack of taxonomic expertise.

If a species is not being recorded for a reasonably long time (e.g. 40 or more years, as suggested by Gravili *et al.*, 2013), a case of putative extinction can be raised (see Executive summary, this volume, for a formal way to do it, developed from paleontology). These putative extinct species have been found in the past at given locations and are associated with one or more habitats. It is possible, with this information, to organize surveys in the same habitats, at the same localities, in the same periods of previous findings, and check if these species are still present. Their absence from the scientific literature, in fact, might be due to simple lack of proper sampling, or to lack of expertise in recognizing them in previous samplings. Another reason for the absence of a given species might be the existence of resting stages that can remain dormant for even centuries and that, when activated, might lead to what paleontologists call the Lazarus effect (Jablonsky, 1986). It is rather important, in this respect, to know the bio-ecology of the species under investigation, especially in terms of life cycle features.

Biotic surveys are increasingly carried out to detect alien species; they may be used also for the purpose of testing the hypothesis of putative extinctions.

Looking for putatively extinct species in Mediterranean Hydrozoa

Gravili *et al.* (2013) applied the above protocol to the 400 non-siphonophoran hydrozoan species known to occur in the Mediterranean Sea (Bouillon *et al.*, 2004). Positive records in the last ten years are available for 156 species (39%), whereas among the remaining 244 species, 67 species have not been recorded since 41 years, 13 are unrecorded since 40-31 years, 79 since 30-21 years, 85 since 20-11 years.

Trycyclusa singularis, the only representative of the genus *Trycyclusa* and of the family *Trycyclusidae* (see Bouillon *et al.*, 2006 for a world list of Hydrozoa) is a striking case of a species that is “absent” from the literature since a very long time. Namely since the time of its description, in 1876, as remarked by Boero and Bonsdorff (2007). The species has been recorded also from northern European Seas (Schuchert, 2006) and is probably not in danger of final extinction, but it is a fact that it is not being recorded from the Mediterranean Sea since 136 years. Being of cold water affinity, and having a restricted distribution to the coldest part of the Mediterranean Sea (the Gulf of Trieste), in shallow water, this species is probably very sensitive to global warming. It might be the case, however, that *T. singularis* is a Lazarus taxon, since its life cycle probably includes a resting stage (Schuchert, 2006). What was proposed by Gravili *et al.* (2013), with the improvement suggested in this volume, can become a standard practice to make lists of putatively extinct species in any group.

Extinction in the Mediterranean Sea

The vertical mixing of Mediterranean waters, at sub-basin scale, is triggered by the so-called “cold engines”: the Gulf of Lions for the Western Mediterranean, and the Northern Adriatic and/or the Northern Aegean for the Eastern Mediterranean. These areas are significantly colder than the rest of the basin, and are sites of “deep water formation” near the surface. They are inhabited by biotas that comprise also species of cold water affinity that are restricted to these colder parts of the Mediterranean (Boero *et al.*, 2008). These areas, thus, are the best candidates for the presence of putatively extinct species in a period of global warming.

Making the lists of species that live only in these areas, for all significant taxonomic groups, might provide a tool for building up lists of putatively extinct species, and surveys at these locations, with the intent of finding these species, can be the best test to ascertain if they are still present, albeit undetected.

The absence of a species is not the final proof of its extinction, though. Many species, in fact, do have resting stages in their life cycles, and they might still be present in the environment, waiting for the return of proper conditions, while not being represented by active specimens. As remarked already, this condition applies also to *Tricyclusa singularis*. The analysis of resting stage banks in the sediments might be a refinement of the surveys (Belmonte *et al.*, 1995), whereas it is extremely difficult to detect resting stages on hard bottoms.

Molecular tools, such as barcoding techniques, might be useful to search for putatively extinct species, if they have been barcoded. It might be useful, if type specimens are available in museum collections, to barcode them.

CONCLUSION

We are very attracted by what we find, and the lists of species are always on the increase, especially in periods of rapid change of biota, like the present one. The "old" lists, in fact, are updated by the addition of the new entries, but the possibly extinct species are seldom, if ever, removed from the lists. This biased picture must be corrected by evaluating also the possibility that species that were present before are not present today. Only taxonomists can accomplish the task of listing putatively extinct species. Conservation biologists, in fact, propose red lists for endangered species whose presence is usually well documented, albeit while being represented by very few specimens. These species must be the object of careful management and protection, but the inconspicuous species that might be in danger should be taken in great consideration too. Simply because they are the bulk of biodiversity.

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Marine mammals and risk of extinction: an overview at local, regional and global scales

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ABSTRACT

The International Union for the Conservation of Nature (IUCN) reports that 25% (32 of 128 species) of marine mammal species are being threatened with extinction. The main threats are of anthropogenic source, including pollution, fishing, invasive species, urban development, harvesting, and climate change. In addition, the conservation status of almost 40% of marine mammals is unknown due to insufficient data. This paper aims to review the current dynamics of extinct and endangered marine mammals, with emphasis on the threats undermining the persistence of vulnerable species, complemented by an overview of specific examples from the Mediterranean Sea and beyond factors and contexts which place marine mammals under risk of local/regional/global extinction.

INTRODUCTION

Extinction happens once an entire species disappears due to natural - over geological time scales (Raup, 1986; 1994) or unnatural causes. It may be a gradual process, with only few species disappearing over long periods of time, or it can happen rather rapidly, causing the disappearance of many species of fauna and flora in short periods of time. Some species of plants and animals may become extinct due to their lower success in finding food and habitat, while other species may disappear due to major changes in their habitat, such as natural catastrophes (climatic, tectonic or cosmic).

Quantifying extinction rates is still highly uncertain because no proven direct methods or reliable data exist for verifying extinctions (Fangliang and Hubbell, 2011). Nonetheless, there is general agreement that rates of species loss have increased over the past 8000 years (Caughley, 1994; Pimm *et al*., 1995), largely as a result of accelerated habitat destruction and degradation, prey depletion, introduction of alien and invasive species, all driven by human activity (Domning, 1999).

Diamond (1989) defined the "*evil quartet*" of extinction drivers: overkill (overexploitation), habitat destruction, introduced species and chains of extinctions. Despite the profound effects that single causes can have on the rate of species loss, recent studies underline that most extinctions involve a synergy of these factors (Koh *et al*., 2004; Ibáñez *et al*., 2006; Mora *et al*., 2007; Brook *et al*., 2008), with individual causes being difficult or impossible to identify.

Scientists estimates that more than 120 species of birds and 60 species of mammals have disappeared over the last 400 years - such as the passenger pigeon (*Ectopistes migratorius*), dodo

(*Raphus cucullatus*), quagga (*Blohemien Quagga*), and great auk (*Pinguinus impennis*). Each year a number of species considered extinct are rediscovered (Fisher, 2011; Scheffers *et al*., 2011). Despite a suggestion (Fangliang and Hubbell, 2011) that the current extinction rate projections of animal and plant species may have been overestimated, there is general consensus that the near-term extinction rates still remain at 400-4,000 times the background rate of species extinction (Brooks *et al.*, 2011; Smith *et al*., 1993; Millennium Ecosystem Assessment, 2007). Recent studies suggest that we are currently in the midst of the sixth mass extinction (e.g. Pimm *et al*., 1995; Wake and Vredenburg, 2008; Chapin *et al*., 2000; Barnosky *et al*., 2011).

Assessing whether a species or a population is to be considered endangered or near extinction is extremely hard and potentially biased, especially in terms of detecting and understanding the biological basis of vulnerability (Dulvy *et al*., 2003). Population size is a relatively easy way to classify a species status, with species such as the vaquita (*Phocoena sinus*) which numbers about 150 individuals only (Jaramillo-Legorreta *et al*., 2007), the North Atlantic right whale (*Eubalaena glacialis*) with only about 300 individuals left (Kraus *et al*., 2005) or the Mediterranean monk seal (*Monachus monachus*), with about 350-450 individuals left (Aguilar and Lowry, 2008).

Once a population reaches very low levels and the rate of decline is very rapid, the probability of extinction in a given time frame is often used to determine its status. The IUCN Red List (IUCN, 2001; 2006) defines '*critically endangered*' those species with a probability of extinction estimated to be at least 50% within 10 years or three generations. Similarly, the '*endangered'* and '*vulnerable'* status is given to those species with a probability of extinction estimated at 20% within 20 years or five generations and 10% within 10 years or three generations, respectively. Another method to forecast population health and extinction risk especially used in conservation biology is the population viability analysis (PVA). It considers both species characteristics and environmental variability such as population size, trends in abundance, life history characteristics, natural variability, trends in habitat loss, and parameter uncertainty (Taylor *et al*., 2006). Considering that each PVA is individually developed for a target population or species and the robust data-sets that this method requires, very few marine mammal species meet the assumptions to be properly evaluated with PVA.

CAUSES OF MARINE MAMMALS EXTINCTION WORLDWIDE

Ocean systems are subject to natural fluctuations on a local and global scale over geological times, leading to fragmentation or loss of most shelf habitats. Such changes could lead to extinctions.

The consequences of anthropogenic impacts on marine mammal biodiversity worldwide remain poorly understood (Davidson *et al*., 2012). The International Union for the Conservation of Nature (IUCN) states that 25% (32 of 128 species) of marine mammal species are threatened with extinction by two or more human impacts, including pollution, fishing, invasive species, development, hunting, and climate change. Nonetheless, the conservation status of nearly 40% of marine mammals is unknown due to insufficient data.

Among marine mammal populations currently considered critically endangered due to very small numbers of individuals one finds cetacean species such as the Indus river dolphin (*Platanista gangetica minor*), the vaquita, North Pacific and North Atlantic right whales, several populations of blue whales (*Balaenoptera musculus*), western North Pacific gray whale (*Eschrichtius robustus*), Cook Inlet and St. Lawrence River beluga whales (*Delphinapterus leucas*), and Arctic bowhead whales (*Balaena mysticetus*); pinniped species such as the Mediterranean monk seal, the Saimaa ringed seal (*Pusa hispida saimensis*), several populations of Atlantic walrus (*Odobenus rosmarus rosmarus*); and sirenian species such as several populations of dugongs (*Dugong dugon*), and West African (*Trichechus senegalensis*) and West Indian manatees.

Very recently the Yangtze River dolphin (the Baiji, *Lipotes vexillifer*) was declared extinct (Turvey *et al*., 2007), making this species the first aquatic mammal species to become extinct since the demise of the Japanese sea lion (*Zalophus californiaus japonicus*) and the Caribbean monk seal (*Monachus tropicalis*) in the 1950s. In addition, this is also the first recorded extinction of a well-studied cetacean species to be directly attributable to human influence.

While commercial whaling effort has been drastically reduced, allowing recovery or partial recovery of several depleted populations (e.g. Paterson *et al*., 1994), other anthropogenic threats and pressures are affecting marine mammal species throughout the world. Ranging from indirect impacts like loss and degradation of habitat, prey depletion and impacts caused by chemical and acoustical pollution, to direct effects such as ship strikes and by-catch, they all have a detrimental effect on cetaceans populations. Climate changes and global warming (e.g. Learmonth *et al*., 2006; Johnston *et al*., 2012) together with the indirect effect of ocean acidification (Bass *et al*., 2006) also have the potential to severely affect marine mammals, and cetaceans in particular.

Whaling and harvesting

Marine mammals exploitation can be considered the main force driving populations to or near extinction (Harwood, 2001). Harvesting of coastal marine mammals by local groups has been widely common, for a long period of time, with a negligible impact on the populations (see Reeves, 2002 for a review). Large marine mammals from remote areas have only recently begun to be endangered from human activities due to the development of commercial operations (18th century for seals and in the 19th century for whales). Commercial, large scale activities have caused several species to reach or being very close to extinction towards the first decades of the 20th century. Among them, we can mention the Steller's sea cow (*Hydrodamalis gigas*), the Caribbean monk seal, and the Japanese sea lion. The Atlantic gray whale (*Eschrichtius robustus*) (Mead and Mitchell, 1984) and the Atlantic sea mink (*Mustela macrodon*) (Turvey and Helgen, 2008) populations have also become extinct over the last hundred years. In 1768 the Steller's sea cow was declared extinct, 27 years after the species was first discovered by Russian explorers in the Commander Islands.

By-catch

By-catch occurs when an animal is incidentally captured and killed by fishing activities. It represents one of the principal causes of death for several marine mammal species (Lewison *et al*., 2004) cases ranging from large baleen whales entangled in lobster pot lines off the East coast of the United States (Johnson, 2005) to Black Sea harbor porpoises (*Phocoena phocoena* ssp. *relicta*) getting entangled in bottom-set gillnets for Turbot (*Psetta maeotica*) (BLASDOL, 1999). Virtually any marine mammal species living where intense fishing activities take place is at risk of being by-caught, but usually the smaller species and those that occur in continental shelf waters are impacted most heavily. In fact, throughout the world, small inshore species such as the harbor porpoise are known to be victims of by-catch in fishing operations, but the level of such by-catches and the likely impacts remain unknown.

Despite evidence of the impacts of this threat in several areas (e.g., NOAA, 2003), our knowledge on the nature and impacts of direct interactions between marine mammals and fisheries on a global scale remains fragmentary (for a comprehensive review, see Read *et al*., 2006).

As an example of the extension of the problem, the capture of pelagic delphinids (*Stenella* and *Delphinus*) by the Eastern Tropical Pacific (ETP) tuna purse seine fishery can be described as one of the first and most important examples of unsustainable levels of by-catch in fishing operations (Gerrodette and Forcada, 2005; Wade *et al*., 2007; Gerrodette *et al*., 2012). In the period between 1960-1972 the impact of this fishing technique on pelagic dolphins, in particular the Pantropical spotted dolphin *Stenella attenuata*, has been extremely severe, with an estimated total mortality of more than 4 million dolphins killed (Wade, 1995).

It required an international public awareness campaign, with the creation of the label 'dolphin safe' on tuna cans, coupled with the development of new techniques to free the dolphins from the nets, to bring about a significant reduction of by-catch levels. Systematic monitoring campaigns organized by the Inter-American Tropical Tuna Commission estimate that mortality has been reduced to less than 1500 individuals per year (Anonymus, 2004). Nevertheless the purse-seine fishery continues to have an impact on dolphin stocks beyond directly observed mortality, with high uncertainty about the degrees of such impacts at the population level (Wade *et al*., 2007).

Two other outstanding examples of species in need of special attention due to the unsustainable by-catch rate on their populations are the Baiji, recently declared extinct (Turvey *et al*., 2007), and the vaquita.

The Baiji or Chinese river dolphin was mainly present in the middle and lower parts of the Yangtze River (China), with an estimated population in the late 1980s of just a few hundred individuals, and with a minimum estimate of only 13 individuals during a survey conducted in 1997-1999 (Zhang *et al*., 2003). The synergistic effect of by-catch in local fishing activities plus extensive habitat degradation and fragmentation, along with dams construction, chemical pollution and heavy traffic volumes have all contributed to the significant decline of the finless porpoise in the river (Wang, 2006), with the former being recognized as the principal causes of mortality for the species. About 45% of all described Baiji deaths have been attributed to snagging in rolling hooks and other fishing techniques such as electro fishing (Zhou and Wang 1994; Zhou *et al*., 1998; Zhang *et al*., 2003). Recently, after an extensive systematic visual and acoustic survey carried in 2006 failed to record any Baiji, the species was declared extinct (Turvey *et al*., 2007).

The vaquita or Gulf of California porpoise is currently the world's most critically endangered cetacean species (Rojas-Bracho *et al*., 2006). This species range is restricted in the upper sector of the Gulf of California in Mexico, and coincides with an area with large and economically important fishing activities, mainly targeting blue shrimp (*Litopenaeus stylirostris*) (Aragón-Noriega *et al*., 2010). Recent abundance estimates describe the vaquita population to be small, with about 245 individuals in 2008 (95% CI 68–884; Gerrodette *et al*., 2011). In this case as well, incidental mortality in fishing operations is the major source of mortality. The yearly mortality rate for vaquita in gill net fisheries has been estimated at around 40-80 per year. Considering the low number of individuals, this rate is clearly unsustainable and will most likely drive the population to extinction within a short time frame. In order to prevent extinction of this species, the Government of Mexico is suggesting economic incentives to eradicate fishing activities from the vaquita distribution area (Morzaria-Luna *et al*., 2012).

Habitat loss and degradation

The great majority of the world's population lives within 100 km from the ocean and three-quarters of the world's big cities are located on the coast (Balk *et al*., 2005). Therefore, coastal areas are affected by threats primarily originated from anthropogenic activities (e.g. Waycott *et al*., 2009; Perkol-Finkel and Airoldi, 2010). While habitat destruction has been increasing for many years understanding its effects on biodiversity still represents a main challenge to science and conservationists (Balmford *et al*., 2002; Airoldi *et al*., 2008; Thrush *et al*., 2009). Although habitat loss and degradation are recognized as a critical threat to global biodiversity, the protection of marine habitats has only recently become an issue of critical importance to conservation efforts.

Harwood (2001) predicted moderate to extreme pressure on marine mammals based on the alteration of their ''critical habitats'' defined as ''functioning ecological units required for successful breeding and foraging''.

In general habitat destruction does not represent a serious threat for most of the large whales. There are, however, some exceptions for those populations which are dependent upon restricted waters adjacent to highly developed coastline, such as the North Atlantic right whale and the Grey whale, where habitat degradation represents a potentially serious issue.

Climate change

Climate change is currently considered one of the most significant factors jeopardizing biodiversity throughout the world (Walther *et al*., 2002; Thomas *et al*., 2004a,b; Isaac and Williams, 2007; Isaac, 2009) likely to enhance the risk of extinction depending on the species geographical range and life history parameters. As a consequence, the marine mammal species more susceptible to extinction risk will be those already vulnerable and with limited climatic ranges, or with specific and restricted habitat requirements (Purvis *et al*., 2000).

Climate change may have direct or indirect impacts on marine mammals, including habitat loss and modifications in prey distribution and accessibility. We can anticipate that climate change, global warming in particular, will have major impacts on several species of marine mammals (e.g.

Learmonth *et al*., 2006; Johnston *et al*., 2012). For example, Forcada *et al.* (2005) described a decline in pup production in South Georgian Antarctic fur seal *Arctocephalus gazella* since 1985, associated with a reported increase in sea surface temperatures, likely associated with low availability of food (krill). Global warming is also impacting sea ice formation and breakup, as well as reducing its thickness and extension, which will affect migration routes.

MEDITERRANEAN MARINE MAMMALS

Eleven species of cetaceans the fin whale (*Balaenoptera physalus*), the sperm whale (*Physeter macrocephalus*), Cuvier's beaked whale (*Ziphius cavirostris*), the Killer whale (*Orcinus orca*), the long-finned pilot whale (*Globicephala melas*), Risso's dolphin (*Grampus griseus*), the rough-toothed dolphin (*Steno bredanensis*), the common bottlenose dolphin (*Tursiops truncates*), the striped dolphin (*Stenella coeruleoalba*), the short-beaked common dolphin (*Delphinus delphis*) and the harbor porpoise (*Phocoena phocoena*) and one species of Pinniped, the critically endangered Mediterranean monk seal (*Monachus monachus*) regularly occur in the Mediterranean Basin. In addition to them, three other species of cetaceans are considered visitors and eight vagrant (Notarbartolo di Sciara and Birkun, 2010).

The Mediterranean sea is recognized as a hotspot of marine biodiversity (Myers *et al*., 2000; Spalding *et al*., 2007; Abdulla *et al*., 2009), but human activities, climate change and the invasion of alien species are the main dangers now threatening its rich marine life (Claudet and Fraschetti; 2010; Bianchi, 2007; Coll *et al*., 2010; Danovaro *et al*., 2010).

In this area, many factors have potential detrimental effects on marine mammal populations, in particular interactions with fishery, injuries and mortality from shipping, direct killing, chemical and noise pollution together with a severe widespread habitat loss and degradation and climatic change (Notarbartolo di Sciara, 2002).

Cetaceans by-catch and entanglement in fishing gear occur throughout the Mediterranean Basin and Contiguous Atlantic, involving mainly high numbers of small-sized species such as the striped, common and bottlenose dolphin (Tudela *et al*., 2005), but also the *endangered* sperm whale in driftnets (e.g. Pace *et al*., 2008). As the effect of species loss due to by-catch at the regional level has not been estimated, the reported numbers certainly represent gross under-estimations (Notarbartolo di Sciara and Birkun, 2010). In some areas the rate of cetacean mortality has been described as unsustainable, causing a drastic declining of local populations (Bearzi, 2002).

Collisions with large vessels represent the main cause of mortally for fin whales and, to a lesser extent, for sperm whales throughout the Basin, with the 82.2% of fin whale mortality occurring within the Pelagos Sanctuary for Mediterranean Marine Mammals (Panigada *et al*., 2006), is represents an important summer feeding ground for the species. 70% of stranded sperm whales along the Greek coasts show evident signs of collisions (Frantzis *et al*., 1999). Ship strikes with sperm whales are likely to represent a serious conservation problem in the Strait of Gibraltar as well, where the high traffic volume overlaps with the species critical habitats in the area (De Stephanis *et al.*, 2005).

The load of chemical contaminants constitutes a serious threat to the species living in the area (Notarbartolo di Sciara and Birkun, 2010). Despite a general improvement noticed by some authors (Aguilar and Borrell, 2005) in relation to contaminants such as DDT and PCB, lately, a serious concern is linked to the high concentrations of xenobiotic chemicals, with very high concentrations reported for most Odontocete species inhabiting the Mediterranean Sea which is surrounded by some of the most heavily populated and industrialized countries in the world. Levels of some xenobiotics are therefore much higher here than in other seas and oceans (Fossi *et al*., 1992; 2001; 2003), with the potential for transgenerational effects, related to exposure of future generations via the placenta and milk, especially in Odontocete and Pinnipeds species (Fossi and Marsili, 2003; Fossi *et al*., 2006).

As an instance, the Adriatic Sea was described as a relatively uncontaminated ecosystem up to the 1970s, despite the presence of high concentrations of certain polluting substances within limited coastal zones (Bearzi *et al*., 2004). The situation got worst in the last thirty years, particularly in western shallow waters (Nasci *et al*., 1999) mostly due to river input and exploitation of fishing resources. The dolphin populations living in the area seem to be strongly affected by the drastic change of their habitat, in conjunction with other man-made ecosystem alterations (Bearzi *et al*., 2004). Another emblematic example from the Basin is the Mediterranean monk seal, where the species has been declining fast as a result of direct killing by fishermen and encroachment in critical habitats (Aguilar and Lowry, 2008).

Mediterranean marine mammals are likely to be severely affected by climatic changes over the next years, considering the relatively small size of the sea, its semi-enclosed status and the fast rate of turnover (Gambaiani *et al*., 2009; Evans *et al*., 2010). An increase in temperature and salinity of Mediterranean waters due to climate change has been reported by several authors (Lejeusne *et al*., 2010; Vargas-Yáñez *et al*., 2010). Climate change and related effects will significantly alter the Mediterranean environment with important consequences on apex predators such as marine mammals (e.g. Giannakopoulos *et al.*, 2009). Gambaiani *et al.* (2009) presented evidence of changes in plankton presence, abundance and distribution; in addition, warmer temperatures will strengthen water stratification, thus reducing vertical mixing and upwelling currents, causing potential lack of recruitment for large predators (Lloret *et al*., 2004). This is the case for the Western Ligurian Sea, for example, where a well-defined cyclonic circulation active all year round enhances strong upwelling currents and maintains lower surface temperatures compared to other Mediterranean areas (Astraldi *et al*., 1995). Due to these oceanographic features, linked to strong atmospheric forcing (i.e. the Mistral wind regime) this region represents an area of high productivity, therefore hosting a richer cetacean fauna compared to bordering regions characterized by lower primary production. As an instance, the area represents the principal feeding grounds for Mediterranean fin whales (Panigada *et al*., 2006). This species may be affected by the impact that increasing temperature may have on several ecological parameters, such as changes in phytoplankton composition, timing of blooms and the northward boundary shifts of warm-water species. For example, the distribution of northern krill *Meganyctiphanes norvegica,* the main fin whale prey in the Mediterranean Basin (Notarbartolo di Sciara *et al*., 2003; Panigada *et al*., 2006), which is located at the southern limit of its ecological tolerance in the western Mediterranean Sea (Tarling *et al*., 2010), may be shifted by an increase in temperature (Druon *et al*., 2012).

Warming of the Mediterranean Sea may also increase the presence, spread and outbreaks of pathogens as suggested by Simmonds and Mayer (1997), who associated the morbillivirus epizootic event that severely affected the Mediterranean striped dolphin population with the increase in temperature recorded during winter 1989-1990.

The Mediterranean and Black Sea subpopulations have been recently assessed following the IUCN Red list criteria and the outcome of this exercise proved to be rather worrying, with one species classified as "*Critically Endangered*" (CR), four species classified as "*Endangered*" (EN), four species classified as "*Vulnerable*" (VU), and three species listed as "*Data Deficient*" (Table 1) (IUCN, 2012).

Table 1. IUCN assessment for marine mammals living in the Mediterranean and Black Seas.

Species-subspecies	Region	IUCN Criterion	Year published
Harbour porpoise *Phocoena phocoena ssp. relicta*	Black Sea subspecies	**Endangered** *A1d+4cde*	2008
Common bottlenose dolphin *Tursiops truncatus ssp. ponticus*	Black Sea subspecies	**Endangered** *A2cde*	2008
Short-beaked common dolphin *Delphinus delphis ponticus*	Black Sea subspecies	**Vulnerable** *A2cde*	2008
Sperm whale *Physeter macrocephalus*	Mediterranean subpopulation	**Endangered** *C2a(ii)*	2012
Short-beaked common dolphin *Delphinus delphis*	Mediterranean subpopulation	**Endangered** *A2abc*	2003
Fin whale *Balaenoptera physalus*	Mediterranean subpopulation	**Vulnerable** *C2a(ii)*	2012
Common bottlenose dolphin *Tursiops truncatus*	Mediterranean subpopulation	**Vulnerable** *A2cde*	2012
Striped dolphin *Stenella coeruleoalba*	Mediterranean subpopulation	**Vulnerable** *A2bcde*	2012
Risso's dolphin *Grampus griseus*	Mediterranean subpopulation	**Data Deficient**	2012
Long-finned pilot whale *Globicephala melas*	Mediterranean subpopulation	**Data Deficient**	2012
Cuvier's beaked whale *Ziphius cavirostris*	Mediterranean subpopulation	**Data Deficient**	2012
Mediterranean monk seal *Monachus monachus*	Mediterranean subpopulation	**Critically Endangered** *A2abc; C2a(i)*	2008

Figure 1 indicates which are the major anthropogenic threats affecting resident marine mammals of the Mediterranean and Black Seas; taken alone these threats may not be particularly worrying, but their synergistic effect may be detrimental for several small populations.

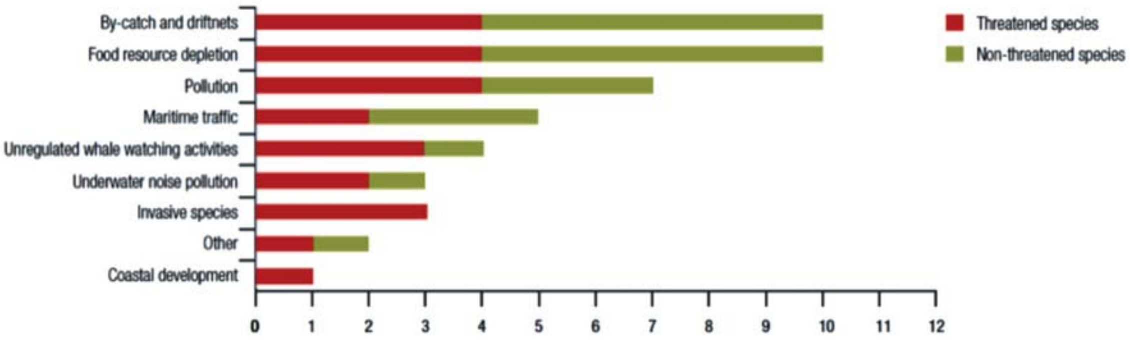

Figure 1. Major threats affecting resident cetaceans of the Mediterranean and Black Seas (from IUCN, 2012).

MEDITERRANEAN CASE STUDIES

Mediterranean monk seal

The Mediterranean monk seal represents the only Pinniped species occurring in the area. Once abundant throughout the region until Roman times (Johnson and Lavigne, 1999), the monk seal is currently on the verge of extinction in the Mediterranean and was extirpated in most of the study areas well before the Second World War (Sergeant *et al*., 1978; Johnson, 2004), with fewer than 500 individuals currently surviving after a major die-off event occurred in 1997 on the Cap Blanc Peninsula on the coast of the western Sahara on the North Atlantic coast of Africa (Costas and Lopes-Rodas, 1998; Harwood, 1998; Hernandez *et al*., 1998; Osterhaus *et al*., 1997; 1998; Forcada *et al*., 1999; Van de Bildt *et al*., 1999). In 2001 the Mediterranean monk seal was ranked as a marine mammal species in imminent peril of extinction (Van Blaricom *et al*., 2001).

The species is listed as "*Critically Endangered*" according to the IUCN Red list criteria (Aguilar and Lowry, 2008) and is included on Appendix I of the Convention on International Trade in Endangered Species (CITES). Other international legal mechanisms which take into consideration the current conservation status of the species include the Bonn Convention (Convention on the Conservation of Migratory Species of Wild Animals), the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats), the Convention on Biological Diversity and the EU Habitats Directive.

In addition to the severe die-off previously mentioned that occurred in 1997, other threats to the population include increased human pressure that displaces seals from their habitat; in particular deliberate aggression by fishermen and by-catch in fishing gear and, to a lesser extent, disease and pollution.

Currently the species distribution is widespread, but fragmented into an unknown but probably relatively large number of very small breeding subpopulations. In the Mediterranean Basin the seal is only present on the Hellenic and Turkish coasts, numbering a few hundred (Güçlüsoy *et al*., 2004), and, out of the region, it occurs in small areas of northern Africa, in the south-eastern North Atlantic area at Cabo Blanco and at the Desertas Islands in the Madeira Islands group (Aguilar, 1999; Gilmartin and Forcada, 2002).

The short-beaked common dolphin

The short-beaked common dolphin was considered relatively abundant in much of the Mediterranean until a few decades ago (Bearzi *et al*., 2003). After a large-scale population decline occurred during the last 30-40 years, in 2003 the Mediterranean population was listed as *Endangered* in the IUCN Red List of Threatened Animals (Bearzi, 2003). Today the species survives only in small portions of its former Mediterranean range and in some areas these dolphins have become rare if not completely absent (e.g. Bearzi *et al*, 2004; 2005). For instance, around the island of Kalamos in the eastern Ionian Sea, where common dolphins presented a high degree of site fidelity when studies began in 1993, the group sizes decreased significantly after 1996. The mean group size was 12 in 1993-96, and dropped to seven in 1997-2002. In the years 1993-2000, the mean sighting frequency was 0.016 groups/km, but it drastically dropped to 0.007 groups/km later (Bearzi *et al*., 2003).

The northern Adriatic Sea represents another interesting case study for this species. In this area, the regular presence of common dolphins was reported and well documented until the 1970s (Bearzi *et al*., 2003; 2004). For largely unknown reasons, they have declined and almost completely disappeared there in the last three decades (Bearzi *et al*., 2000).

Recent studies suggest that common dolphins have declined largely as a result of human impact, the main threat being represented by the depletion of prey caused by overfishing. In the Mediterranean Sea, several fish resources are highly exploited or overexploited (e.g. CIESM, 2000; Lleonart and Maynou, 2003; MacKenzie *et al*., 2009; Coll *et al*., 2010). Ecological extinction caused by overfishing was ranked above by other pervasive human disturbance to coastal ecosystems (Jackson *et al*., 2001). Even though it is difficult to demonstrate a strict correlation between the impoverishment of fish stocks caused by excessive fishing and the disappearance of common dolphins in the Mediterranean Sea, where common dolphins have been studied consistently in the region, exploitative competition with fisheries is a source of concern for the conservation status of the species (e.g. Bearzi *et al*., 2006).

Other factors that may have contributed to the species' decline in the region include habitat degradation, contamination by man-made chemicals, potentially resulting in immunosuppression and/or reproductive impairment, and incidental mortality in fishing gear (Bearzi *et al*, 2003).

CONCLUSION

Marine mammal biodiversity worldwide is threatened by diverse dangers with serious potential detrimental effects on populations and species. While it is often easy to identify the single causes driving species to or near extinction on a local scale, and eventually undertake protection and conservation measures, it is more difficult to achieve the same results on a regional and global scale, due to complex synergistic interactions.

The precarious situation of several marine mammals has been known for a long time, since scientists warned about extinction for some species back in the late 1800s (Eschricht and Reinhardt, 1861; Scammon, 1874). At present, human activity can be certainly identified as the main force causing the loss of species. Pollution, habitat degradation and fragmentation, coastal and off-shore development, overfishing, whaling and hunting all contributed to some extent to the eradication of several marine mammal species, and drive others to the verge of extinction. Currently, 32 species of marine mammals out of 128 are threatened by extinction according to IUCN, while the conservation status of nearly 40% of marine mammals is unknown due to insufficient data.

The lack of baseline information on the biology and ecology of marine mammals hampers the difficulties to assess the correlates and causes of extinction and to implement science-based conservation (Davidson *et al*., 2012). Planning conservation measures to reduce declines in abundance and to facilitate recover of endangered species and populations from extinction, therefore requires a thorough understanding of the life history of the species or population, together with an assessment of the effects of anthropogenic pressures.

In general, a species may be defined endangered and close to extinction once its demographic values are so low that recovery is impossible. Marine mammals are characterized by relatively low reproductive rate and delayed sexual maturity. This implies that if a population reaches low demographic levels, recovery to sustainable levels could be very slow, with populations showing a high degree of geographic and genetic isolation being more susceptible.

During the last century a constant and increasing effort to protect marine mammals biodiversity was put into place, and currently Cetaceans, Sirenians and Pinnipeds are protected by diverse regulations and agreements worldwide, both on a national and international level.

In 1911 the North Pacific Fur Seal Convention was established to protect northern fur seals (*Callorhinus ursinus*) and sea otters (*Enhydra lutris*); in 1931 the Convention for the Regulation of Whaling banned the harvesting of right whales in all oceans; in 1972 the Convention for the Conservation of Antarctic Seals was established; the International Whaling Commission's global moratorium on commercial whaling entered into force in in 1986; in 1991 the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS) was created, entering into force in 1994, while in 1996 the Agreement on the Conservation of Cetaceans in the Black Sea, Mediterranean Sea, and contiguous Atlantic area (ACCOBAMS) was formalized and entered into force in 2001 – both Agreements lie under the umbrella of the Convention on Migratory Species (CMS). Other Memorandum of Understandings (MoUs) within the framework of the CMS have been signed, like that for the Conservation of Cetaceans and their Habitats in the Pacific Islands Region, that dealing with West African Small Cetaceans and Sirenians of the Eastern Atlantic Basin, and the one concerning conservation measures for the Eastern Population of the Mediterranean Monk Seal. Furthermore, other national efforts such as the US Marine Mammal Protection Act (US MMPA) covering all marine mammals within USA territorial waters, the US Endangered Species Act (ESA), and the Canadian Species at Risk Act (SARA) have been established.

Thanks to these Conventions and Agreements, and to a growing and widespread increase in public awareness and consciousness, we have observed a reduction of the harvesting effort, with a partial recovery of some threatened populations (e.g. Alter *et al.*, 2007; Weller *et al.*, 2002). For these species and populations, though, it is imperative to carefully consider future conservation decisions, which will be critical for their long-term status, taking into consideration the fact that extinction continues years, decades and sometimes centuries past the major perturbation (*extinction debt* – Tilman *et al.*, 1994).

Protecting marine mammals represents a challenging goal to conservationists. Being often highly mobile, migratory and mostly at the top of food chains, marine mammals require both species-specific and wide protection and conservation measures.

Marine Protected Areas (MPAs) have been set up to protect vulnerable species and ecosystems, to conserve biodiversity and minimize extinction risk, to re-establish ecosystem integrity, to segregate uses to avoid user conflicts and to enhance the productivity of fish and marine invertebrate populations around a reserve (Pauly *et al*., 2002 ; Hooker and Gerber, 2004). They have progressed beyond the perception as ‘marine parks’ to becoming an important management and conservation tool (CIESM, 2011; Dayton *et al*., 2000). MPAs are also useful in terms of providing a public focus for marine conservation (Agardy, 1997). A given MPA may have any one or several of the above goals. A highly protected MPA set aside as a fishery no-take zone, for example, could be useful for marine mammal conservation by helping predators and preys to recover (Bearzi *et al*., 2006). Also, setting up an MPA around marine mammals which function as umbrella species can often result in positive effects for many other species (Simberloff, 1998; Hoyt, 2005).

Despite MPAs having been advocated for the protection of threatened marine mammals, there is a further need to completely assess their effectiveness and to verify that they are achieving all the expected results in particular when taking into consideration highly mobile species such as cetaceans and other marine top predators (Hoyt, 2005; CIESM, 2011). One of the virtuous examples of the validity of MPAs is represented by the Banks Peninsula Marine Mammal Sanctuary, New Zealand, established to reduce gillnet mortalities of Hector’s dolphin (*Cephalorhynchus hectori*). 21 years after the MPA establishment, a 6% increase in mean annual population growth has been noted in recent studies (Gormley *et al*., 2012).

In the Mediterranean Sea, the Pelagos Sanctuary for Mediterranean Marine Mammals is the only protected area devoted to the protection of the Cetacean and Pinniped species inhabiting the region. It represents the world’s first International High Seas Marine Protected Area and was incorporated in the list of Specially Protected Areas of Mediterranean Interest (SPAMIs) within the framework of the Barcelona Convention in 2001(Notarbartolo di Sciara *et al.*, 2008). While the Pelagos Sanctuary is considered a unique example and opportunity for marine conservation, evidence of its effectiveness is still lacking.

Certainly, enforcement of existing regulations to provide an essential legal safety framework is necessary to prevent the loss of marine mammals worldwide. An ever increasing effort in reducing threats to wildlife, protecting and restoring habitats – especially those where endangered species can be found – a sustainable use of resources and advocating for increased funding and research effort represent crucial interrelated elements necessary to reduce pressure to marine mammals species and their biodiversity loss.

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Extinction vulnerability of chondrichthyans

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ABSTRACT

Chondrichthyan species make up a relatively small group that has functioned successfully in diverse ecosystems for over 400 million years surviving various ecological catastrophes, including “Big five” mass extinctions. This group may now be threatened with extinction as a result of human activities and the conservative life history characteristics of the species. It is suggested that a sixth mass extinction for chondrichthyans is already ongoing, due to a specific level of human activities, particulary fisheries. In the Mediterranean Chondrichthyans are generally declining in abundance, diversity and range and are possibly facing a worse scenario than chondrichthyan populations elsewhere in the world. As chondrichthyans are having small populations with patchy and restricted, geographically distinct distribution, such species have an increased risk of global extinction following local extinction. Thus, it is essential to develop new prognostic tools that will be able to predict extinction risk of chondrichthyan species based on already accessible data.

During the past 300 years only few marine organisms have been globally extinct, compared to on land where more than 800 species have disappeared (Baillie *et al*., 2004; Carlton *et al*., 1999). However, during that period the human impact on the oceans has been significantly increased and widespread, and the two thirds of the world’s human population is expected to live within 60 km of the coast by the year 2020. Most of them depend on marine organisms for their protein intake. Further coastal waters are becoming increasingly polluted, and there is a large-scale loss of coastal habitat where most known marine biodiversity resides. Moreover, marine organisms, especially non-air breathing, are less monitored and investigated than more accessible land species. Therefore, given that the current rate of terrestrial biodiversity loss is several orders of magnitude higher than the background historic extinction and with evidence for poor detection of marine extinctions (Dulvy, 2006; Carlton, this volume) it can be presumed that the number of marine extinctions is largely underestimated. Indeed there is growing concern that marine species are being driven to extinction due to increase of their exploitation and habitat loss or degradation.

Level of extinction will be different as species can be extinct on local, regional or global scale. In areas where there is evidence of local extinction, it is crucial to determine causal factors in case they may impact other species.

Generally (in 80% of cases), there is a single causal factor. Among single causal factors, exploitation (usually fishing) was the primary factor for 55% of reported cases, followed by habitat loss/degradation (37%) (Dulvy *et al*., 2003).

Within marine taxa chondrichthyan species are a relatively small (cca. 1,200 species) group that has functioned successfully in diverse ecosystems for over 400 million years. Despite their evolutionary success, and their survival of various ecological catastrophes, including “Big five” mass extinctions (Bambach, 2006), chondrichthyans are now increasingly threatened with extinction as a result of human activities and their conservative life history characteristics. Although it is assumed that a sixth mass extinction could be reached within next three to 22 centuries (Barnosky *et al.*, 2011) for chondrichthyans it can be said that it is already underway, due to a specific level of human activities impacting precisely this group of marine organisms. A general problem of chondrichthyans, compared with teleost fishes, is that this group of species exhibit strongly K-selected life history strategies: chondrichthyan species are commonly slow growing, late to mature, have low fecundity and productivity, long gestation periods, high natural survivorship of all age classes and long life. Such biological characteristics result in low reproductive potential and low capacity for population increase for many chondrichthyans and, therefore, have serious implications for their populations which limit their capacity to sustain fisheries and recover from declines (Cailliet *et al.*, 2005).

Regrettably, chondrichthyans (as target species or a bycatch) have long been a relatively low priority for fisheries management because catch volumes and values (with the exception of fins) are generally assumed to be low. Consequently, species of greater economic interest, mainly teleost species, have received higher management priority. Recently, the situation has been slowly changing due to increasing conservation concerns, but the efforts are not combined with efficient management due to lack of reliable data needed to make proper stock assessments.

Hence, in most cases, when some kind of management of chondrichthyan species exists, the techniques and enforcement measures used are insufficient to ensure the long-term maintenance of those species and populations. Moreover, the assessment models usually applied are based on teleost fisheries, making such models inadequate to chondrichthyan populations. Subsequently, for the most chondrichthyan species, the absence of required and conventional stock assessment data results in the absence and/or postponing of conservation measures.

Unfortunately, the debate over the potential for fisheries (or other factors) to drive wide-ranging marine fishes (both teleosts and chondrichthyans) to extinction is still ongoing. According to one side, once a species becomes commercially extinct (before becoming biologically extinct), it will be relieved of fishing pressure as targeted fisheries will collapse of their own accord when stocks become so reduced that they are no longer profitable to pursue. Thus, it is presumed that the halt of fishing should allow the species to recover and subsequently increase its population. Nevertheless, the presumption that a fish will reach economic before biological extinction cannot be assured if the value of the species is so high that it is still profitable for fisherman to continue with fishing of an extremely small surviving population. A further problem lies in multispecies fishery where only few species are targeted, while the majority is part of a bycatch. Thus, if a small and less abundant surviving population is a bycatch in fisheries, where target species are still within profitable economical limits, such a fishery will not stop and bycatch populations will be severely depleted and possibly eradicated.

Bycatch species, especially chondrichthyans, in intense fishery may be even more vulnerable than target species, because discards and landings are usually poorly monitored. Therefore, data of declining catches and collapsing stocks may be overlooked. A typical example for a such situation is the case of the North-west Atlantic barndoor skate *Raja laevis*. This species is a large, late-maturing skate taken as bycatch in the bottom trawl groundfish fishery and consequently found extinct in northern Canadian waters, surviving only in small numbers off Georges Bank at the southern edge of its range, where warmer water temperature allows faster growth and presumably earlier maturity (Camhi *et al.*, 1998).

There is much evidence of cosmopolitan and wide-ranging species being locally depleted in some parts of their ranges even as they survive in other regions in relatively high abundance. But it is difficult to assess the cumulative effect of localised depletions on the viability of a species at a global level. Although some argue that immigration from source populations will offset these depletions thereby reducing extinction risk, since very little is known about population dynamics and structure or migratory behavior for most chondrichthyans, such presumption is also unfounded (Camhi *et al.*, 1998).

For threatened species it is essential to find how to estimate the level of extinction risk. Accordingly, various proxies of extinction risk have been proposed that would allow to evaluate the status of species and populations for which abundance or distributional data are either lacking or unreliable. Hutchings *et al*. (2012) studied how to measure extinction risk based on maximum per-capita population growth rate, or r_{max}. They correlated r_{max} with specific life history characteristics to evaluate the degree to which extinction risk differs between fishes and mammals. Life history characteristics, primarily fecundity, maximum body size and age at maturity, were used for 82 chondrichthyan species (23 families and 12 orders), ranging in body size from 0,473 to 3,600 kg. Conclusion was that maximum population growth rate (r_{max}), a metric that is directly related to extinction risk and recovery potential, is similar between teleost fishes and terrestrial mammals, but significantly lower for chondrichthyans and marine mammals, making them particularly vulnerable to human impact (Hutchings *et al*., 2012).

The status of chondrichthyan populations is diverse between regions, so some regions such as the Mediterranean are especially pointed out as areas where chondrichthyans are clearly particularly threatened.

The Mediterranean covers only about 0,7% of the world's ocean surface, but the chondrichthyan fish fauna there is relatively diverse with an estimated 80 species (approximately 7% of total living chondrichthyans). Within those species four batoid species (*Leucoraja melitensis, Raja polystigma, R. radula* and *Mobula mobular*) are considered as endemic for this area (Serena, 2005). The latest available evidence indicates that chondrichthyans in the Mediterranean are generally declining in abundance, diversity and range, and are possibly facing a worse scenario than chondrichthyan populations elsewhere in the world. These declines can be attributed to a number of factors, including the life history characteristics of chondrichthyans in combination with the semi-enclosed nature of the Mediterranean Sea, intense fishing activity throughout its coastal and pelagic waters, effects of habitat loss, environmental degradation, and pollution (Cavanagh and Gibson, 2007). Large coastal species are biologically the most vulnerable to exploitation, and so such species that occur in areas subjected to prolonged and/or intensive fishing pressure are of particular concern. Ferretti *et al.* (2008) concluded that large predatory sharks in the Mediterranean Sea have declined dramatically in abundance over the last two centuries, since only 5 of the 20 large predatory sharks were detected at levels of abundance sufficient for analysis. Moreover, these five species showed rates of decline from >96 to >99.99%. At these low levels large sharks may be considered functionally extinct in coastal and pelagic waters of the northwestern Mediterranean.

Therefore, it is not surprise that the IUCN Red list of threatened species has classified 42% (30 species) of Mediterranean chondrichthyans as threatened within the region. Of these, 18% (13 species) are Critically Endangered (CR), 11% (8 species) are Endangered (EN) and 13% (9 species) are Vulnerable (VU). Most of these species are considered to be more seriously threatened within the Mediterranean region than at the global level (Cavanagh and Gibson, 2007).

Species with highest extinction risk in the Mediterranean include several species of bottom-dwelling chondrichthyans highly susceptible to trawling activities and with vulnerable life histories. All three species of angelsharks *Squatina* spp. are currently seriously threatened (Critically Endangered) with evidence of severe declines and range contractions, although all were historically abundant. Particular concern is on both Mediterranean species of sawfish. Smalltooth sawfish *Pristis pectinata*, large and historically widely distributed sawfish has been wholly or nearly extirpated from large areas of its former range in the North Atlantic (Mediterranean, US Atlantic and Gulf of Mexico) and the Southwest Atlantic coast, by fishing and habitat modification. Remaining populations are now small, fragmented and Critically Endangered globally. In the Mediterranean the species is considered as apparently extinct, as well as in the Northeast Atlantic. A particular problem is that reports of this species outside the Atlantic are now considered to have been misidentifications of other *Pristis* species, which leads to the conclusion that *P. pectinata* is extinct globally. The common sawfish *Pristis pristis* presents a similar case. This species is a large inshore marine and freshwater sawfish that was once common in the Mediterranean and Eastern Atlantic, but has now, along with all other sawfishes, been extirpated from Europe and the Mediterranean. As its status in West Africa is unsurveyed, there is high probability that this species will become extinct in the Mediterranean and Atlantic, if this is not already the case (Cavanagh and Gibson, 2007).

Although there are lots of causal factors responsible for a decline of chondrichthyans in the Mediterranean; the primary causal factor is easily detectable and that is fishing. Generally, it was considered that the commercial value of chondrichthyan catch in the Mediterranean is low compared to that of teleost fishes and other marine organisms, but such presumption could be result of commercial data deficiencies. Due to multispecies characteristic of the Mediterranean fishery, where chondrichthyans are usually considered as a bycatch, landings of those species are mainly not reported. Hence, when landings data are supplied, they are rarely available at species level, as they are provided in generic categories such as “Sharks, rays, skates etc. nei”. The use of generic categories means that accurate species assessments cannot be performed, as the proportion of individual species within these categories is not available. Thus, when landings are declared to these levels, trends in landings or CPUE cannot be detected. Consequently, if stock assessment data would be the only method for the quantification of the degree of vulnerability of the resource, that will remain unknown. However, deficiency of such information, including specific biological and ecological data which are also, in general, still unreliable for most of the Mediterranean chondrichthyans, should not be used as an excuse for lack of conservation action and protection. Comparison of scientific research expedition data from 1948 to 1998 (Fig. 1) in the Adriatic revealed a huge decline of bottom dwelling chondrichthyans in a number of species, species index of biomass, abundance and distribution (Dul i *et al.*, 2009). As bottom-dwelling species are highly susceptible to trawling activities, which constantly intensify in terms of fishing effort and trawable areas, these species are actually taxa at highest extinction risk in the Mediterranean. The case of chondrichthyans, especially large predatory sharks, in the Adriatic, is probably similar. In some areas where they were abundant, there are nowadays extinct and have not been seen for decades (Table 1), e.g. *Isurus oxyrinchus* (Soldo and Jardas, 2002; Soldo, 2006). However, none of those species has been marked as extinct on local or regional scale as there is no agreement on the level of data required for such classification. Thus, it can be proposed that such species should be declared as putatively extinct, until real extinction or occurrence is validated. Consequently, putatively extinct species would receive more attention and effort to collect data for better and faster understanding of their population status in the Mediterranean.

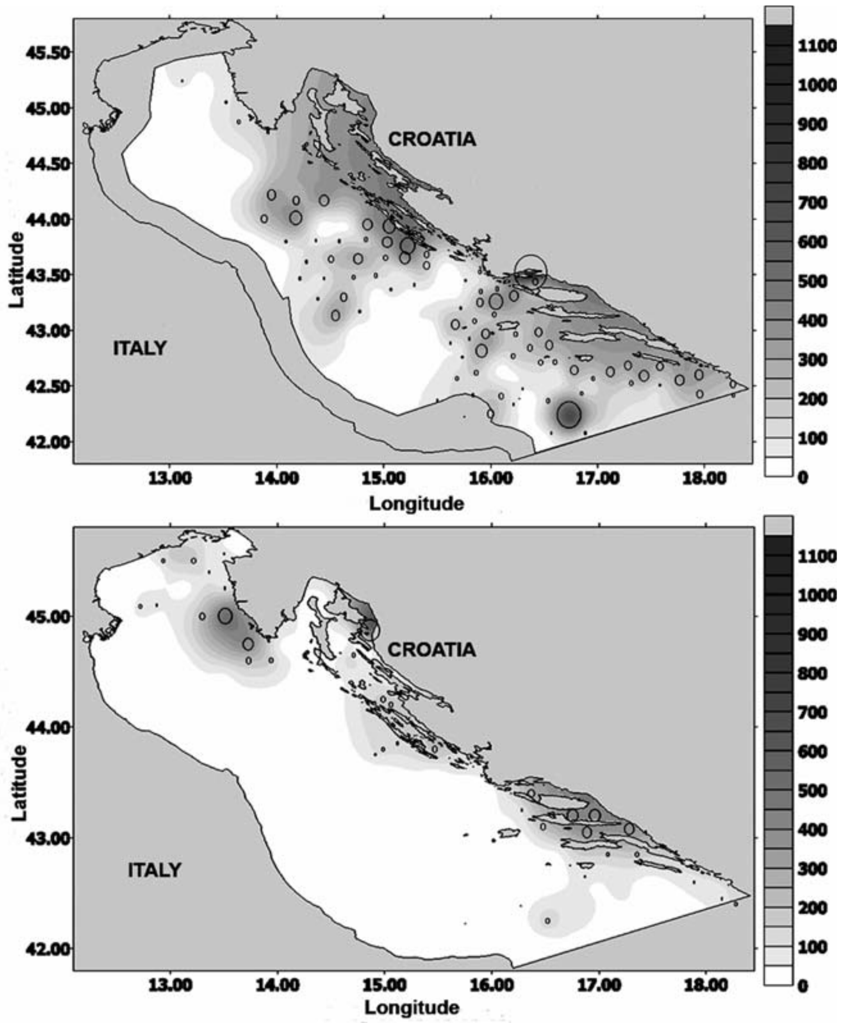

Figure 1. Comparison of abundance and distribution of bottom dwelling chondrichthyans in the Adriatic based on scientific research expedition data from 1948 (up) to 1998 (down).

Table 1. Records of rare chondrichthyans in the Adriatic.

Species with 1-10 records during last 10 years	**Species with no record during last 10 years**	**Species with no record during last 10-30 years**	**Species with no record more than 30 years**
Carcharodon carcharias *Squatina squatina* *Carcharias taurus* *Oxynotus centrina*	*Odontaspis ferox* *Heptranchias perlo*	*Squatina oculata* *Sphyrna zygaena*	*Isurus oxyrinchus* *Pristis pectinata*

Even for some species previously considered as common with a large population, such as the blue shark *Prionace glauca*, latest evidence indicates that such status is no longer valid, as their population are more depleted than previously thought (Soldo and Peirce, 2005). Thus, it is clear that all chondrichthyans in the Mediterranean, whether if they are pelagic or bottom species, are under severe threat of extinction as a result of human impact in whole region, fisheries in particular.

Although it is well-known today that chondrichthyan populations are undergoing severe decline as a result of fisheries, so far no management has been applied to change the pressures on those populations which may lead to further decline resulting in local and regional extinction.

It can be argued that some marine species, after suffering local extinctions, have experienced recolonization. But for Mediterranean chondrichthyans, where fishing pressure is unyielding, such a process is highly unlikely. The next question therefore is whether local extinctions could influence the status of a species on a global scale? While large and abundant populations with a global distribution should not be significantly influenced by extirpation from certain areas, it should be noted that most chondrichthyans have small populations with patchy, restricted, geographically distinct distribution. Matter and Roland (2010) concluded that patchy populations are most likely to exhibit an increase in synchrony following extinction, thus, patchy populations should have an increased risk of global extinction following local extinction. It is already established, that local extinctions of marine species, especially chondrichthyans, tend to be overlooked until long after they have occurred, even when a sort of species management model exists. Therefore, the local extinction factor is probably not included in any calculation. Consequently, warning signs which can predict extinction on a global scale will be ignored or miscalculated, and at a certain point the ability of the species to respond to threats may be compromised by reaching point of no return.

The wider ecosystem consequences of severe decline and local extinctions are unknown and remain to be investigated. Particularly in the case with chondrichthyans since most of them are apex predators, especially large sharks. Top marine predators play an important role in structuring communities by controlling prey populations and preventing ecological dominance (Heithaus *et al*., 2008). Losing top predators can induce strong increases in midlevel consumers, shifts in species interactions, and trophic cascades.

From previously indicated data we can conclude that the status of most chondrichthyan populations is far from stable, and that risk of extinction for those species, and the resulting impact on marine ecosystems, is underestimated. Thus, it is essential to develop new mechanisms and prognostic framework that will allow to predict extinction risk of chondrichthyan species based on already accessible data, and to apply enhanced management measures for their better conservation status at local, regional and global level.

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Assessing neoextirpations in the Adriatic Sea: an historical ecology approach

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1. Background

1.1 The unknown of our present is our past

Historical ecology is a discipline that explicitly acknowledges the need of incorporating time as a fundamental variable into ecological analysis. Indeed "ecology IS an historical discipline" but, quite often, ecologists focus on current bio-ecological systems, with the dangerous assumption that they represent and behave as pristine systems.
What an historical ecologist does is try to reconstruct historical baselines and to investigate changes in ecological patterns and processes over time, aiming at identifying the role played by different driving forces. This applies in particular to those studying biodiversity and its changes over historical times to better understand present ecosystems.

To this end, historical ecologists rely on a range of disciplines that are inherently scientific (in the sense of the so-called "hard science"), including paleoecology, zooarcheology, genetics, etc. To reconstruct baselines and trends in driving forces, it is usually necessary to consider other sources of information (Lotze and Worm, 2009) and establish a dialogue with scholars belonging to disciplines that have different epistemological backgrounds like archaeology, history, and anthropology.

Historical ecology in marine ecosystems rapidly developed in the last two decades, due to the recognition that the understanding of the present status of marine species and ecosystem functioning could be biased by the lack of information on their historical status. As Pauly (1995) highlighted new generations of scientists might have a different perception of marine biodiversity compared to older generations, who had the opportunity to investigate the sea few decades earlier. By posing the issue of the so-called "shifting the baseline syndrome", Pauly clearly showed that it is necessary to define past baselines to understand the present status of biodiversity and the role of different processes that affected it. Another major input of historical ecology in the marine domain the global overview by Jackson *et al.* (2001) on the historical role of driving forces that affected the marine environment, demonstrating that fishery historically preceded all other sources of ecological disturbance.

The historical ecology approach was incorporated into global research actions like the Census of Marine Life that, inter alia investigated biodiversity historical changes in the framework of the History of Marine Animal Populations project (www.hmapcoml.org). This project fostered the collaboration between humanities and science scholars, that put their attention to the recovery of historical records to describe changes in biodiversity and the driving forces that affected it, in particular fisheries. Although some researchers raised concerns on the balance between scientific and historical disciplines in the HMAP project, this initiative had the merit to show the need to reconstruct the impact of humans under the lens of marine environmental history (Bolster, 2003).

1.2 (Neo)extinctions *vs.* (neo)extirpations

Historical ecology can facilitate the understanding of current biodiversity, in particular by tracing historical changes in marine fauna. While the long history of life on our planet has been characterised by five major global processes of extinction commonly named "Mass Extinctions"[1], scientists and the general public are now concerned that the speed of disappearance of species has sharply increased during the current "Anthropocene", with prospects of a "6th Mass Extinction". The current biodiversity crisis is induced by anthropogenic driving forces (Carlton, this volume) but the consequences of this human-induced loss of species are not fully understood.

Thus there is an urgent need of quantifying this process, identifying those species which are at risk of extinction and the role played by humans, in order to prevent or at least alleviate any further negative impact of our species on nature.

There are obviously some practical difficulties in assessing the extinction of a species, particularly in the sea (Roberts and Hawkins, 1999; Purvis *et al.*, 2000; Dulvy *et al.*, 2004). Furthermore, notwithstanding the long history of exploitation of marine biological resources, there are really few known extinctions of marine fishes on a global scale (see Carlton, this volume). Conversely extirpation, which occurs when a species ceases to exist at local or regional scales, is more frequent and has been described for several marine species. Extirpation represents an early warning of species' vulnerability as it is a step towards global scale extinction (Pitcher, 2001).

For consistency with the terminology proposed by Carlton (this volume), we will use the term "neoextirpation" to refer to local or regional disappearance of species in historical time (since 1500). A growing number of marine species have been reported to have declined or even disappeared from discrete areas of their overall historical geographic range (Dulvy *et al.*, 2003) in almost all the seas, including the Mediterranean. The main cause has been identified as fishery exploitation (55%), followed by habitat loss or degradation (37%), introduction of invasive species (2%) and other factors such as climate change, pollution and disease (6% in total). Fishing and habitat loss in particular have caused severe declines at regional and local scales in several Mediterranean Sea taxa (Coll *et al.*, 2010). It is worth noting that neoextirpation is not a peculiarity of mechanized/industrial fishery, since it has been reported even in subsistence and artisanal fisheries (Pinnegar and Engelhard, 2007). Moreover overfishing came much earlier in the historical sequence of events (Bradbury, 2001).

1.3 Extinction risk in the Mediterranean Sea fauna

The Red List of the International Union for Conservation of Nature (IUCN) is a global initiative that aims to assess the conservation status of species/populations worldwide. The selection of species to be included in the assessment is made by regional experts that routinely review the status of species according to different quantitative criteria (IUCN, 2001) that include: reduction in population size, geographic range, absolute population size estimates; probability of extinction.

According to the application of different quantitative thresholds, species are ascribed to different levels of extinction risk, from higher to lower. In particular, "Critically Endangered", "Endangered" and "Vulnerable" species are categories referred to threatened species, while "Near Threatened" and "Least Concern" are used for those species whose extinction risk is limited or negligible. Most often, species may fall into the "Data Deficient" category, since quantitative data may not be available for assessing their status according the Red List criteria.

The analysis of the latest assessments available for Mediterranean Sea species carried out by exploring the IUCN database shows that a total number of 268 Mediterranean species (Kingdom:

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[1] These were abrupt changes in the number and composition of species which shaped, along with the evolutionary process of speciation, the composition and diversity of life as we currently know it. For instance, the 5th mass extinction, which was probably caused by a giant meteor collision, occurred 65 million years ago, at the end of the Cretaceous period, and ended the reptilian dominance of the Earth leading to the current mammalian domination.

Animalia) have been assessed so far, with an increase in the evaluation effort in the last 4 years (Fig. 1). The main taxa considered include fish and elasmobranchs, reptiles, mammals, cephalopods, crustaceans, cnidarians and gastropods. The large majority of species falls in the "Data Deficient" and "Least Concern" categories; however, 50 species are considered to be "Threatened", 14 are "Critically Endangered", 12 are "Endangered" and 22 are "Vulnerable" to extinction.

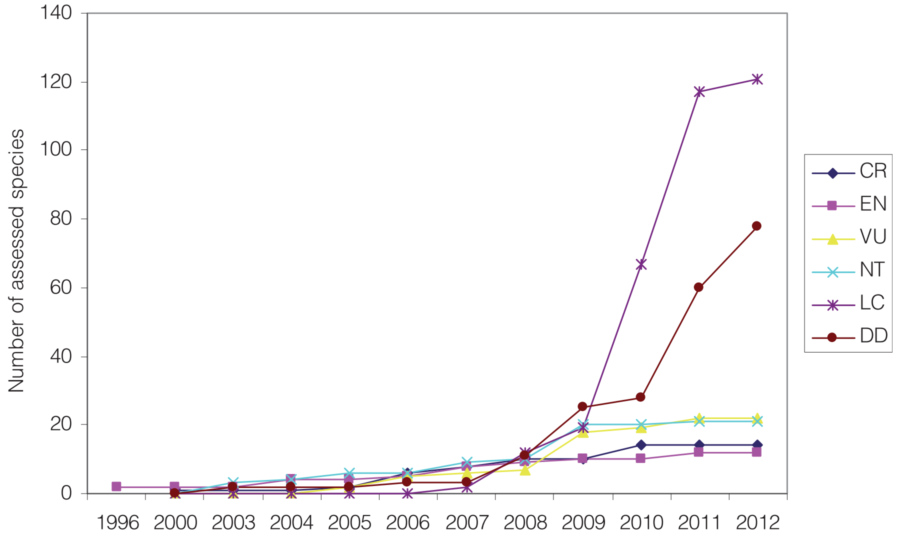

Fig. 1. Cumulative number of Mediterranean marine species (Animalia) assessed in the IUCN Red List since 1996. CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient (Source: http://www.iucnredlist.org/; October 2012).

These data show that, overall, elasmobranchs comprise the highest number of "Threatened" species (29), followed by bony fish (12), reptiles (4) and mammals (3) (Fig. 2). The same pattern applies to the number of "Critically Endangered" species, where 7 species of cartilaginous fishes, 4 bony fish, 2 reptiles and 1 marine mammal make the highest category risk.

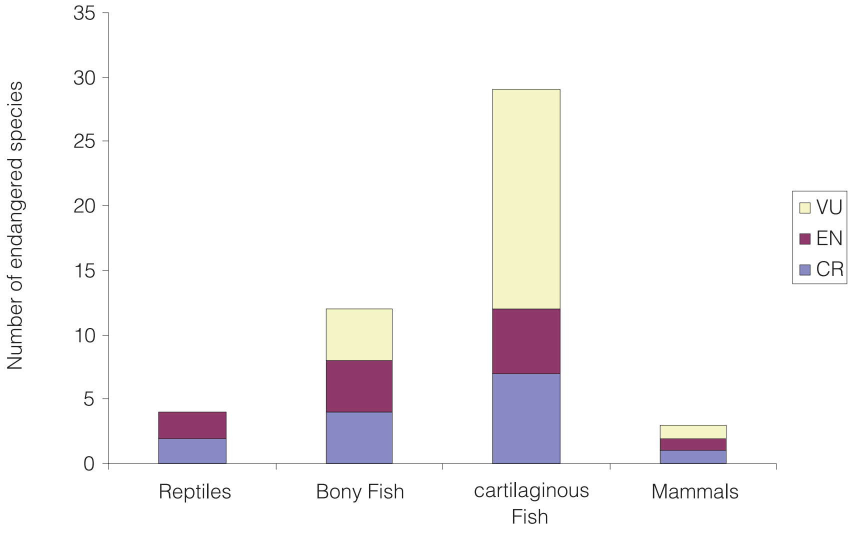

Fig. 2. Cumulative number of threatened Mediterranean marine species referred to different taxa currently assessed in the IUCN Red List (2012). CR = Critically Endangered; EN = Endangered; VU = Vulnerable (Source: http://www.iucnredlist.org/; October 2012).

It is worth noting that the IUCN assessment of the extinction risk of species does not evaluate most Mediterranean species due to a lack of quantitative data (i.e., "Data Deficient" category). The retrieval and analysis of historical data, might contribute to increase the number of assessed species, ascertain their historical range of distribution and, possibly, abundance and biomass.

2. ASSESSING CARTILAGINOUS FISHES NEOEXTIRPATION IN THE ADRIATIC SEA: AN HISTORICAL ECOLOGY APPROACH

This paper focuses on the neoextirpation of elasmobranchs, since they show a high vulnerability to fishery exploitations (Stevens *et al.*, 2000) and are generally considered to be under threat in the Adriatic Sea (see Soldo, this volume).

In a recent study (Fortibuoni *et al.*, 2010) we assessed historical changes in the fish community of the Northern Adriatic Sea considering a long-term timescale, namely the last two centuries. Our aim was to describe long-term changes in fish community by reconstructing time series integrating landing statistics and naturalists' observations by means of an intercalibration process. The study showed relevant changes in fish community structure, with a relative decrease in cartilaginous fishes, as well as a reduction in large-sized, late-maturing and long living species.

On the basis of the dataset acquired in this way we will now infer information on the local neoextinction (i.e., neoextirpation) of species, that deserve a different computational and research approach (i.e., singles species vs. community-based). Our starting point will be, thus, the historical reconstruction of a baseline for elasmobranch occurrence in the Adriatic Sea by using naturalists' accounts.

2.1 Linneus' legacy: Adriatic Sea naturalists' accounts

The introduction of the binomial classification of species, according to a hierarchical approach introduced by Linneus in his *Systema Naturae* (1735), stimulated European naturalists and zoologists to engage in a sort of "race" to describe and name all species. This process was fairly developed even in the Adriatic Sea, where many naturalists visited the region in order to describe marine and coastal species. Among others, we recall Vitaliano Donati, with his "Della storia naturale marina dell'Adriatico (1750)" (On the natural history of the Adriatic Sea), or Alberto Forti, who carried out surveys in the Northern Adriatic Sea in the 1770-1773 and studied the migration of sardines and bluefin tuna. The famous Lazzaro Spallanzani also conducted surveys in the Adriatic, were he studied the production of electricity of the torpedo, as well as the fauna of the lagoon of Chioggia. Other important naturalists who studied the Adriatic Sea fauna include Stefano Chiereghin (1745-1820), Giuseppe Olivi (1764-1795), Stefano Andrea Renier (1759-1830), Fortunato Luigi Naccari (1793-1860), Giovanni Domenico Nardo (1802-1877) and Alessandro Pericle Ninni (1837-1892).

The work conducted by these naturalists represents, to our view, the most valuable legacy of Linneus in the Adriatic Sea, since they provided the earlier available systematic description of species that can be used to set a baseline of marine biodiversity in the area, more than two centuries ago. Moreover, their work was not limited to the description of species according to their morphology (that allows to check the consistency of the species' identification according to modern classification), as they provided additional, (and fundamental) information on species' perceived abundance, seasonality, size, spawning period, behaviour, as well as information on their economic use, especially if they had a commercial value and whether or not they were targeted by fishery and which fishing gears were used to this purpose. Naturalists' knowledge of fish fauna was mainly based on direct observations at fish markets and ports, on interviews of fishermen, on literature and on the analysis of Natural Museums' Collections. For instance, the abbot Stefano Chiereghin's family owned a group of 10 fishing boats in the port of Chioggia, which allowed him to describe the fauna and flora of the Adriatic Sea in the early 19th century in his masterpiece "Descrizione de' Pesci, de' Crostacei e de' Testacei che abitano le lagune ed il Golfo Veneto"[2].

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[2] Interestingly, only one original copy of his study was printed at the time and it is preserved in the "Biblioteca Marciana" in Venice. The large number of volumes, including many hand drawings from Chiereghin, prevented the printing of the book which was too expensive. A reprint of the book is now available thanks to the effort of Cinzio Gibin, and is printed by Editrice Canova.

To the purpose of establishing a historical baseline of elasmobranch species in the Adriatic Sea, we collected and surveyed historical documents from the major archives, libraries and natural museums of the Adriatic area (Venice, Padua, Trieste, Chioggia, Split). We collected 36 naturalists' descriptions of the Adriatic Sea fauna over the period 1818-1956. Species whose identification was unclear, or that were quoted by less than five authors, were excluded from the analysis.

Naturalists' accounts allowed to reconstruct the historical perceived abundance of fish species according to a semi-quantitative scale, including four classes (very rare, rare, common to very common)[3], over a period of approximately one century and a half (1818-1956; for more details, see Fortibuoni *et al.*, 2010). Forty three species of cartilaginous fishes were described, 17 were considered common (10 rays and skates and seven sharks), showing that a rich assemblage of cartilaginous fishes was present in the nineteenth century in the Adriatic Sea (Table 1). We defined as our "historical baseline" the most common class (modal score) of perceived abundance observed in the period 1818-1956, and compared it with the current status and trend of species in the Mediterranean as defined by IUCN (Table 1). It is evident that many species that were formerly considered as common in the Adriatic Sea are now considered under threat in the Mediterranean. For instance, the blue skate (*Dipturus batis*) and the bottlenosed skate (*Rostroraja alba*), once common in the Adriatic, are now assessed as "Critically Endangered" and they show a decreasing trend. The same applies to angelsharks (*Squatina* spp.). We remark that for eight species the IUCN risk status is not defined due to the lack of quantitative data ("Data Deficient" category).

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[3] It is worth noting that this semi-quantitative scale does not represent absolute abundance values, but a hierarchy of abundance that follows a logarithmic scale (see Fortibuoni *et al.*, 2010). Thus, the shift from common to rare category, for instance, implies a logarithmic reduction in perceived abundance.

Table 1. Comparison of the historical baseline (1818-1956) of elasmobranch presence in the Adriatic Sea, defined on the basis of naturalists' descriptions, and their current status and trend in the Mediterranean Sea, as assessed by IUCN. CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient (Source: http://www.iucnredlist.org/; October 2012).

Group	**Scientific name**	**Common name**	**ADRIATIC SEA HISTORICAL BASELINE**	**MEDITERRANEAN CURRENT STATUS (IUCN)**	**TREND (IUCN)**
Rajiformes	*Dasyatis pastinaca*	Common stingray	Common	DD	unknown
	Myliobatis aquila	Common eagle ray	Common	DD	unknown
	Pteromylaeus bovinus	Bull ray	Common	DD	unknown
	Dipturus oxyrinchus	Longnosed skate	Common	NT	unknown
	Dipturus batis	Blue skate	Common	CR	decreasing
	Raja asterias	Starry ray	Common	LC	Stable
	Raja clavata	Thornback ray	Common	NT	decreasing
	Raja miraletus	Brown ray	Common	LC	Stable
	Rostroraja alba	Bottlenosed skate	Common	EN	decreasing
	Torpedo marmorata	Spotted torpedo	Common	DD	unknown
	Dasyatis centroura	Roughtail stingray	Rare	LC	unknown
	Leucoraja fullonica	Shagreen ray	Rare	NT	decreasing
	Torpedo nobiliana	Atlantic torpedo	Rare	DD	unknown
	Torpedo torpedo	Common torpedo	Rare	DD	Stable
	Gymnura altavela	Spiny butterfly ray	Very Rare	VU	decreasing
	Rhinoptera marginata	Lusitanian cownose ray	Very Rare	NT	unknown
	Mobula mobular	Devil fish	Very Rare	EN	decreasing
	Raja radula	Rough ray	Very Rare	DD	unknown
Squaliformes	*Scyliorhinus canicula*	Small-spotted catshark	Common	LC	Stable
	Scyliorhinus stellaris	Nursehound	Common	NT	Unknown
	Squalus acanthias	Piked dogfish	Common	VU	Decreasing
	Squatina oculata	Smoothback angelshark	Common	CR	Decreasing
	Squatina squatina	Angelshark	Common	CR	Decreasing
	Galeorhinus galeus	Tope shark	Common	VU	Decreasing
	Mustelus asterias	Starry smooth-hound	Common	LC	Unknown
	Mustelus mustelus	Smooth-hound	Common	VU	Decreasing
	Alopias vulpinus	Thintail thresher	Rare	VU	Decreasing
	Prionace glauca	Blue shark	Rare	NT	Unknown
	Carcharhinus plumbeus	Sandbar shark	Rare	VU	Decreasing
	Oxynotus centrina	Angular roughshark	Rare	VU	Unknown
	Heptranchias perlo	Sharpnose sevengill shark	Rare	NT	Unknown
	Hexanchus griseus	Bluntnose sixgill shark	Rare	NT	Unknown
	Carcharodon carcharias	Great white shark	Rare	VU	Unknown
	Isurus oxyrinchus	Shortfin mako	Rare	VU	Decreasing
	Sphyrna zygaena	Smooth hammerhead	Rare	VU	decreasing
	Squalus blainville	Longnose spurdog	Rare	DD	unknown
	Cetorhinus maximus	Basking shark	Very Rare	VU	decreasing
	Etmopterus spinax	Velvet belly lantern shark	Very Rare	LC	unknown
	Echinorhinus brucus	Bramble shark	Very Rare	DD	unknown
	Lamna nasus	Porbeagle	Very Rare	VU	Decreasing
	Carcharias taurus	Sand tiger shark	Very Rare	VU	Unknown
	Galeus melastomus	Blackmouth catshark	Very Rare	LC	Stable
	Sphyrna tudes	Smalleye hammerhead	Very Rare	VU	Decreasing

2.2 Historical accounts of commercial fishing activities

Using naturalists' accounts may provide very useful information on historical perceived abundance of species. However, further data are possibly needed to support such evidences. In particular, fisheries-related historical accounts will be useful to this end. The Adriatic Sea is rich in such information (Raicevich *et al.*, 2008; Fortibuoni *et al.*, 2009; Fortibuoni *et al.*, 2010), that can be traced and collected in publications and research journals that were published, in the area in the late 19th and early 20th century.

The description of historical fishing activities can provide important information on several issues including target species, fishing gear and boat technology, fishing seasons and fish markets. All such information can help establish historical presence of a species in a definite area, as well as the capability of fishermen to catch it (and indirectly, the possibility of naturalists to describe them), even allowing to know whether the species was imported from other areas and sold at the local market. The presence of fisheries targeting certain species may support the hypothesis that the species itself was relatively abundant in the area. Most often, unfortunately, detailed data on fishing grounds and target species are lacking.

An extensive search and analysis of historical documents allowed us to reconstruct the fishing activities in the Adriatic Sea and in particular the Chioggia fishing fleet (for details see Botter *et al.*, 2006; Fortibuoni *et al.*, 2009). This picture is rather relevant since the *Chioggiotti* were used to migrate across the whole Adriatic Sea to follow the migration pattern of main target species. Moreover, they were skilled fishermen adopting a range of fishing gears that allowed them to catch both demersal and pelagic species, including cartilaginous fishes (Botter *et al.*, 2006).

A relevant publication of Levi Morenos (1916) was devoted to economic issues related to the context of Austro-Hungarian empire waters in the early 20th century (at that time, from Trieste down to Dalmatia), claiming that the *Chioggiotti* had the right to continue fishing in such areas. In this document the author supports such a request based on a detailed description of the fishing fleets and their activities. It also included maps of the distribution of fishing grounds and reference to the main target species and the fish markets where catches were sold. Levi Morenos maps allow to identify an historical baseline refered to winter and spring, 1910 (Figs. 3 and 4, respectively) for nine elasmobranch species: *Raja clavata*, *R. miraletus*, *Dipturus oxyrhincus*, *Torpedo torpedo*, *Squatina squatina*, *Scyliorhinus canicula*, *S. stellaris*, *Squalus acanthias*, and *S. blainville*.

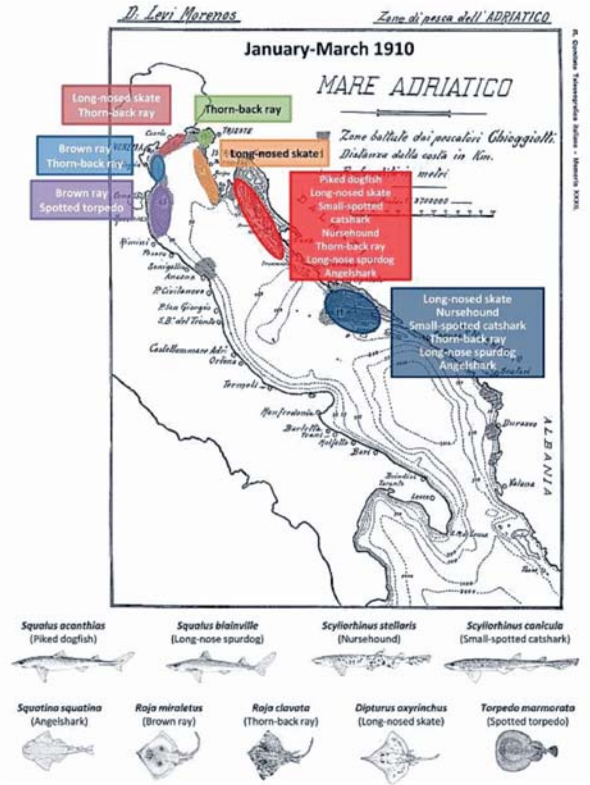

Fig.3. Historical distribution (January-March 1910) of cartilaginous fishes caught as main target species by Chioggia fishing fleet (from Levi Morenos, 1916).

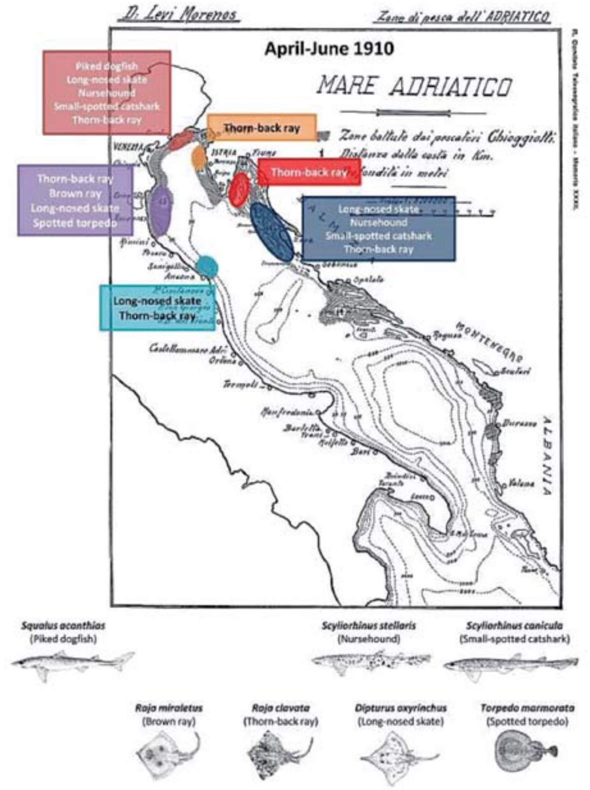

Fig. 4. Historical distribution (April-June 1910) of cartilaginous fishes caught as main target species by Chioggia fishing fleet (from Levi Morenos, 1916).

All these species were described as common in naturalists' accounts (Table 1) and were caught in nearshore areas from the Po river mouth northward and, southward, from Trieste to Dalmatia. Such information the "presence" of relatively high "amount" of a species in the considered fishing grounds, where the cartilaginous fishes were caught (among others) as main target species. On the opposite, we cannot assume that species were "absent" in the other fishing grounds where they were not reported as main target species.

The fish caught relatively close to the fishing ports of Chioggia and Venice was landed there due to the lack of technology to preserve fresh fish and the relatively low speed of the fishing vessels that, at that time, were mainly sailing boats (Botter *et al.*, 2006; Fortibuoni *et al.*, 2010). All this holds true as well for the landings in Trieste market, and thus the landings data should represent the catches in the surrounding area.

2.3 Historical and modern landings data

Quantitative historical data are usually scarce, and the only data available before the second half of the twentieth century in the Adriatic Sea are landing statistics. Before World War II, Trieste and Venice probably represented the most important wholesale fish-markets of the Adriatic area, where most of Adriatic fish caught in the surrounding fishing grounds were sold (Fortibuoni *et al.*, 2010). In 1945, the Chioggia fish market was also established, since the city hosted (and still hosts) the largest fishing fleet of the Adriatic region.

Thus, we scoured libraries and archives searching for landing statistics referred to the Trieste, Venice and Chioggia fish-markets. Being biased toward commercial species and not standardized in terms of fishing effort or fishing gear, landings have the intrinsic limitations of fishery-dependent data. However, quantities sold at fish-markets are correlated to biomass at sea, and thus landings may represent a useful proxy to reconstruct massive changes in fish abundance (Pauly *et al.*, 1998).

Our search allowed collecting landings for the period between 1900 and 2000 of some commercially important groups of cartilaginous fishes at the Trieste and Venice fish-markets (Fig. 5). Data from Chioggia were merged with Venice since after World War II the fishing fleet supplying the fish-market of Venice began to sell fish also in Chioggia (the market will be called Venice-Chioggia hereafter). Here we present data referred to *Raja* spp. (mainly *Raja clavata* and *R. miraletus*), *Scyliorhinus* spp. (*Scyliorhinus canicula* and *S. stellaris*), *Squatina* spp. (mainly *Squatina squatina*) and *Mustelus* spp. (mainly *Mustelus mustelus*). Data are aggregated at genus level since, in most of the cases, landing statistics provide information that are coarse in terms of taxonomic resolution.

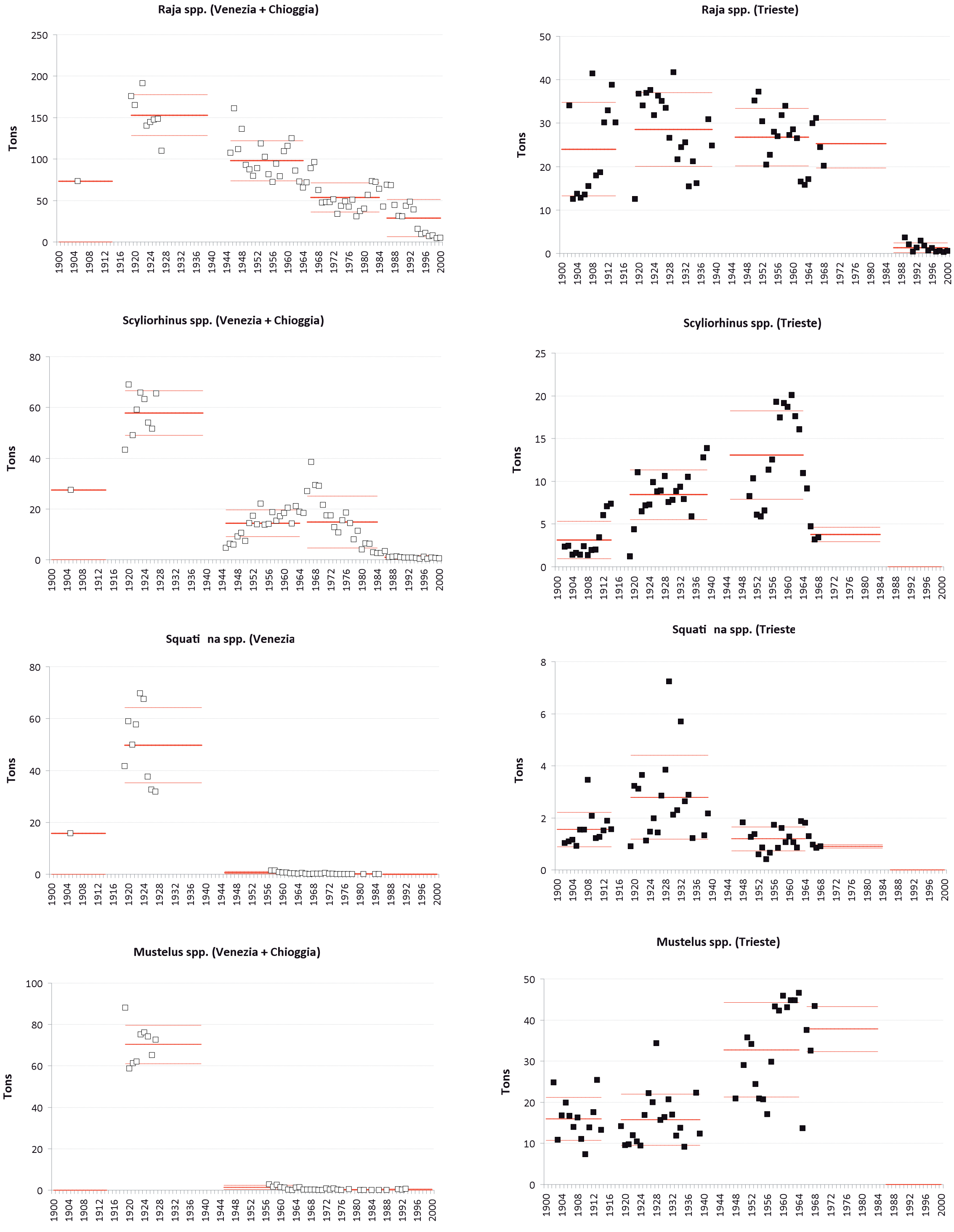

Fig. 5. Landing statistics (tonnes) of (from the top) *Raja* spp., *Scyliorhinus* spp., *Squatina* spp. and *Mustelus* spp. referred to the fish-markets of Venice-Chioggia (white-squares) and Trieste (black-squares) between 1900 and 2000. Mean (± st.dev.) have been estimated and over-imposed (red lines) for the following historical periods: 1900-1914; 1919-1939; 1945-1965; 1966-1985; 1986-2000.

Data show that at the beginning of the twentieth century high quantities of cartilaginous fishes were landed in Trieste and Venice-Chioggia; in most cases historical landings were higher than those recorded after the 1950s, even if fishing effort and capacity were significantly lower at that time (Fortibuoni *et al.*, 2009; Fig. 6). For instance, in the period 1919-1939 in Venice-Chioggia the yearly mean value of landings for rays (*Raja* spp.) was 153 (± 8) tons, while afterwards landed quantities severely declined (Fig. 5). A declining trend of rays in landings was also observed in recent years, both in Venice-Chioggia and in Trieste. The same can be said for angelsharks (*Squatina* spp.), where yearly mean landed quantities were about 50 (± 14) tons in the period 1919-1939, to be followed by a clear reduction in the landings and showing "commercial extinction" in the '60s in Trieste and in the '80s in Venice-Chioggia.

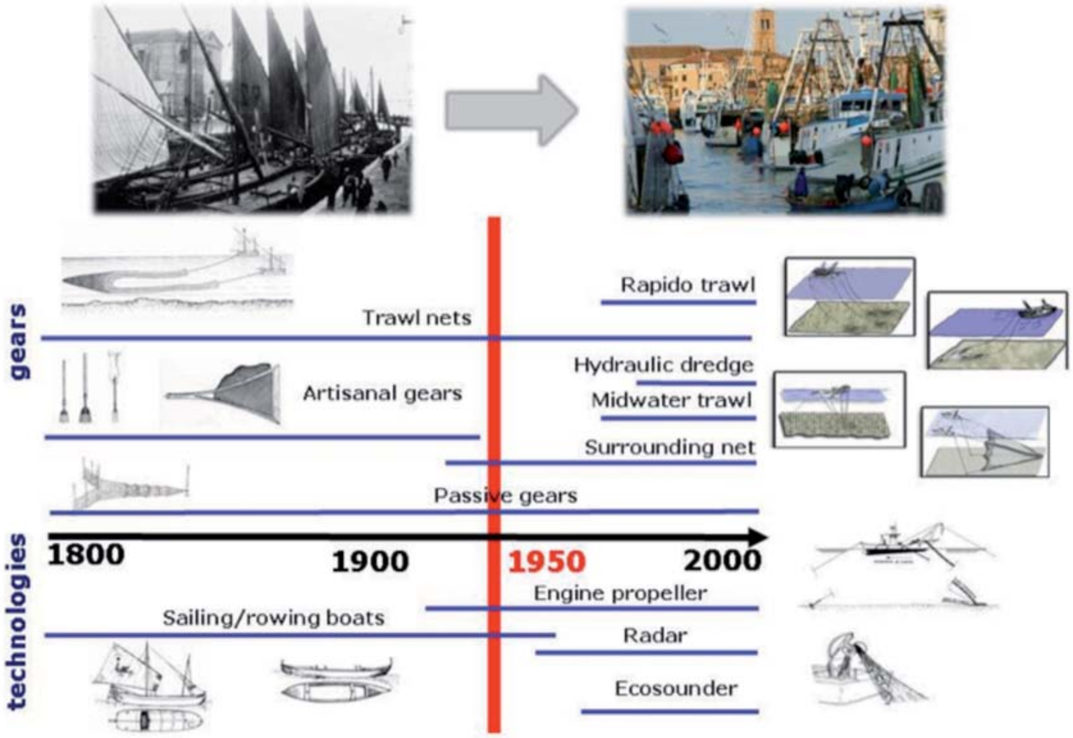

Fig. 6. A conceptual map of changes in fishing gears and technology in the Adriatic Sea (western coast fisheries) from 1850 up to 2000. After World War II, traditional sailings boats were abandoned due to the adoption of engine propeller. The use of new technological devices (e.g., radar, echosounder) and new fishing gears (i.e., mid-water pelagic trawl, rapido trawl, hydraulic dredges) increased the catchability of target species.

Data shown below (Fig. 5) point to a long-term decline in the landings in all considered taxa in the northernmost sector of the Adriatic Sea, in relation to species that were historically caught nearshore. The collateral information that there was an expansion of fishing grounds (in particular from the Chioggia fishing fleet) towards the Northern Adriatic open sea (based on Vessels Monitoring System, Fig. 7) since the '50s, further supports the possibility of a contraction of the species range since historical time.

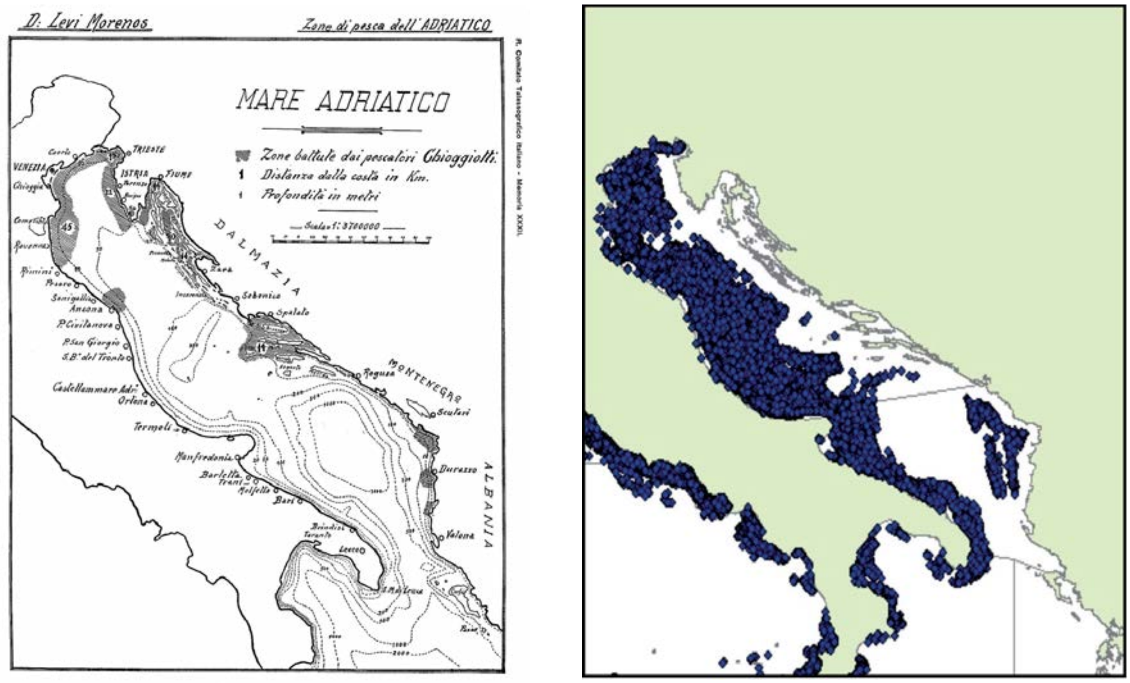

Fig. 7. An example of historical fishing grounds of Chioggia fleet (1910; grey areas) and current exploitation areas of the Italian fishing fleets in the Adriatic Sea (2008; blue dots). Pictures clearly show that the "open sea" is now exploited, while in the past only the coastal areas were impacted by fishing. Data for current fishing activities by Croatian fleets are not available.

2.4 Fishery independent data

In the absence of full accounts of changes in the fishing effort distribution over time and given the inherent difficulties related to the standardization of the landings data, it is difficult to quantify the extent of such changes in cartilaginous fishes.

To this end we examined the historical dataset of the HVAR expedition, the first trawl survey carried out in 1948 and 1949 by Yugoslavian scientists in the central and eastern Adriatic Sea (Karlovac, 1953). These data were compared to modern trawl survey data, i.e the GRUND data (2000-2002) (see Fig. 8), from a trawl survey $^{\text{that}}$ operated from 1982 to 2007 in the Adriatic Sea.

Our aim was to ascertain if the reduction in the landings, and the reduction in the range of distribution of cartilaginous fishes we inferred from the above reported information referred to the coastal northernmost part of the Adriatic Sea, were also detectable in the Central Adriatic Sea. More prominently, we were aiming in particular at identifying changes at species level, rather then genus, since neoextinction should be assessed at this taxonomic level, being the response of species to different sources of disturbance mediated by life-history traits. For consistency in the analysis, we selected those HVAR and GRUND stations that were sampled in the same area and in the same season. We considered four species, namely *Raja clavata*, *R. miraletus, Scyliorhinus canicula* and *S. stellaris*, since they show high catchability to otter-trawl (the sampling gear adopted in both trawl-surveys) and have contrasting life history traits.

As clearly seen in Fig. 8, there were no differences in the index of occurrence (i.e., % of positive hauls where the species was found) of *R. clavata*, while a significant decrease in the average weight of individuals can be clearly seen. This parameter varied from a modal value of nearly 1 kg in 1948 to a modal value of nearly 0.050 g in 2002. On the opposite, *R. miraletus* showed an increase in the range of distribution and a substantial stability in the modal weight.
A different picture emerges for the genus *Scyliorhinus*, where both *S. canicula* and *S. stellaris* show a clear reduction in the index of occupancy. In particular, the formerly widespread *S. canicula* showed a reduction from 50% to about 10% of the index of occupancy (although this was mirrored

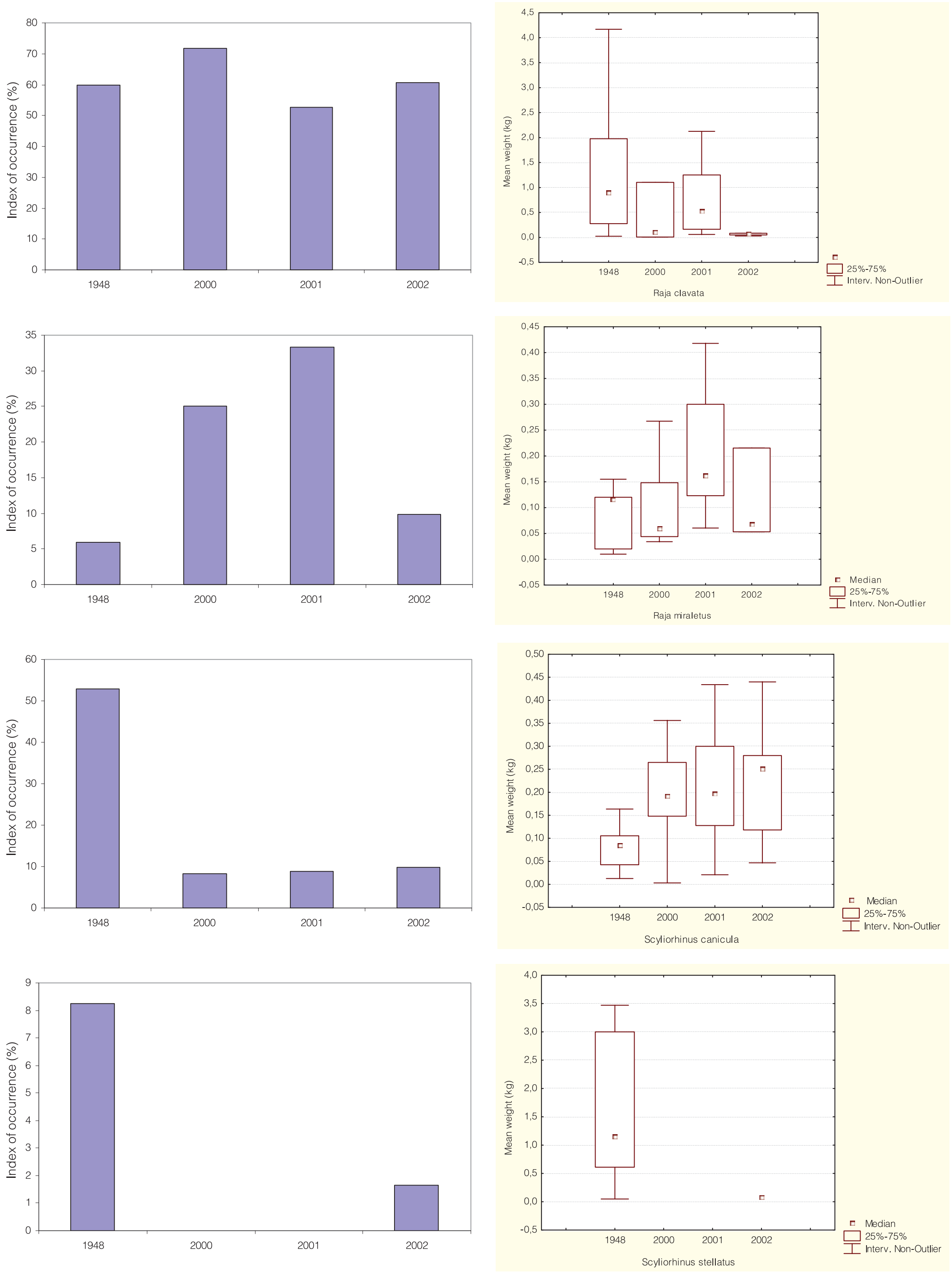

Fig. 8. A comparison of the index of occurrence (left panels) and average weights (right panels) of four selachians species (from top to bottom: *Raja clavata, Raja miraletus, Scyliorhinus canicula, Scyliorhinus stellaris)* in the Central Adriatic Sea in the HVAR expedition (1948) and GRUND trawl surveys (2000-2001-2002). Average weight (Median, interquartile range and max-min range) was estimated in each sampling station as ratio between total number of individuals and total weight.

by an increase in the average weight of individuals), while *S. stellaris* almost disappeared from the investigated area.

It is worth noting that, when taking into account the life-history traits of such species, the observed patterns can be rationalized, since *R. clavata* and *S. canicula* has lower L_{max} (and related life-history traits like L at maturity) compared to *R. miraletus*, and *S. stellaris* which points to lower vulnerability to fishing pressure of the former two species (Dulvy *et al.*, 2003).

Our analysis is also confirmed by a study carried out by Jukic-Peladic *et al.* (2001) that compared HVAR data with another trawl survey (MEDITs) carried out in the 1998, and clearly showed a reduction in the number of cartilaginous fishes species, as well as in their relative importance in the catches in the Central and Eastern Adriatic Sea, also confirming the reduction in *R. clavata* and *S. canicula*. Moreover a recent publication of Piccinetti *et al.* (2012), that reports the average spatial persistence of species in the 1994-2010 period based on MEDITs trawl-survey, confirm that the four species considered are now present only in the eastern part of the basin.

2.5 A general overview: can multiple evidence be a proof?

In this work we showed the range of information that an historical ecology approach can use to trace neoextirpation, focusing on elasmobranchs in the Adriatic Sea as a case-study. Our activity allowed us to list a number of "evidence" that we can summarize as:

1) naturalists' accounts enabled us to reconstruct an early baseline for the Adriatic Sea cartilaginous fishes (since 1800), indicating that 43 different species were present in the area, many of which were common and are, nowadays, considered to be threatened;

2) historical accounts confirmed that, in the early twenty century, many of these species were exploited, and that fishery was carried out mainly in relatively coastal areas;

3) historical documents permitted also to describe the discrete areas where some cartilaginous fishes were abundant and thus exploited as target species;

4) landing statistics confirmed that in the past the yield of elasmobranchs was high in the Northern Adriatic Sea, but the low taxonomic resolution of landings partially prevented to assess changes in the relative abundance of species within a definite genus. However, clear signs of reduction in landings after World War II were recorded, especially in the last decades;

5) further historical accounts show that an expansion of fishing grounds from the coast to the open sea occurred in the meanwhile, fostered by sharp changes in fishing technology;

6) fishery-independent data confirmed that, for some species, a reduction in the index of occupancy or in the average weight happened in the last 60 years, showing the presence of a neoextirpation process;

7) the exploration of other published records based on trawl-surveys, also shows that most of the cartilaginous fishes once abundant in the western side Adriatic Sea can now be found only on the eastern side of the basin.

Our question, now, is whether the degree of coherence of such "evidence" collected from historical accounts, landings and trawl-survey data can be considered as final proof of a serious neoextirpation process occurring in the area. We believe that the overall data and sources presented indeed show that the current date status of Adriatic Sea elasmobranchs is a "shadow" of what the naturalists used to see few generations ago.

However, answering the same question at the species level is more complex. In our view, only by considering each single species, one by one, will be able to provide a final word on single species neoextirpation. For instance we can confirm that *Raja clavata*, *Scyliorhinus canicula* and *S. stellaris* are under threat, while for *R. miraletus* the answer is less certain.

Even less trivial is to assess the status of such species according to quantitative criteria such as those adopted by the IUCN Red List. The challenge is how to incorporate historical accounts into a formal process of species' risk evaluation.

In any case, we should recall that the pattern reconstructed has a deep ecological relevance since it allows us to say that the Adriatic ecosystem has changed, many top predators are gone, and therefore current day macroecological analysis should acknowledge the fact that we are now studying an “unnatural ocean”. Our warning is that, most likely, the resilience of the Adriatic Sea elasmobranch group might have been hampered, and that the spectacular rise reported by Umberto D’Ancona (1926) after World War I fishing ban (that was studied by Vito Volterra to propose the so-called Lotka-Volterra equations, Volterra, 1926), might not occur nowadays, or take too long. A question that only time will be able to answer, if management best practices to protect cartilaginous fishes are introduced.

3. Moving forward

This contribution could only scratch the surface of a “gold mine” that needs to be exploited if we really intend to describe changes in biodiversity and understand the reality of the current 6th Mass Extinction. A further source of data that we did not take into account, but that is currently under assessment in the Adriatic Sea, is the fishermen’s traditional knowledge whose value to describe changes in biodiversity is now widely recognised (Raicevich *et al.*, 2010). Other sources of data are Natural History Museums, that in turn may provide samples that could be used for genetic analysis, to determine historical trophic levels as well as population growth in the past, etc.

When dealing with marine species, and questioning their possible neoextinction, the issue of geographical scale is very relevant. The reduction in the number of species in a defined sector is the prerequisite to extirpation, while to infer information on possible neoextinctions we would need to widen our picture and move beyond the Adriatic Sea area. Therefore we consider that the development of a wider historical ecology approach in the Mediterranean Sea, that encompasses the several areas where naturalists’ accounts and Natural History Museums were and are still active, as well as the retrieval of historical sources and the exploration of fishermen traditional knowledge, could allow reaching the geographical boundary where evidence became clear and neat proofs.

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Life history correlates of marine fisheries vulnerability: a review and a test with tunas and mackerel species

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ABSTRACT

The vulnerability of a species is a combination of its degree of exposure to extrinsic threats, such as fishing, and of its intrinsic sensitivity to the threatening process. While there is broadening support for the idea that life histories and demography relate to measures of vulnerability including decline, extinction risk and population collapse, the efficacy of different traits to predict vulnerability varies greatly. This study, first reviews current understanding of the life history traits that have been identified as useful biological correlates of vulnerability in marine fishes. Second, potential life history correlates of vulnerability for scombrid species (tunas and mackerels) are identified. We found that age at maturity is the most consistent and reliable biological correlate of species intrinsic sensitivity, suggesting that this variable might be the most reliable predictor of species maximum per-capita growth rates (r_{max}). While maximum body size is the most reliable correlate of species vulnerability to fishing, suggesting that it might be the most reliable predictor of species declines, recoveries and threat status in marine fishes. The review also confirms, contrary to a widely-held perception, that fecundity is not a predictor of either species sensitivity or vulnerability to fishing, suggesting that the production of large number of eggs does not protect marine fishes from extinction risk. Moreover, we found that longevity is the best predictor of population rates and extent of declines in adult biomass in scombrid species. The longest-lived scombrid populations, rather than the largest, appear to have experienced the fastest rates of decline and the greatest extent of decline in adult biomass over the last 50 years. Identifying and quantifying the relative importance of biological and ecological correlates of vulnerability in fishes continues to be a challenge and is poorly understood. Understanding the intrinsic biology of species vulnerability and extinction risk appears crucial to build tools to predict species responses to fishing and their risk of depletion or extinction.

1. Introduction

The number of exploited fish species far exceeds the number of existing stock assessments available to guide scientific decision-making. Stock assessments are data intensive and it is unlikely that there will ever be sufficient information to develop quantitative stock assessments for all exploited species. Therefore, a key challenge is to develop methods for informing management over the large majority of stocks for which there is simply not enough data with which to develop traditional data-hungry stock assessments (Dulvy *et al.*, 2004; Pardo *et al.*, 2012). One way to approach this challenge has been to identify potential biological and ecological correlates of species vulnerabilities to extrinsic threats such as population trajectory, threat status or extinction risk (Jennings *et al.*, 1998; Dulvy *et al.*, 2004; Reynolds *et al.*, 2005a; Pardo *et al.*, 2012) which are useful to predict the species capacity to respond to fishing. The vulnerability of a species is a combination of its degree of exposure to extrinsic threats, such as fishing and habitat destruction, and its intrinsic sensitivity to the threatening process (Dulvy *et al.*, 2004; Reynolds *et al.*, 2005a). The intrinsic sensitivity of a species to external threats is determined by species characteristics, such as life history and ecology traits, which underlie the productivity of the species and their capacity to recover from known threats (Hutchings *et al.*, 2012). In marine systems, overfishing is the leading primary threat to extinction in marine fishes (Reynolds *et al.*, 2005a). For example, highly vulnerable species to fishing would have sensitive life histories prone to low productivity and recovery rates that are also exposed to levels of fishing mortality greater than can be sustained by the species. There may be a real opportunity to rank species vulnerabilities, by using intrinsic traits combined with a measure of possible exposure to a threatening process and this is the basis for ecological risk assessment frameworks (Hobday *et al.*, 2011). This information could be used to identify and select sensitive species to prioritize management and efforts to protect and recover the most threatened species.

Beverton and Holt (1959) recognized long ago that understanding the range of life histories across environments can be profoundly useful for assessing fish populations. The intrinsic characteristics of a species, for example its life history, are critical to understand how species respond to anthropogenic threats such as fishing and recover from depletion (Hutchings, 2002; Dulvy *et al.*, 2004). Generally, species with life history strategies characterized by high rates of growth and high natural mortality, early age at maturity and short life span are generally able to sustain higher fishing mortality rates. On the other hand, species characterized by slow growth, late maturity, short spawning period and long life are more sensitive to fishing and may only sustain lower rates of fishing mortality (Adams, 1980; Roff, 1984). While the broad theory has been understood for decades, it is only recently that sufficient comparative population trends and life history data have become available to allow empirical testing (e.g. Reynolds *et al.*, 2005a). With the objective of identifying biological correlates of species vulnerability to fishing, empirical testing has proceeded on two fronts: linking life histories to demography, particularly maximum per capita population growth rates r_{max} (e.g. Denney *et al.*, 2002; Garcia *et al.*, 2008; Hutchings *et al.*, 2012), and linking life histories to population status, usually measured as trends in population trajectories, threat status, extinction risk or probability of collapse while controlling for exposure to fishing (e.g. Jennings *et al.*, 1998; Jennings *et al.*, 1999b; Anderson *et al.*, 2011; Pinsky *et al.*, 2011). The metric - maximum per capita population growth rate r_{max} is a standard measurement of population productivity which summarizes many biological and ecological aspects of a species and depicts the species intrinsic sensitivity to external threats (Musick, 1999). It is negatively associated with extinction probability (Lande, 1993; Dulvy *et al.*, 2004) and positively associated with the fishing mortality necessary to drive a species to extinction ($F_{extinct}$) (Garcia *et al.*, 2008). However, the estimation of r_{max} requires detailed demographic information, typically lacking for the majority of species. For these reasons, multiple empirical studies have attempted to quantify potential correlation between r_{max} and several life history traits of species in order to use the more easily available life history information to identify species that have low r_{max} and therefore are more sensitive to external threats and might face higher risk of extinction (Hutchings *et al.*, 2012). On the other hand, studies linking life histories to population status, while controlling for fishing exposure, provide the quantitative basis to develop tools for predicting species responses to fishing, their threat status and probability of extinction in data-poor situations (Jennings *et al.*, 1998; Anderson *et al.*, 2011; Pardo *et al.*, 2012).

While there is broadening support for the idea that life histories and demography relate to measures of vulnerability including, decline, extinction risk and population collapse, the efficacy of different traits to predict vulnerability varies greatly. For example, Jennings *et al.* (1998) showed that after accounting for differences in fishing mortality (exposure), fish populations in the Northeast Atlantic characterized by large body size and late maturity showed faster rates of population decline than smaller-bodied species. Yet, other life history traits such as fecundity and von Bertalanffy growth rate did not correlate with population declines. The spatial variation in tropical reef fish species abundance along a fishing pressure gradient further supported that maximum body size is a strong correlate of species responses to exploitation (Jennings *et al.*, 1999b). In contrast, other studies found maximum body size (or maximum body weight) to be uncorrelated or weakly correlated to population status, measured either as abundance trends (Russ and Alcala, 1998), national threat status (Anderson *et al.*, 2011) or proportion of stocks collapsed within species (Pinsky *et al.*, 2011) while controlling for the exposure to fisheries. Although multiple life history traits have been identified as potential biological correlates of vulnerability to fishing in marine fishes, their wide use and general applicability as predictors of vulnerability continues to be a challenge given the different type of methods and data, and the diverse taxonomic and spatial scopes used in the analyses (Anderson *et al.*, 2011).

This study has two aims. First, we conduct a literature review to summarize current understanding of the life history traits that have been identified as useful biological correlates of vulnerability in marine fishes. Second, we identify potential life history correlates of vulnerability for scombrid species. Scombrids – commonly known as tunas, Spanish mackerels, bonitos and mackerels – sustain some of the most important fisheries in the world and probably are among the best studied group of marine fishes (Juan-Jorda *et al.*, 2011; Juan-Jordá *et al.*, 2012). Thus, scombrids are both rich in biological information and provide one of the longest, large-scale fisheries data set for testing the role of intrinsic life histories in predicting species responses to fishing while accounting for exposure to fishing mortality rates.

2. METHODOLOGY

2.1 Literature review of biological correlates

We assembled a wide range of published documents that examined the relationship between a suite of life history traits and various measures of species vulnerability, in order to identify potential biological correlates to predict population and species level responses to fishing, threat status, and extinction risk. In graph and models we do not distinguish between population and species-level responses. Given that the vulnerability of a species is a function of the species intrinsic sensitivity and its exposure to those threats, we distinguished studies focusing on the links between life histories and demography so as to identify potential life history correlates of species intrinsic sensitivity versus those focusing on the links between life histories and population trajectories and status. At the same time we controlled for exposure to fisheries in order to identify biological correlates of vulnerability to fishing.

The 25 studies assembled exemplify the different metrics commonly used to depict species intrinsic sensitivity and species vulnerability to fishing. Estimates of the maximum per-capita population growth rates (r_{max}) derived from established methods (Myers and Fowlow, 1997; Hutchings *et al.*, 2012) is the most common measure used as a metric of species intrinsic sensitivity (Table 1). Extinction fishing mortality ($F_{extinct}$) which is the fishing mortality required to bring a species to extinction, is also used as a metric of species sensitivity since it is equivalent to $r_{max.}$ Moreover, population trajectories of marine fishes quantified as declines, recoveries and collapses typify how species respond to fishing and are common metrics of vulnerability (Table 2). Population declines are commonly estimated as rates of change and extent of declines within a given time interval (e.g. Jennings *et al.*, 1998). However, definitions of population recovery and collapse are more data – driven and study-specific. For example, Hutchings (2000) defined recovery as any increase in population size after a 15-year decline (approximately equal to three generation spans for the species studied) and Pinsky *et al.* (2011) define a population collapse when biomass falls below 20% of the biomass that provides the long term maximum sustainable yield (B_{MSY}). Another common vulnerability metric is the threat status according to IUCN Red List criteria.

Table 1. Review of biological correlates of species intrinsic sensitivity.

Taxonomy	**Scale**	**# of sp. or pop.**	**Sensitivity metrics**	**Potential life history correlates**	**Life history correlates of species sensitivity**	**Ref.**
Teleost fishes	Global	38 sp.	Maximum generational growth rate for the population (r_{max})	Body mass	No associated with body mass	(Ginzburg *et al.*, 2010)
Teleost fishes	Global	47 sp.	Maximum per capita population growth rate (r_{max})	Fecundity, body mass, and age at maturity	Late age at maturity	(Hutchings *et al.*, 2012)
Chondrichthyan fishes	Global	82 sp.	Maximum per capita population growth rate (r_{max})	Fecundity, body mass, and age at maturity	Large body size and late age at maturity	(Hutchings *et al.*, 2012)
Chondrichthyan fishes (sharks and skates)	Global	33 pop.	Potential rate of population increase (index of r_{max})	Body size, age at maturity and growth	Large body size and late age at maturity	(Frisk *et al.*, 2001)
Chondrichthyan fishes (sharks)	Global	41 pop.	Annual population growth rates (lambda)	Body size, age at maturity, generation time	Late age at maturity and large generation time	(Cortés, 2002)
Chondrichthyan fishes (sharks, rays and chimaeras)	Global	127 pop. 105 sp.	Extinction risk ($F_{extinct}$)	Body size, size at maturity, age at maturity, longevity, growth, litter size, interbirth interval, reproductive mode	Deep water habitat species (slower growth, later age at maturity and higher longevity). Reproductive mode (matrotrophically viviparous)	(Garcia *et al.*, 2008)
Chondrichthyan fishes (sharks)	Pacific	20 sp.	Rebound potential at MSY (index of r)	Body size, age at maturity, maximum age	Late age at maturity, large maximum age (weak)	(Smith *et al.*, 1998)
Teleost fishes	NE Atl. Ocean	63 pop.	Maximum rates of recruits at low population size (alfa)	Body size, age of maturity, growth and fecundity	Large size, late age at maturity, slow growth and large fecundities (this is because fecundity is correlated with size). After removing the size effect on fecundity, fecundity was not associated..	(Denney *et al.*, 2002)
Teleost fishes	NE Atl. Ocean	63 pop.	Adult production per adult at low population sizes (alfa standardized)	Body size, age at maturity, growth and fecundity	Large size and slow growth	(Denney *et al.*, 2002)
Teleost fishes (Atlantic cod)	Atlantic Ocean	20 pop.	Maximum per capita population growth rate (r_{max})	Age at maturity	Late maturity	(Myers and Fowlow, 1997)

We examined all assembled studies to identify the most reliable and consistent biological correlates of both species intrinsic sensitivity and species vulnerability to fishing. We also evaluated whether life history correlates (a) differed between vulnerability and sensitivity metrics; (b) differed between teleost and chondrichthyan fishes; and (c) were consistent across the several metrics of vulnerability.

We ranked the life history traits in Figures 1-4 according to the three main axes of life history variation described in fishes: size, speed and reproductive allocation (Rochet *et al.*, 2000; Juan-Jordá *et al.*, 2012). Maximum body size, together with other size-related traits such as length at maturity or maximum weight, governs the first axis of life history variation ranking species along a *small-large* continuum of life histories. Time-related traits such as longevity, age at maturity and growth rates underlie the second axis of a *slow-fast* continuum. Fecundity-related traits such as fecundity at length at maturity and the rate of change of fecundity with size underlies the third axis describing the schedule of reproductive allocation in fishes (Rochet *et al.*, 2000; Juan-Jordá *et al.*, 2012). Thus, traits in Figures 1-4 were ordered as follows: (1) the maximum per-capita population growth rate (r_{max}), followed by (2) size-related traits [maximum size (L_{max}), maximum body weight (W_{max}) and length at maturity (L_m)], (3) time-related traits [longevity (T_{max}), age at maturity (T_m), von Bertalanffy growth rate (k), and generation time (GT)], and (4) reproductive traits [fecundity, egg size and reproductive mode].

Table 2. Review of biological correlates of species vulnerability to fishing.

Taxonomy	**Scale**	**# of sp. or pop.**	**Vulnerability metrics**	**Potential life history correlates**	**Life history correlates of species vulnerability**	**Fisheries exposure accounted**	**Potential ecological and biogeographical correlates**	**Ecological and biogeographical correlates of species vulnerability**	**Ref.**
Teleost and chondrichthyan fishes	Global	12477 sp.	IUCN Red List Categories	Body size	Large size	Yes			(Olden *et al.*, 2007)
Teleost fishes	Global	386 sp.	IUCN Red List Categories	Body size	Large size	Yes	Habitat (demersal, pelagic, reef-associated), range, environmental temperature (temperature, tropical, deep-water)	Small range, environmental temperature (deep-water species) and habitat (reef-species)	(Field *et al.*, 2009)
Chondrichthyan fishes	Global	227 sp.	IUCN Red List Categories	Body size	Large size	Yes	Habitat (demersal, pelagic, reef-associated), range, environmental temperature (temperate, tropical, deep-water)	Small range size	(Field *et al.*, 2009)
Chondrichthyan fishes (skates)	Global	230 sp.	Locally extinct	Body size	Large size	No	Latitudinal range and depth range	None	(Dulvy and Reynolds, 2002)
Teleost and chondrichthyan fishes	Canada	34 sp.	IUCN Red List Categories	Body size, age at maturity	Late age at maturity and large body size (weak effect)	Yes	Latitude midpoint, depth point	Deeper waters	(Anderson *et al.*, 2011)
Teleost fishes	Global	90 pop.	Population trajectories (declines and recoveries)	Several taxonomic groups with different life histories (Demersal vs pelagic clupeids vs other pelagics)	Demersal benthic species seem more vulnerable to fishing exploitation. Pelagics such as clupeids seem more resilient and have better recovery rates than the rest of the species or families.	No			(Hutchings, 2000)
Teleost fishes	Global	90 pop.	Population trends (declines and recoveries)	Several taxonomic groups with different life histories (Demersal vs pelagic clupeids vs other pelagics)	Demersal benthic species seem more vulnerable to fishing exploitation. Pelagics such as clupeids seem more resilient and have better recovery rates than the rest of the species or families.	Yes			(Hutchings, 2001)
Teleost fishes	Global	120-458 sp.	Population trends (collapses)	Longevity, age at maturity, maximum weight, growth rate, fecundity, egg diameter	Fast growing	No	Trophic level	None	(Pinsky *et al.*, 2011)
Teleost fishes	Global	120-458 sp.	Population trends (collapses)	Longevity, age at maturity, weight, growth rate, fecundity, egg diameter	Fast growing, long lived (weak effect)	Yes	Trophic level	None	(Pinsky *et al.*, 2011)
Teleost fishes	NE Atl. Ocean	9 sp., 18 pop.	Population trends (abundance trends)	Body size, age at maturity, growth rate, fecundity at length of maturity, potential rate of population increase (a proxy of r_{max})	Large size, late maturity and lower potential rates of population increase	Yes			(Jennings *et al.*, 1998)
Teleost fishes	Fiji	33 sp.	Population trends (abundance at several sites)	Body size	Large size	Yes			(Jennings *et al.*, 1999b)
Teleost fishes	Philippines	Various families	Population trends (density and biomass trends)	Body size	Large size	Yes			(Russ and Alcala, 1998)
Teleost and chondrichthyan fishes	North Sea	23 sp.	Population trends (cpue trends)	Body size, length and age at maturity, growth, average annual fecundity, potential rate of population increase (a proxy of r_{max})	Large size, larger and late maturity, slow growing, lower potential rates of population increase	Yes			(Jennings *et al.*, 1999a)
Chondrichthyan fishes (skates)	UK waters	7 sp.	Population trends (abundance and biomass trends)	Body size, growth rate, length of maturity	Large size	Yes			(Dulvy *et al.*, 2000)

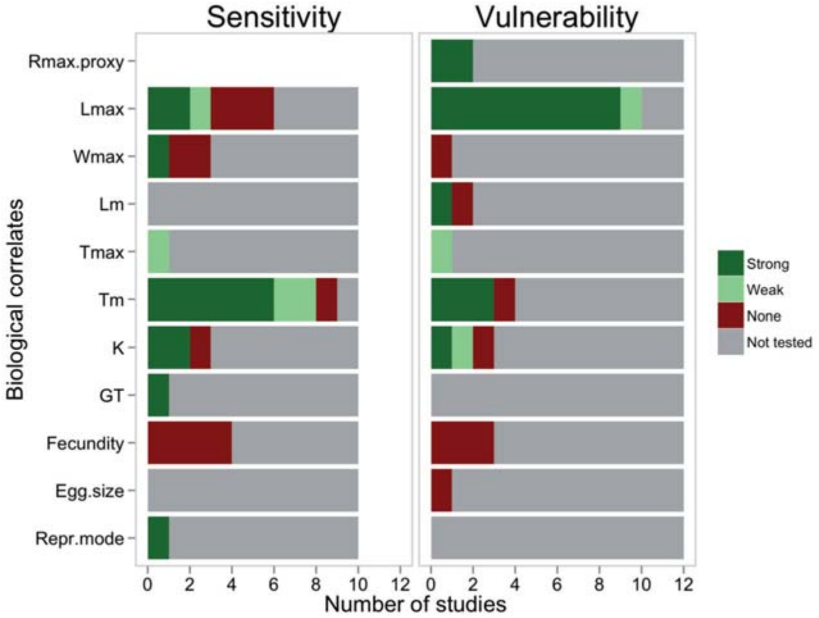

Figure 1. Most common life history correlates of (a) species vulnerability to fishing and (b) species intrinsic sensitivity. Total number of studies assembled (x axis). Colors illustrate life history traits that have been strongly associated with vulnerability and sensitivity metrics (dark green), weakly associated (light green), not associated (dark red) and not included in the analyses (grey). Table 1 and 2 illustrate measures used as sensitivity and vulnerability metrics. Maximum per-capita population growth rate (Rmax.proxy), maximum body size (L_{max}), maximum body mass (W_{max}), length at maturity (L_m), longevity (T_{max}), age at maturity (T_m), growth rate (K), generation time (GT), fecundity, egg size and reproductive mode.

2.2 Biological correlates of vulnerability in scombrid species

2.2.1 Metrics of vulnerability

We compiled age-structured stock assessment models with more than 15 years of data for scombrid species and populations globally, from which we extracted time series of adult biomass, fishing mortality rates and standard biological reference points, $B_{current}/B_{MSY}$ and $F_{current}/F_{MSY}$, if available from the assessments (Juan-Jorda *et al.*, 2011). We ended up with stock assessments for 26 scombrids populations representing 11 species: 17 principal market tunas (7 species), five mackerels (two species), and four Spanish mackerels (two species) (Table 3).

We used three metrics to describe the responses of scombrid populations to fishing over the last 50 years of exploitation. The first metric consisted in calculating the average annual rates of change in adult biomass for each population. Most of the time, series of adult biomass showed non-linearity and temporal autocorrelation. Therefore, we converted the raw time series of adult biomass of each population to annual rates of change (r_i), $r_i = \ln(AB_{i+1}/AB_i)$, where AB_i is the adult biomass in year *i*. Such differencing or taking the ratios in log-space is a common method of removing temporal autocorrelation from a time series (Shumway and Stoffer, 2006). Then, we estimated the average annual rate of change in adult biomass across all years for each population, using a generalized least-squares model of the form $r_i = b_o + e_i$., where r_i is the dependent variable, interpreted as the annual (*i*) rate of change in adult biomass; b_o, the intercept, is interpreted as the average annual rate of change in adult biomass across all the years; and e_i is the residual error. We used maximum likelihood to fit all the generalized least-square models and we examined the residuals of all the models, further correcting for temporal autocorrelation with AR1 and AR2 processes when necessary. The second metric consisted in estimating the total extent of decline in adult biomass over the entire time period of exploitation for each population. We estimated the extent of decline for each individual population as follows: $(1 - \exp(b_o \cdot n)) \cdot 100$, where b_o is the

Table 3. List of scombrid populations.

Ocean	Taxonomic group	Latin name	Population common name
Atlantic	Mackerels	*Scomber scombrus*	Atlantic mackerel, North East
Atlantic	Spanish mackerels	*Scomberomorus cavalla*	King mackerel, Gulf of Mexico
Atlantic	Spanish mackerels	*Scomberomorus cavalla*	King mackerel, U.S. Atlantic
Atlantic	Spanish mackerels	*Scomberomorus maculatus*	Spanish mackerel, Gulf of Mexico
Atlantic	Spanish mackerels	*Scomberomorus maculatus*	Spanish mackerel, U.S. Atlantic
Atlantic	Tunas	*Thunnus alalunga*	Albacore tuna, North Atlantic
Atlantic	Tunas	*Thunnus alalunga*	Albacore tuna, South Atlantic
Atlantic	Tunas	*Thunnus thynnus*	Atlantic bluefin tuna, East
Atlantic	Tunas	*Thunnus thynnus*	Atlantic bluefin tuna, West
Atlantic	Tunas	*Thunnus obesus*	Bigeye tuna, Atlantic
Atlantic	Tunas	*Thunnus albacares*	Yellowfin tuna, Atlantic
Indian	Tunas	*Thunnus obesus*	Bigeye tuna, Indian
Indian	Tunas	*Thunnus maccoyii*	Southern bluefin tuna
Indian	Tunas	*Thunnus albacares*	Yellowfin tuna, Indian
Pacific	Mackerels	*Scomber japonicus*	Chub mackerel, Chilean
Pacific	Mackerels	*Scomber japonicus*	Chub mackerel, Japanese
Pacific	Mackerels	*Scomber japonicus*	Chub mackerel, North East Pacific
Pacific	Mackerels	*Scomber japonicus*	Chub mackerel, Tushima Current Pacific
Pacific	Tunas	*Thunnus alalunga*	Albacore tuna, North Pacific
Pacific	Tunas	*Thunnus alalunga*	Albacore tuna, South Pacific
Pacific	Tunas	*Thunnus obesus*	Bigeye tuna, East Pacific
Pacific	Tunas	*Thunnus obesus*	Bigeye tuna, West Pacific
Pacific	Tunas	*Thunnus orientalis*	Pacific bluefin tuna
Pacific	Tunas	*Katsuwonus pelamis*	Skipjack tuna, West Pacific
Pacific	Tunas	*Thunnus albacares*	Yellowfin tuna, East Pacific
Pacific	Tunas	*Thunnus albacares*	Yellowfin tuna, West Pacific

model estimated average annual rate of change for each individual population and n is the length of the time series of each individual population. Finally, the third metric described the current exploitation status of scombrids using the standard fisheries reference point, $B_{current}/B_{MSY.}$ that illustrates the current adult biomass relative to the adult biomass that would provide the maximum sustainable yield. When $B_{current}/B_{MSY} \leq 1$, the population is considered overfished, while when $B_{current}/B_{msy} \geq 1$ the population is not overfished.

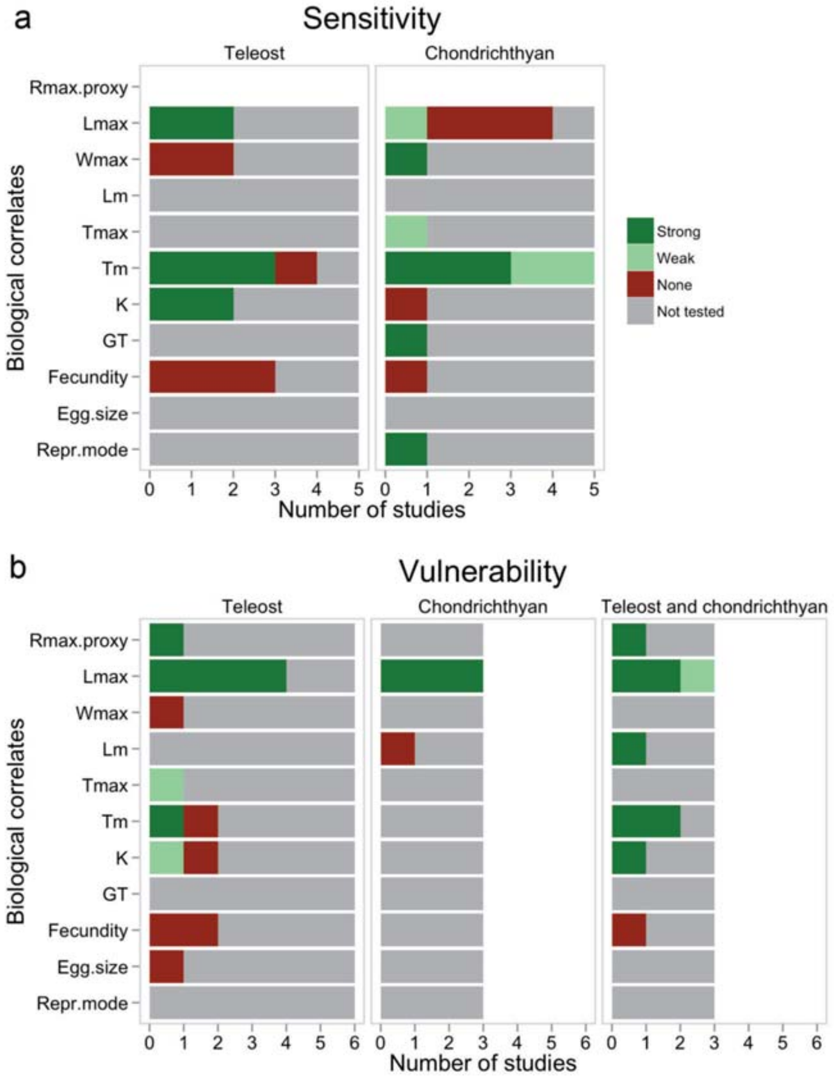

Figure 2. Life history correlates of (a) species intrinsic sensitivity and (b) species vulnerability to fishing, in teleost fishes, chondrichthyans fishes, and teleost and chondrichthyans fishes together. Total number of studies assembled (x axis). Colors illustrate life history traits that have been strongly associated with vulnerability and sensitivity metrics (dark green), weakly associated (light green), not associated (dark red) and not included in the analyses (grey). Table 1 and 2 illustrate measures used as sensitivity and vulnerability metrics. Maximum per-capita population growth rate (Rmax.proxy), maximum body size (L_{max}), maximum body mass (W_{max}), length at maturity (L_m), longevity (T_{max}), age at maturity (T_m), growth rate (K), generation time (GT), fecundity, egg size and reproductive mode.

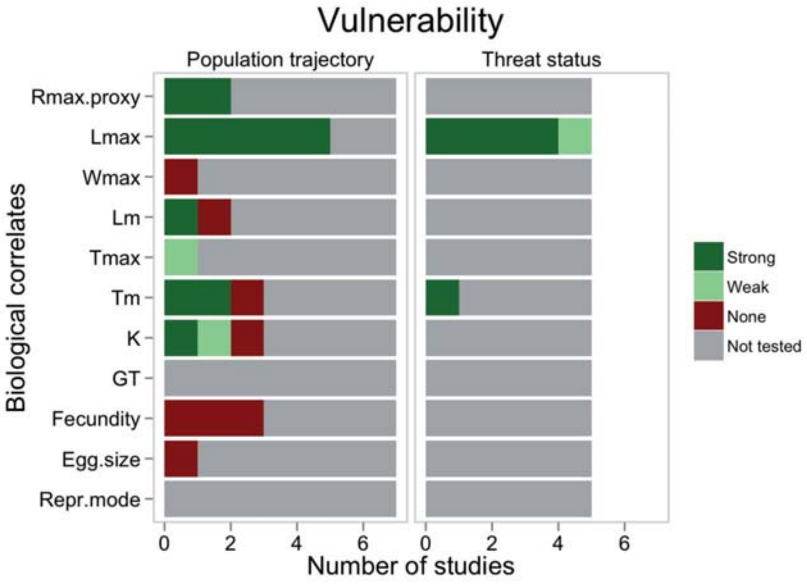

Figure 3. Life history correlates of species vulnerability to fishing illustrating the two main metrics of vulnerability, population trajectories and threat status. Population trajectories of marine fishes quantified as declines, recoveries and collapses typify how species respond to fishing, using metrics of vulnerability. Threat status is commonly assigned according to IUCN Red List criteria Colors. Total number of studies assembled (x axis). Colors illustrate life history traits that have been strongly associated with vulnerability and sensitivity metrics (dark green), weakly associated (light green), not associated (dark red) and not included in the analyses (grey). Table 1 and 2 illustrate measures used as sensitivity and vulnerability metrics. Maximum per-capita population growth rate (Rmax.proxy), maximum body size (L_{max}), maximum body mass (W_{max}), length at maturity (L_m), longevity (T_{max}), age at maturity (T_m), growth rate (K), generation time (GT), fecundity, egg size and reproductive mode.

2.2.2 Potential biological correlates

We used the scombrid life history data set described by Juan-Jorda *et al.* (2012) from which we extracted life-history data for the 26 populations of scombrids analyzed in this study. The life history traits included were maximum body size (L_{max}, cm), length and age at maturity (L_m, cm and T_m, years) longevity (T_{max}, years), growth rates described with the growth coefficient *k* (1/year) extracted from von Bertalanffy growth functions, generation time (*GT*, years), fecundity (absolute and relative batch fecundities), spawning interval (Spw_{int}, days) and spawning season (Spw_{season}, months). In order to describe fecundity in scombrids which spawn repeatedly over the spawning season, we used three measures: (1) the absolute batch fecundity at the length of maturity (F_{Lm}, number of oocytes at L_m) estimated by using the fecundity-length equation (Fecundity = a · Length^b) and length at maturity; (2) the exponent *b* of the fecundity–length relationship (or slope of the log–log fecundity-length regression), which describes the increase of fecundity with size (F_{slope}); and (3) the relative batch fecundity (F_{rel}, number of oocytes per gram), which describes reproductive effort. Generation time (*GT*, years), defined as the average age of the adult population, was calculated for each population using the time series of abundance for each age class and the vector of age of maturity available from each stock assessment. We report length-based estimates as fork lengths throughout the study.

In order to aggregate the life history parameters from multiple studies at the population level, we selected data for analysis based on the following rules: (a) we chose the maximum value for those traits at the extreme of the life cycle (maximum length and empirical longevity); (b) we calculated a sample-size weighted average for those reproductive traits within the lifecycle (maturity, fecundity and spawning interval); and (c) for the growth coefficient *K* derived from von Bertalanffy growth functions, we calculated a simple arithmetic mean (giving equal weight to all the studies), because this parameter is more difficult to combine across studies due to the differing methodologies used to estimate age and growth among studies. In our life history analysis we preferentially used the female estimates whenever the traits were reported separately for sexes. Complete data were missing for some populations. Therefore, in order to maximize the number of populations included in the analyses, we filled the missing information following two criteria: we combined all available studies from the multiple populations and calculated a species average for each life history trait; and we substituted the population's missing traits using the species average value of each trait.

2.2.3 Linking population responses to fishing and life histories

We first explored the association between all life history traits and the current exploitation status of scombrid populations using frequency distributions of all the potential biological correlates of exploitation status using beanplots (Kampstra, 2008). Second, we fitted linear regressions to test for the relationship between the species responses to fishing and their life history traits, and to identify what life history trait, or suites of life history correlates, are better predictors of fish responses. The linear model can be expressed as: $Y_i = B_o + B_1 X_{1,i} + \ldots + B_k X_{k,1}$, where Y_i ,the dependent variable, is the metric describing the responses of scombrid populations (*i*) to fishing. We used two metrics (average annual rate of change in adult biomass and extent of decline in adult biomass) to describe the species responses to fishing. Therefore, we repeated the following modeling approach for each of the two response variables. In the linear model, B_o is an intercept, and B_1 through B_k are the coefficients of the independent variables $X_{1,i}$ through $X_{k,1.}$ The k covariates (life history traits) used to fit the models were selected based on the following criteria: their potential importance based on the literature review undertaken in this study; their collinearity with one another, and the data coverage of each trait for each population. Thus, we excluded collinear life history traits that were highly correlated ($r > 0.9$) with one another and traits with missing data. The vulnerability of a species not only depends on the intrinsic characteristics of the species, such as their life histories and ecology, it is also determined by their exposure to extrinsic threats such as fishing or habitat loss. The magnitude and extent of these extrinsic threats also need to be taken into account to determine the vulnerability of the species. Therefore, we included as a covariate a measure of fishing mortality in the linear models, to account for the different rates of fishing mortality that populations have been exposed during their history of exploitation. In the model, fishing mortality was expressed as the average fishing mortality for the period over which abundance trends were calculated for each population. In these analyses, we log-transformed (natural logarithm) all the life history traits prior to the analysis to approximate normality, except the slope from the fecundity–length relationship that was already estimated from log-transformed data.

For the purpose of our analysis, we only examined the relationship between negative average rates of change in adult biomass and their respective extent of decline and the suite of life history traits; thus excluding positive rates of change and positive extent of change in adult biomass. Among all the scombrid populations, only four Spanish mackerels populations showed positive average annual rates of change and a concomitant positive change in adult biomass. These populations have been under a recovery and management plan for the last 30 years and currently their current biomasses are considered recovered to target levels (B_{MSY}).

As a result, we constructed a set of candidate models reflecting particular *a priori* hypotheses to identify the most important biological correlates of vulnerability for scombrids accounting for the different levels of fishing mortality that populations have been exposed during their history of exploitation. We fitted all the candidate models with the k potential covariates as main effects. The models did not include interactions between variables because of the large number of potential combinations and the small size of our data set. We evaluated all candidate models and generated an average predictive model by ranking the models according to their Akaike's Information Criterion corrected for small sample sizes (AICs) (Burnham and Anderson, 2002). We retained the minimal adequate models with AICs within four of the lowest values. The relative likelihoods of candidate models were calculated using AIC weights (wAICc) (Burnham and Anderson, 2002). We also assessed and reported the relative importance of each life history variable.

Data management, analysis and figures were all done using the R statistical software v.2.14.2 (R Development Core Team, 2010), including the R packages "MuMIn" (Bartón, 2009) and "ggplot2" (Wickham, 2009).

3. RESULTS

3.1 Literature review of biological correlates

Table 1 and 2 provide a summary of the current understanding of biological correlates of species intrinsic sensitivity and species vulnerability to fishing in marine fishes. We found that a total of eight potential biological correlates have been tested against the main metrics of species intrinsic sensitivity and eight potential biological correlates against the main metrics of species vulnerability to fishing (Figure 1). Maximum body size and age at maturity have been the most commonly-tested traits while the rest of the traits, particularly generation length or the reproductive mode of the species, have been tested less often. Among all the traits, maximum body size and age of maturity have been most frequently identified as useful biological correlates of both species sensitivity and vulnerability. However, it appears that age at maturity is a better correlate of the species sensitivity while maximum body size is a better correlate of species vulnerability to fishing (Figure 1). Fecundity has never been identified as a useful biological correlate of species sensitivity or species vulnerability to fishing. Moreover, there is surprisingly little evidence for the usefulness of maximum weight, length at maturity, longevity, and von Bertalanffy growth rate as biological correlates of sensitivity or vulnerability to fishing.

In both teleost and chrondrichthyan fishes, age at maturity remains the most reliable correlate of species sensitivity, while maximum body size continues to be the most reliable correlate of species vulnerability to fishing (Figure 2a). In addition, we find mixed evidence for the reliability of maximum size and weight as reliable predictors of species intrinsic sensitivity in both teleost and chrondrichthyan fishes (Figure 2b).

Maximum body size is the most consistent correlate of species vulnerability to fishing irrespective of the metric used, such as decline rates, recovery rates, collapses or IUCN threat status (Figure 3). In addition, we also find that a large majority of studies linking species life histories with any of the vulnerability metrics had controlled for the exposure of the species to fisheries (Figure 4). Even after controlling for exposure to fisheries in the analyses, maximum body size remains the most useful biological correlate of species vulnerability to fishing.

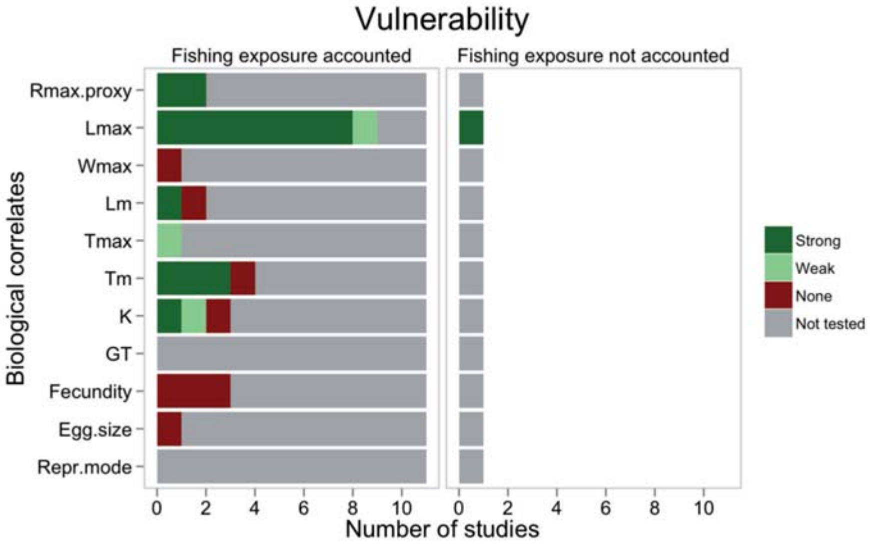

Figure 4. Life history correlates of species vulnerability to fishing illustrating whether or not the fishing exposure was controlled for in the analyses. Total number of studies assembled (x axis). Colors illustrate life history traits that have been strongly associated with vulnerability and sensitivity metrics (dark green), weakly associated (light green), not associated (dark red) and not included in the analyses (grey). Table 1 and 2 illustrate measures used as sensitivity and vulnerability metrics. Maximum per-capita population growth rate (Rmax.proxy), maximum body size (L_{max}), maximum body mass (W_{max}), length at maturity (L_m), longevity (T_{max}), age at maturity (T_m), growth rate (K), generation time (GT), fecundity, egg size and reproductive mode.

3.2 Biological correlates of vulnerability in scombrid species

3.2.1 Rates of decline, extent of decline and exploitation status in scombrids

Most scombrid populations (21 out of 26 populations analyzed) have experienced negative average annual rates of change with their corresponding extent of decline within their respective histories of exploitation (Figure 5). In addition, there is a strong link between exploitation status and population trajectory: the overfished populations exhibite the steepest and largest extent of declines compared to not overfished populations, although there are some exceptions.

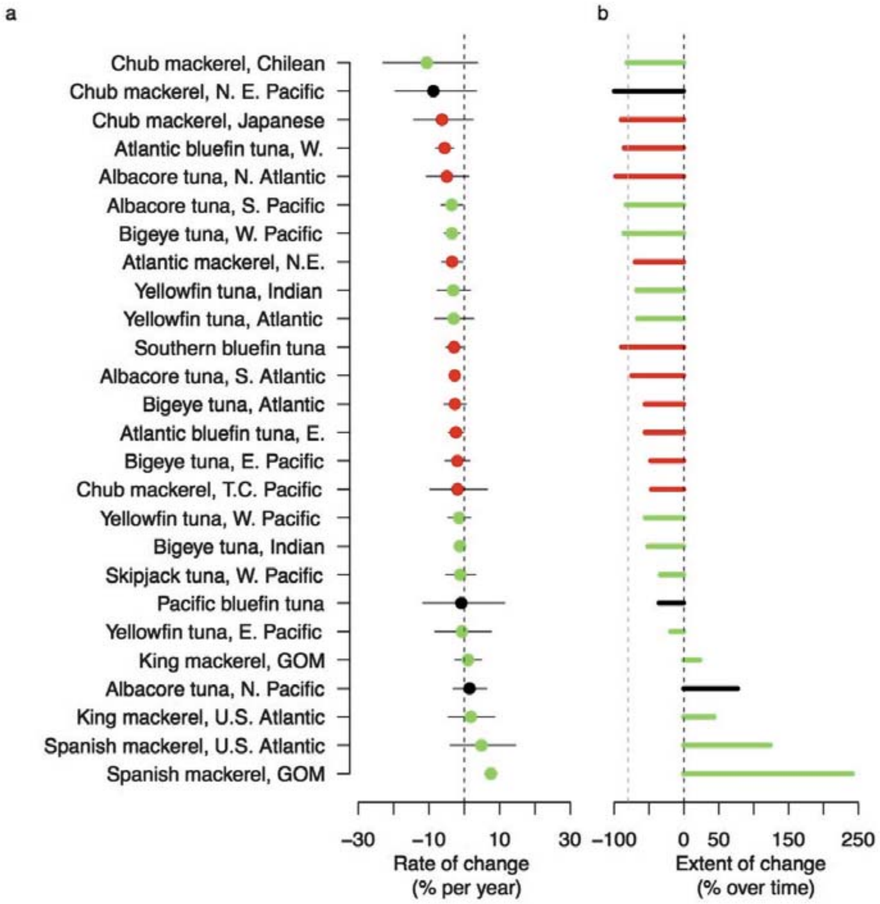

Figure 5. Scombrid population responses to fishing as metrics of vulnerability. (a) Average annual rate of change in adult biomass (mean ± 95% CIs) and (b) overall extent of decline or recovery in adult biomass for each population estimated over the entire time span of the time series data. Full name of populations available in Table 3. Colors depict whether populations are overfished ($B_{current} < B_{MSY}$, red), not overfished ($B_{current} > B_{MSY}$, green) and current status unknown (black).

3.2.2 Life history correlates and current exploitation status

We explored the association between a suite of potential life history correlates of vulnerability and the current exploitation status of scombrids with beanplots for visual comparative purposes (Figure 6). We find that overfished populations tend to mature at larger sizes and later, be longer-lived, have shorter spawning seasons, slower growth rates, and longer generation times than populations that are not currently overfished. At this scale of analysis, there is no apparent difference in maximum size between overfished and not overfished populations. We also find that overfished populations have been exposed to lower average rates of fishing mortality than not overfished populations. It might be that currently not overfished populations are made up of species with lower intrinsic sensitivities.

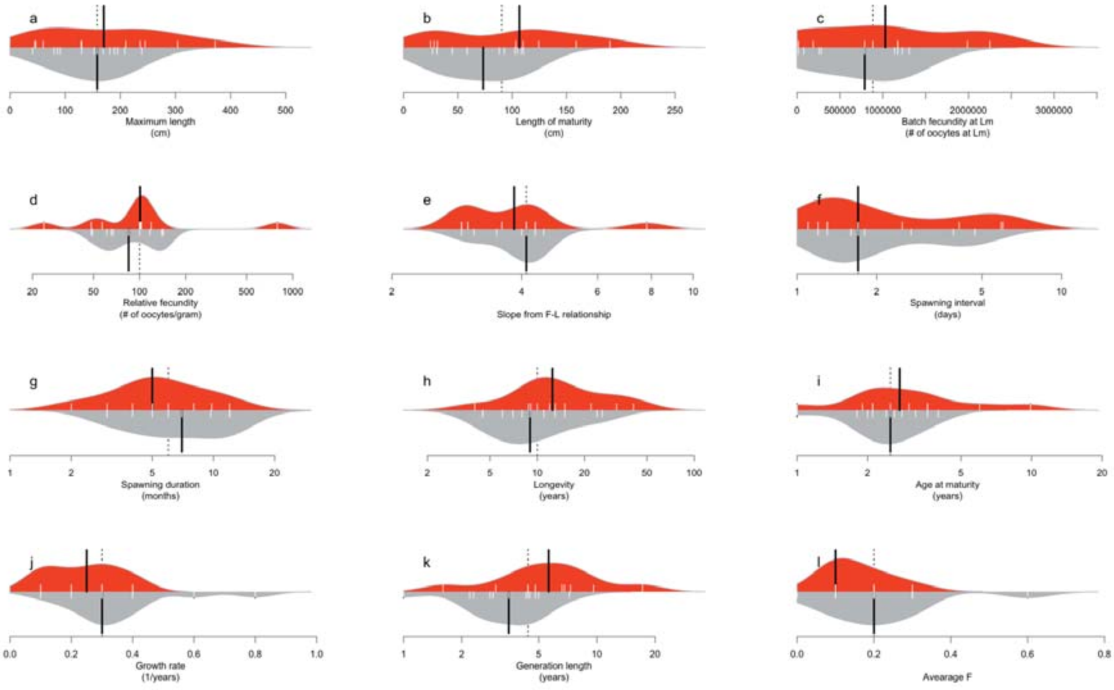

Figure 6. Beanplots of potential life history correlates of vulnerability in scombrid populations. Curve polygons (beans) illustrate the estimated density of the distribution in the life history values for overfished ($B_{current} < B_{MSY}$, red) and not overfished ($B_{current} > B_{MSY}$, grey) populations. The long vertical black line shows the median of each distribution. The long vertical dashed black line shows the median for the data combined. The short vertical white lines depict the populations for which data are available.

3.2.3 Biological correlates of responses of populations to fishing

In order to identify the most important biological correlates of vulnerability to fishing in scombrids, we constructed a full model, which excluded variables that were highly correlated ($r<0.9$) and variables that had missing information for most of the populations. Length at maturity and fecundity at length of maturity were positively and highly correlated ($r>0.9$) with maximum body size and were excluded therefore. The full model ended up including the following traits: maximum body size, longevity, age at maturity, growth rate, generation time, and spawning duration. Average fishing mortality was also included to control for the different mortality rates experience by each populations over their history of exploitation.

Our analysis revealed support for more than one model for each of our vulnerability metrics (between 3 and 7 models with $\Delta_i < 4$) (Table 4, left side). Therefore, we included all of the candidate models into the averaged model for each vulnerability metric (Table 4, right side). Among all the life history traits examined, longevity was consistently the most important correlate (negatively so) of both rate and extent of decline in adult biomass (relative importance = 0.6 and 0.67, respectively). Long-lived populations have experienced the steepest declines and largest extents of adult biomass. Generation time was also negatively correlated (although less importantly so) with both rate of decline and extent of decline (relative importance = 0.3 and 0.13, respectively), suggesting that populations with the largest generation time also experienced the steepest and largest declines in adult biomass. In the models of rates of decline, our data also suggested a weak positive correlation between decline rates and maximum size, indicating that large-bodied species have experienced the slowest rates of decline. However, the correlate of maximum size should be better interpreted in conjunction with longevity (see in Table 4.a the model with the second highest W_i is $L_{max}+T_{max}$). This candidate model suggests that longer-lived populations, even after accounting for their larger maximum sizes, have experienced the steepest rates of decline. Moreover, average fishing mortality rate, was not included in any of the highest ranked candidate models, suggesting that the average fishing mortality experienced by each population throughout its history of exploitation is not a particularly useful correlate of rate or extent of decline.

Table 4. Summary of the linear models using (a) rate of decline as vulnerability metric and (b) extent of decline as vulnerability metric. Left side: Models having the greatest support are shown. K, the number of parameters; loglik, the value of the maximized log-likelihood function; AICc, Akaike's information criterion with a correction for small sample sizes; W_i Akaike weights. The models are ordered by decreasing W_i and only those with $\Delta_i < 4$ are shown. Right side: Scaled model parameters estimates with standard errors from the averaged predictive linear models are shown. The parameters have been ordered by their relative importance to the average model on a scale of 0 to 1. The parameters were scaled by subtracting the mean and dividing by two standard deviations to allow for comparisons among parameters.

(a) Rate of decline

Models for the greatest support:							**Model-averaged coefficients:**							
Model	**k**	**loglik**	**AIC$_c$**	**Δ_i**	**W_i**			**Estimate**	**Std. Error**	**Adjusted SE**	**z value**	**Pr(>|z|)**	**Significance codes**	**Relative variable importance**
T_{max}	3	34.3	-59.8	0.0	0.37		(Intercept)	-0.031	0.005	0.006	5.10	3.00E-07	***	
L_{max}+T_{max}	4	35.6	-58.1	1.7	0.16		z.T_{max}	-0.029	0.012	0.013	2.23	0.026	*	0.6
GT+Lmax	4	35.1	-57.1	2.7	0.09		z.L_{max}	0.027	0.016	0.018	1.54	0.124		0.39
$Spw_{seaso}n$+T_{max}	4	34.9	-56.9	3.0	0.08		z.GT	-0.025	0.013	0.015	1.69	0.092	.	0.2
L_{max}+T_m	4	34.9	-56.9	3.0	0.08		z.T_m	-0.033	0.015	0.017	1.89	0.059	.	0.14
GT	3	32.4	-56.1	3.7	0.06		z.Spw_{season}	-0.014	0.014	0.015	0.93	0.353		0.08
GT+L_{max}+T_{max}	5	37.3	-56.0	3.8	0.05									

(b) Extent of decline

Models for the greatest support:							**Model-averaged coefficients:**							
Model	**df**	**loglik**	**AIC$_c$**	**Δ_i**	**W_i**			**Estimate**	**Std. Error**	**Adjusted SE**	**z value**	**Pr(>|z|)**	**Significance codes**	**Relative variable importance**
T_{max}	3	-48.7	106.4	0.0	0.56		(Intercept)	-64.63	4.71	5.34	12.10	<2e-16	***	
GT	3	-50.2	109.3	2.9	0.13		z.T_{max}	-24.25	9.94	11.25	2.16	0.031	*	0.67
T_{max}+Spw_{season}	4	-48.0	109.6	3.2	0.11		z.GT	-17.37	10.44	11.87	1.46	0.143		0.13
							z.Spw_{season}	-12.21	11.11	12.82	0.95	0.341		0.11

4. DISCUSSION

4.1 Biological correlates in marine fishes

Our literature review of life history correlates of species sensitivity and vulnerability revealed important insights into the relative importance of several life history traits as reliable biological correlates. First, age at maturity has been consistently identified as the most useful biological correlate of species intrinsic sensitivity, suggesting that age at maturity might be the most reliable predictor of species maximum per-capita growth rate (r_{max}). We find this outcome to be consistent in teleost and chondrichthyan fishes. Given that age at maturity is a commonly estimated parameter in marine fishes, in the absence of demographic data to estimate r_{max}, age at maturity can be used as an indicator of species productivity and capacity to recover from depletion and to rank species according to their productivity and resilience and therefore risk of extinction (Hutchings *et al.*, 2012) . In contrast, multiple studies showed no link or a weak link between maximum body size or weight and the metric of r_{max} suggesting that maximum body size or weight are not good predictors of r_{max} either in teleost or chondrichthyan fish species, thus, are not good predictors of species productivity and resilience. There are methodological reasons the metric of r_{max} may not be strongly related to body size. r_{max} is usually estimated with age-dependent demographic models, such as Euler-Lotka or rebound potential, and hence there is no size dependency in the estimation of r_{max}. Although we know theoretically and empirically that r_{max} scales negatively with maximum body mass with an exponent of -1/4 (Savage *et al.*, 2004; Jennings and Dulvy, 2008).

Second, the literature review revealed that maximum body size has been most frequently identified as a reliable biological correlate of species vulnerability to fishing, suggesting that maximum body size might be the more reliable predictor of species declines, recoveries and threat status in marine fishes. This outcome is consistent across teleost and chondricthyan fishes. These findings concur with a previous review of biology of extinction risk in marine fishes which comprised 15 sensitivity and vulnerability studies (Reynolds *et al.*, 2005a). Our review included 23 studies and distinguishes between sensitivity and vulnerability studies. The key finding of Reynolds *et al.* (2005a) was that large body size and late age at maturity are the most reliable biological correlates of declines, recovery, and threat status. In our review, we still expected time-related traits (such as age at maturity or growth rate) to be good predictors of species vulnerability. However, they have been less frequently tested given that they are harder to measure than maximum body size. A recent global study found, contrary to expectations, that small, short-lived species, commonly presumed to be less vulnerable to fisheries, have collapsed as often as large, higher trophic-level species even after controlling for fishing mortality (Pinsky *et al.*, 2011). We caution that this study had very low power because the authors did not correct for multiple comparisons, risking false positives, and also because fishing mortality was not included as a main covariate in the models; it was analyzed instead using regression of residuals (Freckleton, 2002).

Third, our review confirms, contrary to widely-held perceptions, that fecundity is not a predictor of either sensitivity or vulnerability. Although multiple empirical studies have repeatedly shown how different measures of fecundity (average fecundity, maximum fecundity per breeding season, fecundity at length of maturity) are not reliable correlates of species vulnerability to fishing in marine fishes, concluding that the production of large number of eggs does not protect marine fishes from extinction risk (Jennings *et al.*, 1998; Jennings *et al.*, 1999b; Denney *et al.*, 2002; Reynolds *et al.*, 2005a; Hutchings *et al.*, 2012).

Fourth, life history studies in fishes, birds, mammals and reptiles have shown that most of the life history variation can be explained along at least two main axes or dimensions (Gaillard *et al.*, 1989; Saether *et al.*, 2002; Bielby *et al.*, 2007; Juan-Jordá *et al.*, 2012). The first axis, governed by body size and length-related traits such as length at maturity, ranks species along a small-large continuum of life histories, while time-related traits, such as longevity, growth rates, age at maturity and generation underlie the second axis ranking species along a slow-fast continuum. Given that length and time-related traits govern the first two axes of life history variation in fishes, we would expect length-related traits highly correlated with maximum body size such as length at maturity, and time-related traits highly correlated with age at maturity such as growth and longevity, to arise as important biological correlates as they become increasingly tested and available in more marine fish species. We found no clear evidence that maximum body mass, longevity, length of maturity, and growth rate are reliable biological correlates of either species sensitivity, or vulnerability to fishing. This may be due to the small number of studies testing these parameters as potential biological correlates.

Our literature review focused on identifying the relative importance of several biological correlates in marine fishes rather than freshwater fishes. However, we would also like to highlight some of the work carried out in freshwater systems to identify biological correlates of vulnerability in freshwater fishes (Angermeier, 1995; Duncan and Lockwood, 2001; Reynolds *et al.*, 2005b; Olden *et al.*, 2007; Anderson *et al.*, 2011). While large body size is a good biological correlate associated with fisheries vulnerability in marine fishes, in freshwater systems small body size is a better predictor of freshwater threat and extinction risk due to habitat loss (Reynolds *et al.*, 2005b; Olden *et al.*, 2007). The very different types of threats present in these two systems may drive the observed disparity in the usefulness of body size as a biological correlate of vulnerability in marine and freshwater fishes. Overexploitation is the leading primary threat to extinction in marine fishes (Reynolds *et al.*, 2005a). In contrast, the primary threats in freshwater systems are wider, and tend to include habitat loss, pollution, introduction of invasive species and over-exploitation (Olden *et al.*, 2007). These threats tend to interact in complex ways that are generally species and location-specific (Olden *et al.*, 2007), and therefore their effects may be harder to predict for freshwater species.

4.2 Biological correlates of vulnerability in scombrid populations

The analysis of biological correlates of scombrid species revealed that long-lived scombrid populations have experienced the steepest declines and the largest extents of decline in adult biomass within their period of exploitation. Among all the traits tested, longevity was highly correlated with rates of decline and extent of decline, suggesting that longevity was the most reliable predictor of scombrid responses to fishing. Our findings differ from empirical studies which suggest that maximum size is the best predictor of population status in marine fishes, (e.g. Jennings *et al.*, 1998; Jennings *et al.*, 1999a; Jennings *et al.*, 1999b; Dulvy *et al.*, 2000). This may be due to the small number of studies testing longevity as a potential biological correlate. To our knowledge, only two studies have tested for the importance of longevity as a biological correlate of species vulnerability to fishing or species intrinsic sensitivity (Smith *et al.*, 1998; Pinsky *et al.*, 2011). The first found that the intrinsic rebound productivity in 20 shark species in the Pacific Ocean was primarily affected by age at maturity, and secondarily affected by maximum age. The latter found that the proportion of population collapses within species (measured with landings data) were slightly more common among long-lived marine fish species than short-lived species. However, this trend was absent when population collapses were calculated using biomass data derived from stock assessment models. Yet, why was longevity the most reliable predictor of scombrid responses to fishing rather than maximum size? There is increasing evidence that the age-structure of longer-lived species has an effect on the productivity and stability of populations and that therefore maintaining natural age-structures is essential for the successful management of fish populations (Longhurst, 2002; Berkeley *et al.*, 2004). Perhaps, size-selective fishing pressure on the larger and older individuals may be causing substantial changes in the age structure of scombrid populations, making longer-lived populations the most vulnerable to fishing.

The average fishing mortality experienced by each population throughout its history of exploitation was not a useful correlate of either rate of decline or extent of decline in scombrid populations. These findings are counterintuitive, given that prolonged levels of high fishing mortality rates have been associated with higher and faster rates of decline and are expected to affect extinction probability in fishes (Hutchings and Reynolds, 2004). Our results do not imply that fishing mortality is not the primary cause of the declines in adult biomass across populations; our analysis suggests instead that it is not a useful correlate of vulnerability to fishing. Perhaps, by averaging fishing mortality rates over the entire history of exploitation of each population, we lose all the fine temporal details of how fishing rates directly affect abundance levels over time and therefore the history of exploitation may be too complex to be reduced easily into a single metric of average mortality rate. Past studies have also revealed that the fishing intensity experienced by populations did not change the relationship between the life history of the species and the probability of collapse or risk of extinction (Field *et al.*, 2009; Anderson *et al.*, 2011; Pinsky *et al.*, 2011). Future analysis could attempt to link species responses to fishing and their life histories by examining changes in abundance over time in combination with the changes in fishing mortality rates over time.

4.3 Conclusions

Our comparative review of biological correlates reveals that maximum body size is the primary biological correlate, and age at maturity the secondary biological correlate, of species vulnerability to fishing in marine fishes. In addition, age at maturity appears to be the primary biological correlate of species intrinsic sensitivity in marine fishes. Both findings are consistent across teleost and chondrichthyan fishes. Moreover, patterns of life history correlates of decline in scombrids suggest that longevity is the best predictor of population rates and extent of declines. The longest-lived scombrid populations, rather than the largest, appear to have experienced the fastest rates of decline and the greatest extent of decline, even after accounting for the different mortality rates experienced by each population. Identifying and quantifying the relative importance of biological and ecological correlates of vulnerability in fishes continues to be a challenge and is poorly understood. Understanding the intrinsic biology of species vulnerability and extinction risk is crucial to build tools to predict species responses to fishing and their risk of depletion or extinction. Overall limits to exploitation could then be calculated for any population, even in data-poor situations, bringing a realistic precautionary ecosystem-based approach to fisheries management one step closer**.**

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The Gulf of Gabes, southern Tunisia: an endemic fish hotspot under threat

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While representing only 0.32% of the global oceanic volume, the Mediterranean Sea, contains 6-8% of all known marine species with an endemism rate of 10% for fishes (Quignard and Tomasini, 2000). The Suez Canal and the Gibraltar Strait that connect the Mediterranean Sea to respectively the Red Sea and the Atlantic Ocean, are two exotic species spillways making this ecosystem the largest receptacle of exotic species in the world (CIESM, 2013; Streftaris *et al.*, 2005).

On a global scale, species invasion has been recognized as a major threat to biodiversity, even though a causal link between the introduction of exotic species and the risk of local extinction has not yet been demonstrated (e.g. Davis, 2003).

There is ample evidence indeed to warrant the claim that exotic invasions can, at the very least, reduce the abundance of native species, alter disturbance regimes and basic ecosystem processes, impose large economic costs, introduce new pathogens to indigenous populations and modify food webs structure and energy flows (e.g. Libralato *et al.*, 2002). Further, native species can be driven to extinction by competitive interactions (e.g. Olden *et al.*, 2006), by predation (e.g. Roemer *et al.*, 2002), or simply by demographic stochasticity when many new individuals enter the community and occupy part of the carrying capacity of native species (Lande, 1993).

Endemic species, that are native species restricted to a given area, are more endangered by exotic invasions because they cannot escape and establish elsewhere. Thus, the intensity of interaction between exotic and endemic species is of major concern for the conservation of biodiversity as it may contribute to the breakdown of the regional distinctiveness of the Earth's biota (Vitousek *et al.*, 1997; MacKinney and Lockwood, 1999). In this respect, the Mediterranean Sea provides exceptional material for a case study by virtue of its biodiversity and its high percentage of endemic species.

The Mediterranean Sea is currently becoming warmer: in the last decades, temperature has been rising in deep and surface waters (Diaz Almela *et al.*, 2007; Schroeder *et al.*, 2013).

The geographic distribution of fish taxa is strongly clustered in the Mediterranean Sea: subtropical species occur in the south-eastern area, where water temperatures are higher than average (Theocharis *et al.*, 1993), whereas cold-adapted species inhabit northern areas (Bianchi and Morri, 2000). However, as a result of global warming, fish species that were typically found in the warm waters of the southern areas have been observed more frequently in the north (Sabatés *et al.*, 2006; CIESM, 2008). In parallel, the abundance of certain boreal species has markedly decreased (Quignard and Raibault, 1993).

The increase of Lessepsian species introductions as well as those of Atlantic species from lower latitudes in correlation with the increasing temperature of the Mediterranean Sea suggest that this sea is acting as a catchment basin for exotic thermophilic species (Ben Rais Lasram and Mouillot, 2009). This is corroborated by the recent invasion of the western basin of the Mediterranean, colder than the other areas, by Lessepsian species.

Moreover, the comparison of exotic fishes richness maps generated more than 20 years apart (before and after the significant climatic warming period), reveals a clear modification in the species distribution pattern. After the 1980s, some exotic fishes reached the coldest areas of the Mediterranean Sea, such as the Adriatic Sea, which is a major hotspot of endemism (Ben Rais Lasram and Mouillot, 2009). The number of exotic species in the Mediterranean is now about double of what it was 20 years ago.

It is now obvious that sea surface warming is expected to drive a general northward shift of fish ranges in the Mediterranean Sea leading to the gradual replacement of cold temperate species by thermophilic species. Hence, the coldest parts of the Mediterranean Sea (Gulf of Lion and northern Adriatic) could initially serve as a sanctuary for cold-temperate species; but, with intensified warming, those areas might become a "dead end", from which cold-temperate species could not escape. This process would be critical to endemic species, because the trapping effect would lead to species extinction (Ben Rais Lasram *et al.*, 2010).

According to projections derived from climatic envelope models for 2041–2060 (Ben Rais Lasram *et al.*, 2010), 53% of endemic fish species would be considered as "looser" i.e. reducing their habitat and 47% would be considered as "winner". By 2070–2099, there would be 64% of looser species and 36% of winner species.

By 2041–2060, 3/4 of the looser species are expected to qualify for the IUCN Red List. 20% of them are expected to become extinct and 20% are expected to become highly threatened. By 2070–2099, 90% of the looser species are expected to qualify for the IUCN Red List. 33% of them are expected to become extinct.

By the middle of the current century, all the species now expected to become extinct would be of low prevalence and encountered in the coldest areas of the Mediterranean Sea (Ben Rais Lasram *et al.*, 2010).

Four scenarios for species predicted to lose part of their geographic range can be distinguished (Ben Rais Lasram *et al.*, 2010): (i) a high probability of immediate extinction (e.g. *Corcyrogobius liechtensteini* and *Didogobius schlieweni*), (ii) a high probability of extinction by the end of the 21st century after severe climatic niche reduction (e.g. *Gobius geniporus* (see Fig. 1), (iii) severe habitat fragmentation (e.g. *Arnoglossus kessleri* (Fig. 1) and (iv) migration to the coldest areas, associated with habitat reduction (e.g. *Cyclothone pygmaea*).

Among the winner species, 77% are predicted to experience high range extensions, reaching 80% or even 100% increase. This is for example the case of *Solea aegyptiaca* (Fig. 1) that is currently distributed along the southern and the eastern sides of the Mediterranean (from Tunisia to Turkey) as well as the Adriatic Sea and the Gulf of Lion. By the middle of the century, it could reach the Aegean Sea, the Tyrrhenian Sea and the Catalan coasts. Its distribution area projected using its climatic niche is expected to extend by 88%. By the end of the century, this species would be distributed in the whole Mediterranean except the extreme west of the Alboran Sea and an enclave in the northern part of the Aegean Sea (Ben Rais Lasram *et al.*, 2010).

Sea water warming would lead to a total modification of endemic species assemblages: as a whole, 25% of the Mediterranean Sea is predicted to experience a total modification of endemic species assemblages by the end of the 21st century. At that point, global warming would be so marked that none of the endemic fish assemblages of the Mediterranean would be identical to those of the 1980s.

According to climate envelope models projections, the Gulf of Gabes (southern Tunisia) together with the Levantine Basin and the southern side of the eastern basin would undergo the highest turnover rate in species composition i.e. close to 100% (Ben Rais Lasram *et al.*, 2010). That is, all endemic species in those areas would disappear (by extinction or migration) and be replaced by others.

Tunisia and the Gulf of Gabes in particular are actually under scrutiny in a context of global change and provide an interesting case study. Indeed, Tunisia lies at the transition between the warm

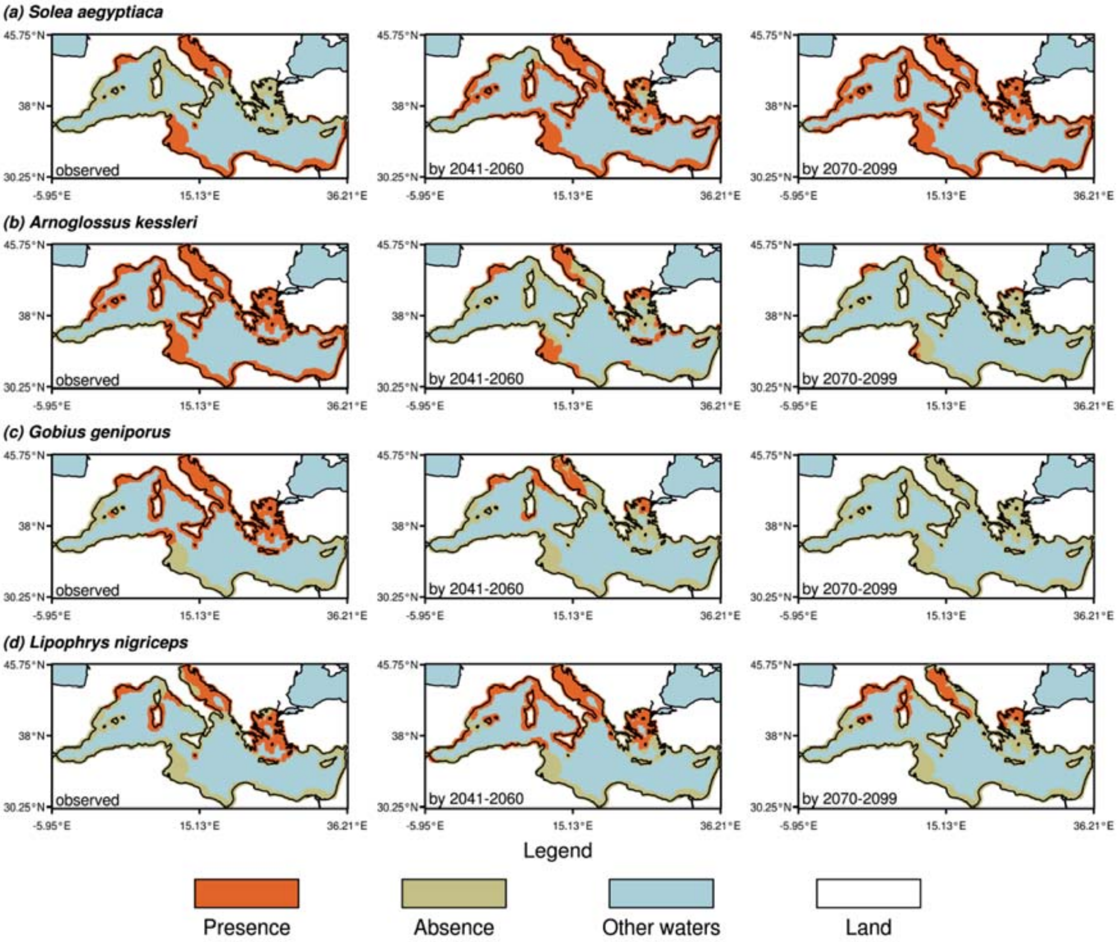

Fig. 1. Observed (1980s) and predicted (by 2040-2060; by 2070-2099) distribution areas of four endemic Mediterranean Sea fish species, and potential future thermal habitats projected with climate envelope models. The axes indicate degrees of latitude (X-axis) and longitude (Y-axis).

Levant basin and the cooler western part of the Mediterranean Sea and consequently exhibits both thermophilic and cold water species assemblages.

According to an updated inventory of the Tunisian ichthyofauna (Bradai *et al.*, 2004), 327 fish species inhabit the Tunisian coastal waters. The major part (86.24%) is of Atlantic origin, 7% are endemic species and nearly 2% are Lessepsian migrants. The latter are more frequent in the Gulf of Gabes where their frequency is increasing.

Considering the thermal affinities of the fish species present in Tunisia, 67% of them are temperate and thermophilic species and 14% are cold water species (Bradai *et al.*, 2004). In the Gulf of Gabes, we count nearly 73% of thermophilic species and 12% of cold water species.

It is now obvious that these assemblages are expected to undergo an intense reorganization due to species turnover induced by sea water warming.

Tunisian waters, as for the rest of the Mediterranean Sea, are experiencing the effects of global change: studies carried out on historical databases revealed positive trends in water temperature and salinity during the last century (Ben Mahmoud and Harzallah, 2009). The trends differ spatially: salinity increases in the southern Sicily Channel but decreases in the north; temperature increases particularly in the Atlantic water layer. These variations indicate a warming of the surface layers and a more active thermohaline circulation with more entries of Atlantic water at the surface and more exits of Mediterranean water at the intermediate layers (Ben Mahmoud and Harzallah, 2009).

The ecological consequences of global change consist in the arrival of exotic species favored by the changing abiotic conditions: *Trachypenaeus curvirostris* and *Metapenaeus monoceros* (Missaoui and Zaouali, 1995), *Pisodonophis semicinctus, Parexocoetus mento, Seriola fasciata* and *Pempheris vanicolensis* (Bradai *et al.*, 2004), *Fistularia commersonii* and *Parexocoetus mento* (Ben Souissi *et al.*, 2004), *Cheilopogon furcatus* (Ben Souissi *et al.*, 2005) etc. and recently *Lagocephalus sceleratus* (Jribi and Bradai, 2012).

The Gulf of Gabes seems to be the most affected Tunisian ecosystem by global change. Indeed, in this area overfishing, pollution and introduction of exotic species operate in synergy and affect directly the structure and composition of species communities.

The Gulf of Gabes covers a continental shelf area of 35 909 km2 and is the second largest ecosystem in the Mediterranean Sea (the Adriatic Sea being the largest). The 200 m isobath is reached at 250 km off the shoreline. The ecological originality of the Gulf of Gabes (high diversity, *Posidonia* meadows) and the accessibility (very shallow slope of the continental shelf, soft bottoms) are suitable for bottom trawling and have contributed to a considerable increase in the number of fishing fleets. The Gulf of Gabes has become the main area in which fishing activity in Tunisia is concentrated.

The high biodiversity of the Gulf of Gabes, favored by the *Posidonia* meadows, is threatened by three factors: unsustainable fishing, pollution and global change resulting in an increasing number of exotic species.

First, irresponsible fishing, and particularly bottom trawling, causes a progressive but systematic destruction of *Posidonia* meadows. The regression of the meadows that give the Gulf of Gabes its reputation, has been reported in the literature since 1925 (Le Danois, 1925). Trawling has led to bare bottoms in many areas of the Gulf and some studies estimate that the fishing effort exceeds the optimum by 33% (Missaoui *et al.*, 2001).

Second, the Gulf of Gabes undergoes severe problems of pollution especially from the phosphate industry. Discards of chemical complexes led to the accumulation of a thick black deposit on a completely azoic surface. The combined effect of pollution and overfishing has resulted in large changes in the Gulf of Gabes ecosystem. Large areas of *Posidonia* have disappeared, *Cymodocea nodosa* is scarce and *Caulerpa prolifera* has almost completely disappeared. Regression of the vegetation cover by 90% led to biological communities characterized by flora and fauna of degraded environments (Ben Mustapha *et al.*, 1999).

Third, the Gulf of Gabes is being invaded by alien species as a consequence of global change: several species, mainly Indo-Pacific, have emerged, such as the bivalve *Pinctada radiata* currently abundant (Bradai, 2000), the shrimps *Metapenaeus monoceros* and *Trachypenaeus curvirostris* that strongly compete with the native shrimp *Penaeus kerathurus* (Missaoui and Zaouali, 1995), the green alga *Caulerpa racemosa* (Ben Alaya, 1971) and the Brachyura *Eucrates crenata* that became very abundant (Zaouali, 1992). There are about twelve exotic fish species including *Siganus luridus, Siganus Rivilatus, Parexocoetus mento, Seriola fasciata* and *Pisodonophis semicinctus.*

Projections derived from climatic envelope models and carried on endemic species (Ben Rais Lasram *et al.*, 2010), revealed that the Gulf of Gabes would undergo the highest turnover rate in the Mediterranean Sea with the loss of some species and the appearance of some others. Among the looser species we can cite *Ophidion rochei* and *Raja polystigma* that are expected to undergo a severe reduction of their thermal habitat in the Gulf of Gabes by 2070–2099. Conversely, *Didogobius bentuvii* and *Panturichthys fowleri*, that are both present at the extremity of the Levantine Basin, are projected to extend their thermal habitat and to reach the Gulf of Gabes by the end of the century.

Currently, excepting the case of the Lessepsian shrimps *Metapenaeus monoceros* and *Trachypenaeus curvirostris* that strongly compete with the native shrimp *Penaeus kerathurus* and are now commonly commercialized but with lower prices that *P. kerathurus*, there is no evidence of competition nor extirpation of the Gulf of Gabes native species by exotic species. However, those species have to be under scrutiny because the biological consequences remain challenging to predict.

Endemic marine Mediterranean species are thus likely to undergo a biotic stress materialized by exotic species and an abiotic stress materialized by global warming. The former being favored by the latter, it is likely that both pressures add up and act in synergy leading to the increase of vulnerability of endemic species. This is even more critical in a highly impacted area such as the Gulf of Gabes where overfishing and pollution exacerbate the consequences of global change.

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Food for thought – A general framework for an ecosystem approach to fisheries in the Mediterranean Sea

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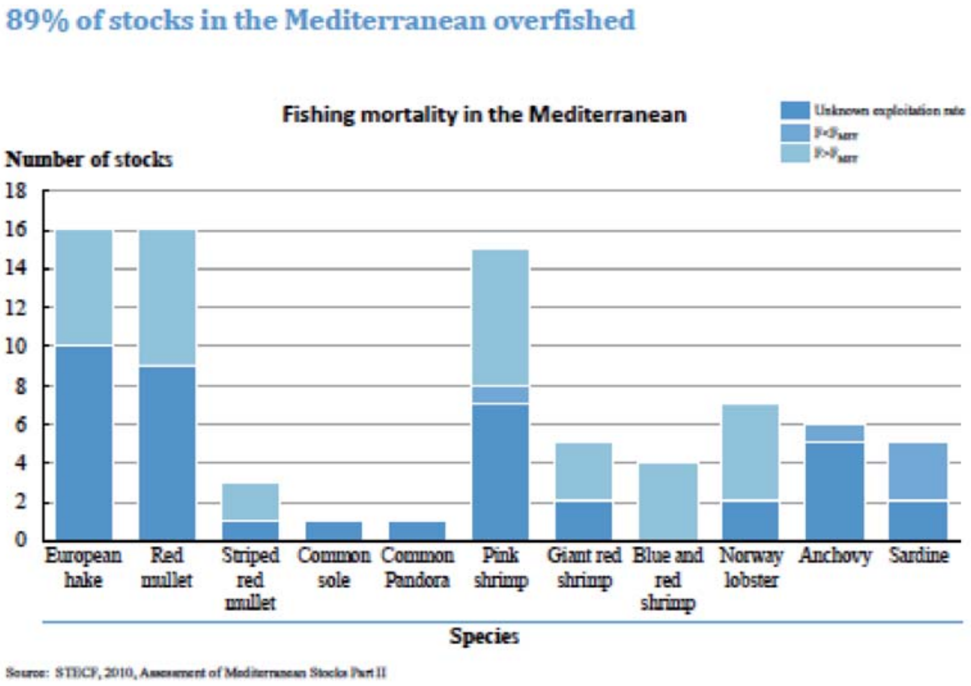
THE MEDITERRANEAN SEA IS OVEREXPLOITED AND BIODIVERSITY IS AT RISK

The Mediterranean Sea, is the largest and deepest enclosed sea, represents a hotspot for marine biodiversity. Currently it is known to host more than 17,000 described marine species and contributes an estimated 7% to the world's marine biodiversity, including high percentages of endemic species. This rich ecosystem has been altered in many ways throughout its history particularly through overexploitation and habitat loss which represent the main human drivers of historical changes. These pressures have grown exponentially and at present they constitute, together with well as extraction, pollution, eutrophication, the introduction of alien species, and recently, climate change, the most important threats (Coll *et al.*, 2011). Mediterranean fisheries produce today about one million tonnes of marine products with a decreasing trend of 15% during the last 25 years. In this global context managing marine resources in the Mediterranean represents a challenge as scientists need to improve the science-policy interface, using relevant assessments and integrating multidisciplinary knowledge, encompassing physics, ecology, biology and natural, social and economic sciences.

The long held misconception that marine biodiversity is inherently less susceptible to extinction risk than terrestrial species has been broadly demystified through widespread application of IUCN Red List Criteria in the Global Marine Species Assessment (http://sci.odu.edu/gmsa/index.html). Fisheries exploitation is, by far, the most serious extinction threat to marine biodiversity (McClenachan *et al.*, 2011). An astonishing 89% of Mediterranean fish stocks are overexploited (STECF, 2012, Fig. 1.), which contrasts with the global estimate of 30% of exploited marine fish stocks at the world level (SOFIA, 2012) although a recent study reveals that most stocks are also at risks (Costello *et al.*, 2012). The state of unassessed stocks in the Mediterranean Sea (CEA Report, 2011) shows that the mean biomass ratio is less than 0.6 (B/Bmsy) for the Mediterranean Sea and the Black Sea (Fig. 2).

Top predators like sharks, tuna, sword fish, marine turtles, marine birds, etc. play an essential role in marine ecosystems as they regulate the flow of energy through the food webs and control the population of species at lower trophic levels. Due mainly to overfishing, the population of these marine top predators has experienced a decline without precedent over the last decades. As a result, the survival of these species is under threat and a major concern for species conservation (see for example Figs 3 and 4). The steeped decline of these species can have unpredictable effects on marine ecosystems, leading to trophic cascades through the food webs which in turn can induce regime shifts (Sheffer *et al.*, 2005), and promote for example invasion by high turn-over species such as jellyfish. Meta analyses can help in identifying patterns at a global scale relevant for

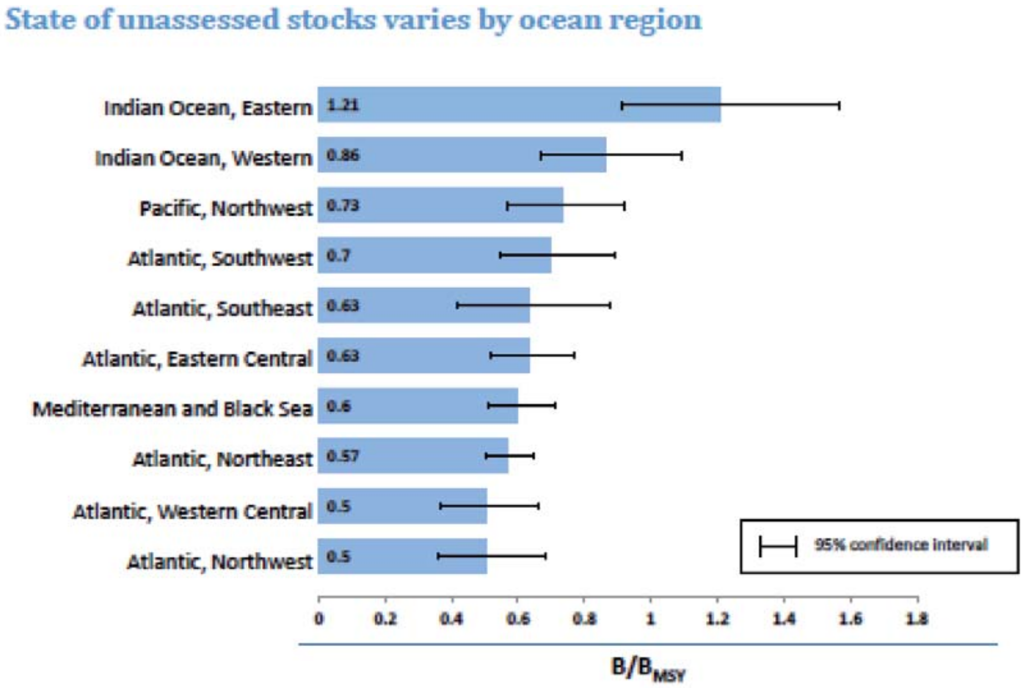


89% of stocks in the Mediterranean overfished

Fishing mortality in the Mediterranean

Source: STECF, 2010, Assessment of Mediterranean Stocks Part II

Figure 1. The Mediterranean resource are in decline and overexploited (89% overexploited - STECF Report on EU Fishing Fleet (2012).



State of unassessed stocks varies by ocean region

Figure 2. (CEA Report, 2011) the state of unassessed stocks in the Mediterranean Sea shows that the mean biomass ratio is less than 0.6 for the Mediterranean Sea and the Black Sea.

determining the form of key predator-prey relationships in marine ecosystems which is critical for understanding marine ecosystem dynamics. Using a comprehensive global database, it is possible to quantify for example the effect of fluctuations in food abundance on seabird breeding success and to identify threshold in prey (fish and krill, termed "forage fish") abundance below which seabirds experience consistently reduced and more variable productivity (Fig. 5).

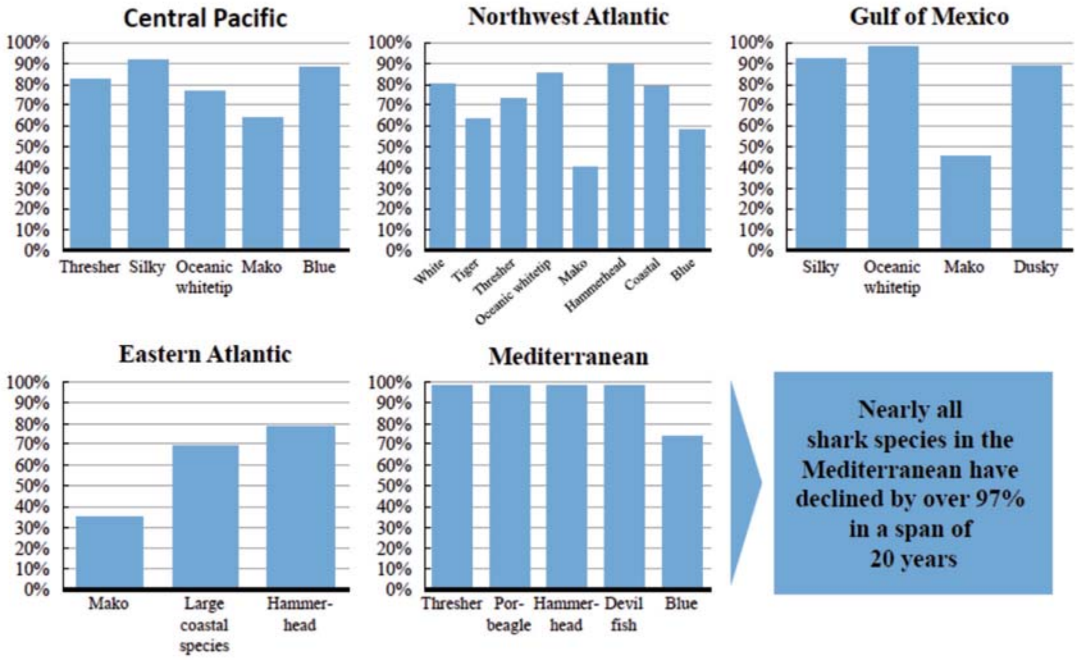


Figure 3. Shark populations continue to decline globally and catastrophycally in the Mediterranean where most sharks species have declined by 97% during the last two decades (Baum *et al.*, 2003; CEA Report, 2011).

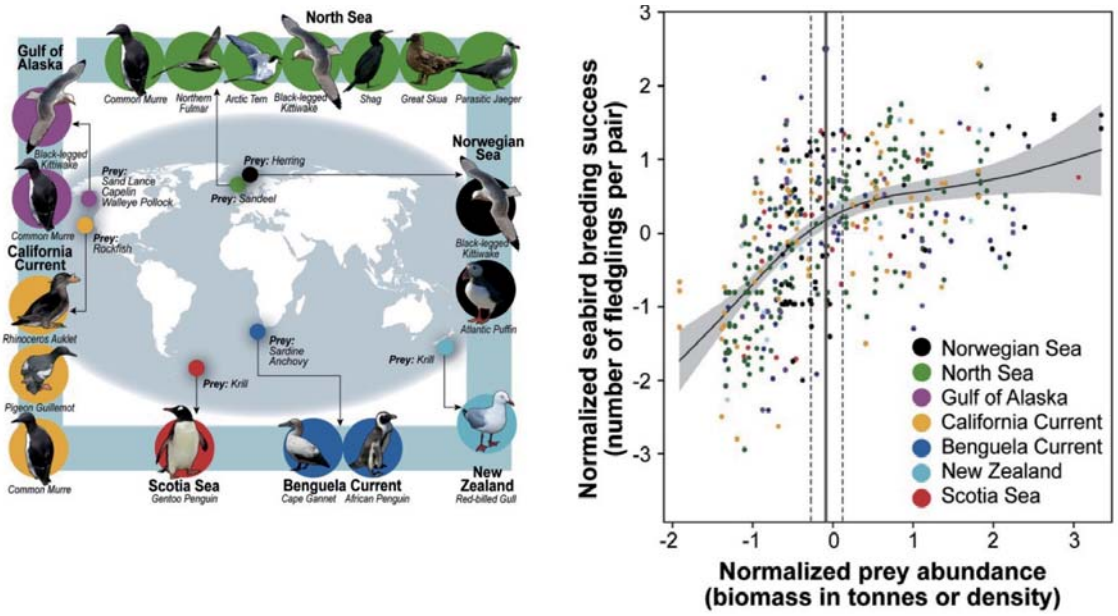


Figure 4. Relationship between breeding success and abundance of forage fish for 14 birds species in 7 marine ecosystems. The plot shows that bred threshold in prey (fish and krill, termed "forage fish") abundance below which seabirds experience consistently reduced and more variable productivity. The threshold approximated one-third of the maximum prey biomass observed in long-term studies. This provides an indicator of the minimal forage fish biomass needed to sustain seabird productivity over the long term (Cury *et al.*, 2011).

Despite the essential role played by top predators many gaps remain regarding their biology and ecology, their interactions with other species, and how marine ecosystems can be affected by the declining of their populations. Research is also needed to improve the knowledge on the migratory behaviour of these species which are not well understood, in order to establish appropriate management measures taking into account the regional dimension. In addition, the effects of climate change on the migration patterns, distribution, feeding behaviour, survival and reproduction of these species are still largely unknown.

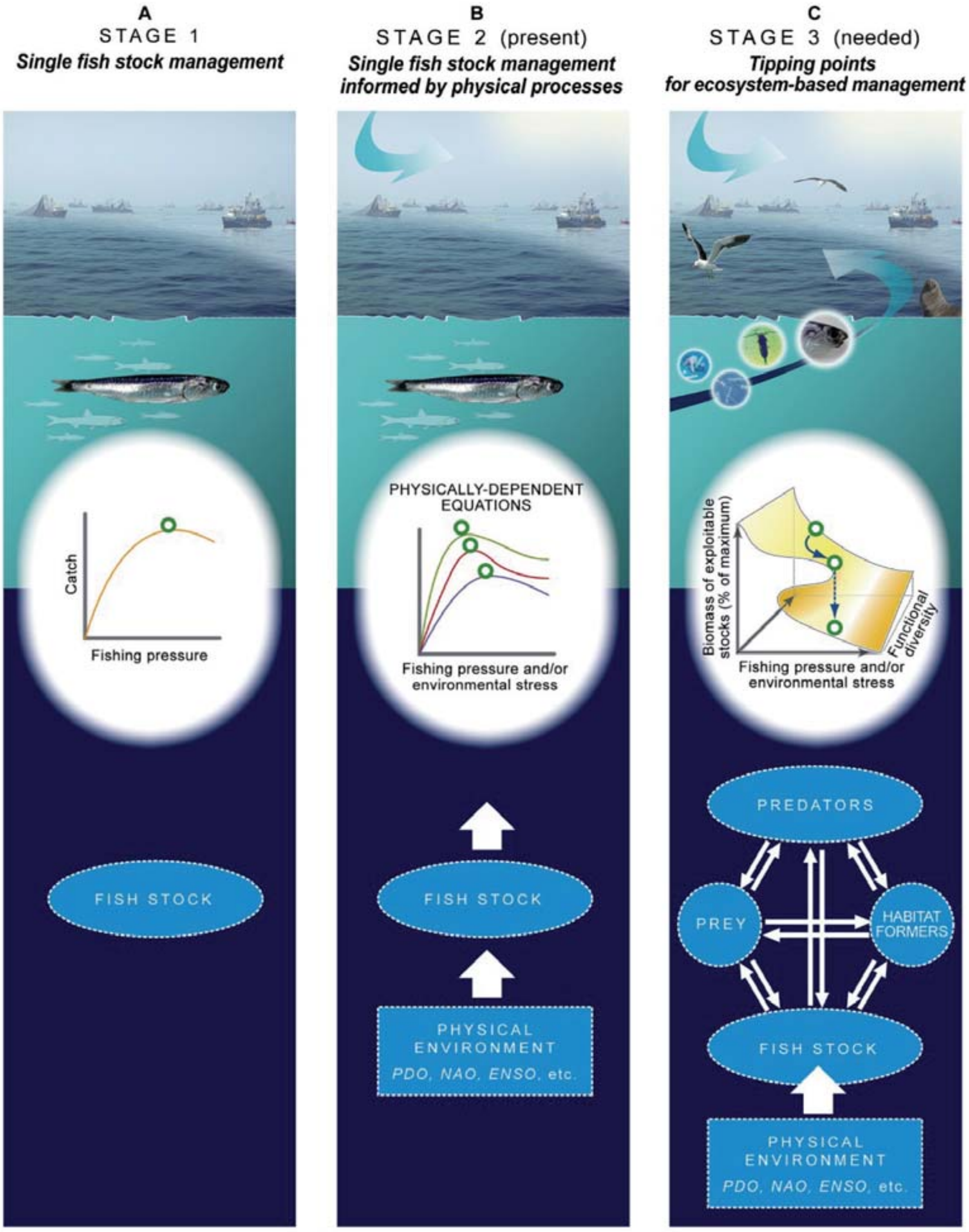


Figure 5. The paradigm shifts in fisheries management: past, present and future. Left panel (A) characterizes the early stages of conventional fishery science, in which stocks are managed as isolated entities towards a maximum sustainable yield (small circle). The middle panel (B) reflects the current state of affairs, in which bottom up forcing from physical oceanographic variation (e.g., PDO, NAO, and El Niño/La Niña events) modifies expected maximum (three small circles) sustainable yields. The right panel (C) portrays our view of how fishery science should be expanded to include direct and indirect species interactions along a diversity gradient and their consequences for population and community dynamics. Due to strongly nonlinear responses to increasing environmental stress and anthropogenic forcing, sudden phase shifts (shown in offset) can result especially at low species diversity.

TOWARDS IMPLEMENTATION OF THE ECOSYSTEM APPROACH TO FISHERIES

There is an urgent need to develop methodologies to efficiently manage human impacts on biodiversity and the services that ecosystems provide, in particular if we are to progress at all towards targets set during the 2002 Johannesburg World Summit, of restoring fish stocks to maximum sustainable yield by 2015. The Reykjavik Declaration of 2001, reinforced at the World Summit on Sustainable Development in Johannesburg in 2002, requires nations to base policy related to marine resource exploitation on an ecosystem approach. The Ecosystem Approach to Fisheries (EAF) aims to reconcile conservation and exploitation of renewable resources in an ecosystem context. Such a framework requires the integration of ecological analyses so as to provide the scientific basis for understanding human impacts on whole ecosystems.

Fisheries science diverged in the 1950s from its parent discipline of ecology as quantitative models of fisheries population dynamics were developed to estimate sustainable yields and control exploitation. A major revolution occurred with the recognition of how the physical environment affects larval transport, and survival (Hamilton *et al.*, 2008; Mullon *et al.*, 2002). In the meantime, aquatic ecology evolved toward trophodynamics (Curry *et al.*, 2005) and took a leap forward with models capturing the indirect repercussions of species interactions (Briand and McCauley, 1978; Wootton, 1994). These indirect effects contribute to feedback loops and the resultant complex dynamics and tipping points; it is around them that fisheries science and ecology need to coalesce (Fig. 5).

A global Marine Protected Area network is still in its infancy. In 2008 data collected by the World Conservation Monitoring Centre indicated that only 1.5% of global ocean area was under any form of protection. The same data show that around 7% of territorial seas (to 12 nautical miles) and around 3% of Exclusive Economic Zones (EEZs) are protected. In Areas Beyond National Jurisdiction (ABNJ) there has been negligible progress, with only 0.5% under any form of protected-area designation. The world's governments have, for more than a decade, recognised that more MPAs are needed if further loss of marine biodiversity is to be avoided and functional marine ecosystems are to be maintained. In a significant step forward, the 10th Conference of the Parties to the Convention on Biological Diversity (CBD) agreed to bring about effective protection of 10% of marine environments (both near-shore and off-shore) by 2020, focusing especially on areas of particular importance for biodiversity and ecosystem services.

Recently large investments in marine conservation have concentrated on protected areas and spatial management, both in the developed and developing countries, along with fisheries management, education, outreach and market-based incentives (CEA Report, 2011). They are playing an important role in marine conservation, but important gaps must be filled as the UN objectives have not be enreached. Furthermore fisheries management has not been considered a top priority for conservation by most countries. This transition should shift from national objective to regional focus, which means for the Mediterranean: (i) document and coordinate scientific initiatives, (ii) promote the sharing of scientific information and capabilities, (iii) promote data availability, integration, harmonization, and interoperability, (iv) promote training capabilities and capacity building of the scientific community and stakeholders, (v) establish mechanisms to disseminate knowledge, and communicate EAF benefits, and (vi) promote concrete regional scientific initiatives.

A series of regional and pan-European policies are relevant for the Mediterranean Sea including the Integrated Maritime Policy (IMP), the Marine Strategy Framework Directive (MSFD), the Water Framework Directive (WFD), the Common Fisheries Policy (CFP) and the Barcelona Convention and its Mediterranean Action Plan (UNEP-MAP). These policies have set a series of monitoring obligations to contracting parties but have also introduced new research needs in specific areas. This is especially the case for the recently implemented MSFD that calls the EU member states to implement the necessary measures in order to reach/ maintain Good Environmental Status (GES) of our seas. The long list of descriptors and indicators associated with GES are setting new research priorities to fill knowledge gaps and require new monitoring programs to be designed and implemented. Although the implementation of MSFD is a national obligation, MSFD is generally considered as an overarching driver and a major priority recognizing the important gaps that exist in southern European seas.

Climate change is affecting the biological, chemical and physical characteristics of the marine, atmospheric and watershed environments with significant impacts on human populations. Topics of immediate concern are coastal zone management, fisheries, invasive species and ocean acidification. Large programs to understand these problems are underway, including SESAME (European Commission) and MISTRALS (France), the EU programs Medsea (acidification MS & BS), VECTORS (invasive) and PEGASO (Integrated Coastal Zone Management MS & BS). There exist other regional Bodies or international programs that address the issues of the EAF in a more focused manner: European Commission (DG RTD, MARE, ENV, etc.), FAO (including Regional Projects e.g. ADRIAMED, COPEMED, EASTMED), as well as RFMOs (e.g., GFCM, ICCAT, EFARO) that are aimed at studying or implementing the EAF.

The Marine Strategy Framework Directive (MSFD, 2008/56/EC) is the environmental pillar of the IMP designed to achieve the full economic potential of oceans and seas in harmony with the marine environment. The MSFD was adopted in order to protect the marine environment across Europe more effectively. It aims to achieve GES of EU marine waters by 2020 and to safeguard the resource base upon which marine-related economic and social activities depend. EU Member States must progressively develop *"Marine Strategies (that) shall apply an ecosystem-based approach to the management of human activities, ensuring that the collective pressure of such activities is kept within levels compatible with the achievement of good environmental status (GES)…"*.

The Common Fisheries Policy (CFP) was set up in 1983 and underwent a significant review in 2002, which put a significant emphasis on the reduction of the environmental impact of fisheries. The overall objective of the CFP is to ensure economically, environmentally and socially sustainable use of fisheries resources. A further revision of the CFP (effective in 2013) will adapt it to the new challenges lying ahead for the fishery sector.

To integrate such initiatives into a Mediterranean global approach all aspects relevant to ecosystem services and the exploitation of marine resources could be viewed through the newly launched IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) that aims to incite the scientific community to build scenarios of biodiversity change.

While we cannot see the future, we can influence it by assigning desired objectives and exploring innovative solutions, particularly via the ecosystem approach to fisheries. However, responding to the challenge of the newly launched IPBES will require building a global scientific strategy.

Scientists will have to play a more visible role in bringing their work to public attention and into policy (Briand, 2012). Fisheries scientists have been communicating through target or limit reference points (e.g., using Maximum Sustainable Yield (MSY) or threshold limit fish biomass (BLim) using media such as maps, texts and figures. Communicating with scenarios constitutes a new challenge as a daunting amount of information needs to be conveyed to a large audience in a very limited time within the framework of the ecosystem approach to fisheries. A new strategy is required if we want to communicate scenarios to stakeholders. For this purpose we will need dedicated scenario laboratories, places where we can visualize, experiment and discuss facts, assumptions and options between stakeholders and envision our shared future and policy options regarding ecosystem services using scenarios (see Fig. 6). In this perspective we will have to adopt new communication tools such as 3D gaming engine to real-time visualization of scientific simulations (Briand and Giuliano, 2012) in order to make simulation more vivid and accepted by the stakeholders.

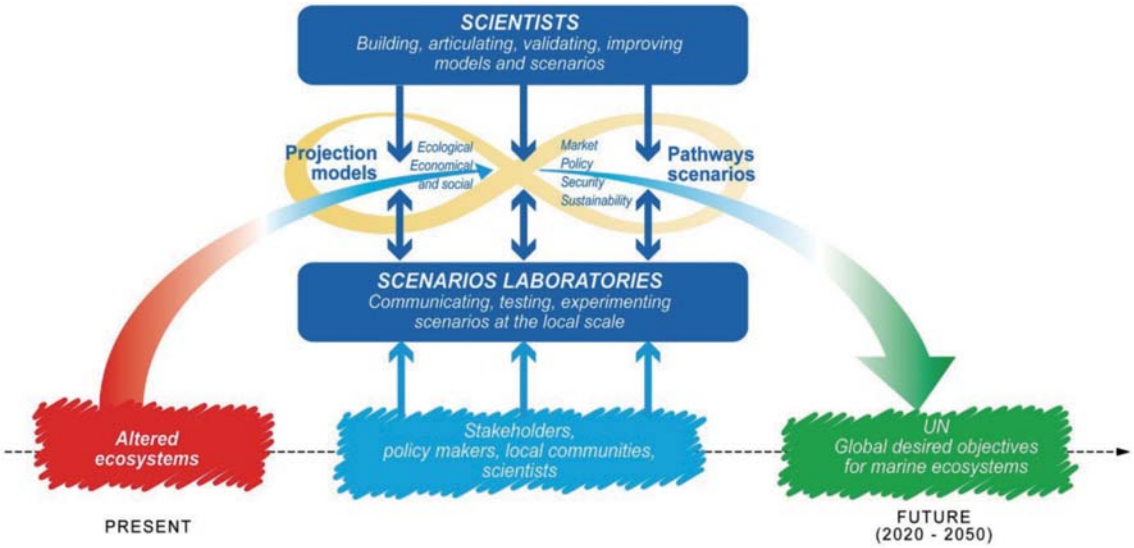


Figure 6. Consilience Scenario Laboratory (Cury and Reygondeau, 2013.)

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