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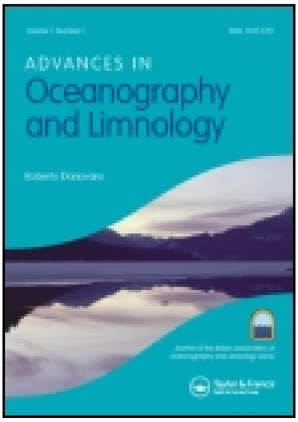

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The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context

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The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context

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High-level predators have been depleted in the oceans worldwide following centuries of selective fishing. There is widespread evidence that high-level predators' extirpation may trigger trophic cascades leading to the degradation of marine ecosystems. Restoration of large carnivores to former levels of abundance might lead to ecosystem recovery, but very few pristine ecosystems are left as baselines for comparison.

Marine protected areas (MPAs) can trigger initial rapid increases of high-level predator abundance and biomass. Nevertheless, long term protection is needed before the ecosystem's carrying capacity for large carnivores is approached and indirect effects on lower trophic levels are observed.

The Mediterranean is probably very far from its pristine condition, due to a long history of fishing. Today small to medium-sized consumers (e.g. sea breams) are the most abundant predators shaping coastal benthic communities, while historical reconstructions depict abundant populations of large piscivores and sharks inhabiting coastal areas. Mediterranean MPAs are following a promising trajectory of ecosystem recovery, as suggested by a strong gradient of fish biomass increase. Consistent monitoring methods to assess relative variations of high-level predators, together with food-web models aimed at disentangling the indirect effects of their recovery, could be useful tools to help set up appropriate management strategies of MPAs.

Keywords: high-level predator; top predator; trophic cascades; MPAs; ecosystem shift; overfishing; baseline; ecosystem recovery

1. Introduction

High-level predators, a category including top predators, are generally large-sized long-living animals like marine mammals, sharks and large teleosts that occupy the higher trophic levels in the food web. They are commonly characterized by late sexual maturity and their abundance, at adult stage, is usually not subject to predator control. Together these characteristics result in low resilience to demographic perturbation and high risk of extinction, conditions making them highly vulnerable to fishing [1]. In a number of regions worldwide, their almost complete extirpation from marine ecosystems is a direct consequence of fishing that has disproportionately targeted them for centuries [2,3]. Today we face a situation where almost no pristine marine ecosystems are left and where historical information on pre-exploitation abundance of high-level predators is very rare. In many places, high-level predators have been absent or rare for so long that scientists and managers have never realized how important they were in the ecosystem. In this con-

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text a clear understanding of their ecological role is limited by the fact that our observations are restricted to already altered ecosystems, affected by the decline and, in some cases, disappearance of top predators. Historical data from coastal ecosystems are more abundant and suggest that losses of large predatory fish and mammals were especially pronounced here and led to marked changes in coastal ecosystems structure and function [2]. In fact, the fauna of predators we have today in many coastal ecosystems is a 'ghost' [4] of what it was before human impacts. Such ecosystems nowadays are often controlled by medium-sized predators, although larger carnivores originally preying upon them likely controlled the trophic web in the past [5]. In terrestrial ecosystems, medium-sized predators have sometimes replaced top predators: i.e. coyotes are mesopredators where wolves have been reintroduced, while they have ascended to the role of apex predators where larger predators have been extirpated [6–8]. Due to this possible shift between mesopredators and apex predators, we will here use the term 'top predator' to qualify the highest level trophic category of predators.

Management of marine ecosystems should consider how they looked in the presence of top predators to be able to set meaningful conservation targets. The Mediterranean is an especially interesting area in this context. This sea has a history of thousands of years of exploitation. In fact, the first evidence of fishing in the shallow Mediterranean comes from prehistory, with the Mediterranean dusky grouper being among the target fishes fished for more than 10,000 years and the blue fin tuna, being an important part of Mediterranean culture for 12,000 years, for millennia exploited by many coastal artisanal fisheries [9]. Apparently first local fish depletions started during Roman times [10], due to rising human population and food demand. During medieval times, strong human population growth resulted in the depletion of fisheries in coastal waters [11]. In the late nineteenth century fishing capacity grew exponentially and in the twentieth century it expanded offshore and to deeper waters. Today most, if not all, of Mediterranean important stocks are overexploited and this sea is very far from the pristine condition depicted in antiquity.

Here we will analyse the reasons that stand for the largely accepted hypothesis that high-level predators have an important ecological role in shaping marine communities, as shown by empirical observations on the far reaching impacts caused by their depletion, which is especially heavy in coastal ecosystems. Subsequently, we will review the effects of Marine protected areas (MPAs) implementation, in terms of high-level predator recovery and their impact on food webs. We will specifically focus on the Mediterranean region, signed by the previous extinction of many top predators and by a general lack of historical data. As a conclusion we will try to answer the following questions: are high-level predators currently recovering in marine protected areas? What are the indirect consequences of such a recovery? Are increasing levels of these predators a good signal of increasing ecosystem health? We will finally suggest possible ways to overcome the general lack of data and knowledge on high-level predators.

2. The importance of high-level predators

2.1 Trophic cascades and pristine ecosystems

In a seminal paper published in 1960, Hairston, Smith and Slobodkin proposed that predators have the potential to maintain global plant biomass by limiting the densities of herbivores ('The world is green' hypothesis) [12]. For the first time, it was stated that predators at the upper trophic levels might control the abundance of consumers and primary producers at lower trophic levels.

Following the 'The world is green' revolution, the idea that ecosystems might be shaped by apex predators stimulated several avenues of research.

In 1966 Paine stated the hypothesis that 'local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites of one species'. Paine experimentally demonstrated that the removal of the apex sea star predator *Pisaster ochraceus* from the rocky intertidal (Pacific Coast of North America) resulted in a pronounced decrease in diversity, with local extinctions of certain benthic invertebrates and algae due to outcompetition from more efficient space occupiers (mussels) [13]. This was one of the first experimental evidences about the role of a keystone predator and showed that in communities controlled by the natural predation of a top predator, the sea star, prey abundances were controlled and local diversity was higher.

The strength of carnivore effects generally depends on the strength of the link between the predator and its prey [14] and often relates to the predator's body size [15]. In a system of strongly interacting links, large top predators frequently initiate the top-down control leading to indirect effects on food webs (i.e. trophic cascades) [16].

Clearly, experimental demonstration is logistically impractical for large animals. What we observe today in marine systems is a situation of generalized absence of large top predators, which have long been reduced or extirpated from much of the world [2,17,18] and whose depletion has triggered trophic cascades that sometimes led to dramatic ecosystem shifts. Trophic cascades are generally a signature of the vast and growing human impact on natural systems and since the 1960s they have been demonstrated in a wide variety of systems, as witnessed by the number of reviews written on the subject [18–22].

A review from the end of the 1990s [19] provided evidence that trophic cascades were no longer limited to sole simple systems like lakes, streams and intertidal zones, as previously reported [23]. Discoveries of trophic cascades were reported from previously unexpected systems, such as the open ocean, tropical forests, fields, and soils. The amplitude of such phenomenon was assessed in several benthic marine ecosystems [20], showing that trophic cascades range from Mediterranean rocky sublittoral, kelp forests and rocky subtidal to coral reefs, rocky intertidal and soft bottoms. A comparison of six different ecosystems, demonstrated that trophic cascades were strongest in lentic and marine benthos and weakest in marine plankton and terrestrial food webs [21]. Evidence of oceanic top-down control from large high trophic level piscivores was also found [22]. Substantial marine mammal, sharks and large piscivorous fish depletions led to mesopredator and invertebrate predator increases and in some cases to trophic cascades negatively impacting commercial species. A more recent empirical study on top predators [18] revealed the unanticipated impacts of trophic cascades on processes as diverse as the dynamics of disease, wildfire, carbon sequestration, invasive species, and biogeochemical cycles defining the loss of these animals as humankind's most pervasive influence on nature.

When fishery data or ecologists' observations are available from a time when top predators were still present, the far reaching impacts of high-level marine carnivore depletion on the ecosystem appear clear.

One of the most well studied examples of such phenomena comes from the Aleutian Islands, where variations in sea otter abundances due to overfishing and subsequent protection have been responsible for dramatic variations of sea urchin population density. These changes have determined the alternation between the natural kelp forest systems and the impoverished condition of overgrazed rocky reefs. Moreover, diet switching of killer whales in this area and subsequent increased predation on sea otters has demised sea urchins from otter predation ultimately causing the destruction of kelp forests [24,25].

The depletion of cod (*Gadus morhua*) followed by the shifting of the fishery to lower trophic levels (fishing down the food web [26]) caused a transition towards a kelp forests ecosystem that superficially looked like its initial state, but *de facto* was very different [5]. The ecological extinction of cod in Canadian coastal zones led to dramatic increases in sea urchin populations, which overgrazed kelp forests leaving widespread barrens [27]. The subsequent shift of the fisheries towards sea urchins allowed kelp forests to recover [28]. The combination of abundant kelp without high-level predators was ideal for a population increase of the predatory crab *Cancer borealis* [29]. Today this mesopredator crab is the dominant species of the ecosystem and is only limited by the availability of nursery habitats (bottom-up control), as opposed to predation on adults (top-down control) [5].

Sharks are one of the largest predators in the oceans, generally foraging on large areas. Today they are still subject to catch and mortality rates that are far exceeding the estimated rebound rates for many populations, causing their worldwide decline and the consequently relevant ecological consequences [30,31]. In some cases (New England, South Africa) the dramatic depletion of large sharks has resulted in the proliferation of smaller elasmobranchs, of which large sharks were the sole predators, and the decline of bony fish at lower levels in the food web [22].

The diversity of species within each trophic level is a type of insurance against the disruption of the ecological functions that species assemblages perform [32]. A long history of fishing down the food web has left Caribbean coral reefs with low species diversity and few functional players at each trophic level (low functional redundancy) [21]. Predators such as sharks, large groupers and snappers have been extirpated from many reefs and many herbivorous fish have been removed by selective fishing. Thanks to the reduction in population density and the size of its predators and competitors, the sea urchin *Diadema antillarum* was left as the primary herbivore in this system. The very high abundance of *Diadema* favoured the explosion of a disease that induced mass mortality of urchins in the 1980s, with resulting uncontrolled macroalgal growth and overcompetition on hard corals. This was one of the world's most rapid and widespread shifts in community state ever documented [5,33]. This shift was probably possible because of the historical overfishing and consequently reduced low functional redundancy of Caribbean reef communities, a condition that negatively affected the resilience of this ecosystem to catastrophic and unpredictable events [34,35].

In many areas only medium–upper trophic level predators are left to control the ecosystem, since their original predators have long been depleted. These are today the main fishing target and are subject to strong fishing pressures. In Kenyan coral reefs, the main keystone species we can identify today is the triggerfish (*Balistapus undulates),* the single most important predator of sea urchins. Where this fish is overfished, sea urchin densities largely increase and turf filamentous algae overgrow corals bioeroded by the sea urchins' grazing activity. Sea urchins can outcompete important grazer fish such as parrotfishes and hard corals cover decreases sharply [36–39].

Deleterious effects of sea urchin predator depletion have been observed also in the Canary Islands, where it has been demonstrated that losses in the diversity of predatory fish species lead to a loss of functional roles and cascading effects that constrain ecosystem processes, leading to the spread of barren grounds [40].

Although the last mentioned species are not top predators, examples of their effects on the ecosystem need to be mentioned in order to imagine the role that previously abundant and larger top predators probably had. In fact, if removing a few species of small scale fishes can change the underwater landscape so dramatically, it is unavoidable to ask oneself what were the consequences of removing large predators from such ecosystems [41] and how these looked in their presence.

There are very few examples left in the world of pristine ecosystems but their observation has provided fundamental information on the shape of an ecosystem in the presence of top predators.

The observation of Shark Bay, Australia, a remote subtropical location characterized by healthy sea grass communities and large population sizes of many large-bodied taxa [42], released important information on the role of tiger sharks as top predators. It was demonstrated that tiger sharks have widespread risk effects on both large-bodied herbivores and mesopredators (sea turtles, dolphins, dugongs, pied cormorants). Behaviour-mediated cascades leading to effects on the micro-habitats of the area have been supposed. In fact risk-induced heavy grazing by large herbivores led to reduced seagrass quality in habitats of lower incidence of tiger sharks, and increased quality in areas of higher shark abundance.

Recent studies revealed the structure of two pristine ecosystems, the Palmyra and Kingman atolls in the Line Islands (central Pacific) and the North Western Hawaiian Islands [43–46]. At both locations large high-level predators (specifically large piscivorous snappers, groupers, carangids and sharks) account for 55% to 85% of total fish biomass, with sharks accounting for 57% and 74% of total piscivore biomass in the Line Islands. Despite enhanced predation, high biomass of herbivores is also supported by the coral reefs, together with higher coral cover when compared to nearby fished islands of the same archipelago [46].

The Palmyra and Kingman atolls and the North Western Hawaiian Islands ecosystems have been described as characterized by an inverted trophic pyramid with most fish biomass at top levels, a structure that, due to historical overfishing of our oceans, had never been observed before by ecologists. Even if the existence of inverted pyramids has recently been questioned due to size-based constraints [47], it is undeniable that these pristine ecosystems set new baselines for evaluating present and historical human impacts and provide new targets for MPA conservation efforts.

2.2 High-level predators in the Mediterranean: historical reconstruction and degradation

The actual state of the Mediterranean is characterized by a paucity of high-level predator species both in richness and abundance and with medium-sized fish like sea breams left alone to control ecosystem shape. In fact the Mediterranean harbours a classical example of a trophic cascade controlled by a medium-sized fish [48]. Here the rocky sublittoral is characterized by the shift between a developed community with high fish and macroalgal biomass (e.g. *Cystoseira* forests, the Mediterranean ‘kelp’) and an overgrazed community with high abundance of sea urchins and low algal biomass (e.g. encrusting coralline algae and barren grounds). It has been largely demonstrated that overfishing of sea breams (*Diplodus* spp.), the most effective sea urchin predators in the Mediterranean, led in many areas to large increases in sea urchin population densities with consequent algal overgrazing and shift to low diversity coralline barrens [49,50].

Our understanding of Mediterranean food webs is actually based on a mix of unnatural, simplified communities, dominated by small species, where megafauna has been virtually eliminated by overfishing. [2,17,41]. This impoverished state is supposedly very far from the pristine conditions.

In fact, the Mediterranean has not been pristine since long before the onset of industrial fishing, but it is signed by a millenary history of exploitation, thus it is very difficult to evaluate the current state of this sea. Historical reconstructions have proved to be a useful strategy to fill this gap for many ecosystems, as already reviewed by several authors [51,52], but they are still scarce in the Mediterranean.

Archaeozoological reconstructions based on the study of fish bone remains (i.e. osteometry) allowed investigation of the history of fishing in times preceding the advent of writing. The data have revealed how Mediterranean shallow waters were once dominated by large sized piscivores which attained much bigger sizes than nowadays [53]. Desse and Desse-Berset proposed that these observations allow us to chronologically set the beginning of overexploitation [53].

The analysis of a large amount of fish bones recovered from a Neolithic coastal site of Cap Andréas Kastros, Cyprus, revealed evidences of early exploitation of pristine populations. Here selective fishing conducted from the coast was directed to large specimens of tunas and groupers [54]. Similarly, other Neolithic coastal Mediterranean sites revealed large specimens, attaining sizes that are not comparable with the mediocre dimensions of fish captured by fishermen today [53]. Fish remains from a Spanish cave revealed how fish fauna diversity and size decreased over the last 12,000 years [55]. Osteometry studies also revealed the presence of almost locally extinct species, such as the sturgeon (*Acipenser sturio*), and some elasmobranch species that appear to have been very abundant in coastal waters, contrary to the current situation.

Until the end of the Mesolithic and during Neolithic eras the groupers were very abundant in the coastal systems between the 35th and 40th parallel, accounting for 30–80% of the examined bony remains. Sites in Spain, Tunisia, Corse, Cyprus, Sicily and other Italian sites revealed the presence of healthy populations of *Epinephelus* spp., with all size ranges represented [56].

Anecdotal research has also led to very interesting discoveries on this topic. A survey of ancient Greek, Etruscan and Roman mosaics and paintings depicted large groupers often reaching the size of a man, being caught at the water surface by fishermen using poles or harpoons from boats, a technique that would yield no grouper catch today [57]. As illustrated in ancient frescoes many Mediterranean top predators (e.g. dolphinfish *Coryphaena hippurus*) may have been all actively fished in antiquity [51].

An especially striking implication of these studies is that not only in ancient times much larger individuals were commonly fished, but that their abundance in coastal waters was high, allowing humans to fish them directly from land [57] or from little boats [57]. Current groupers' bathymetric distribution shows well how populations actively respond to human exploitations. Largest individuals of this species indeed find refuge at depths that exceed the diving limit of most of the recreational spearfishermen [53,58,59].

A recent study coupling historical reconstruction and modelling delivered a detailed account of successive waves of fish depletions in the Adriatic sea and shows well the trajectory of degradation undergone by the Mediterranean ecosystem [10]. Marine mammals at the top of the food web were largely common in antiquity and have been depleted or are very rare today. The common dolphin (*Delphinus delphis*), bottlenose dolphins and the monk seal were hunted in classical Greek, Roman and medieval times and are today ecologically extinct in almost all the Mediterranean Sea.

Predilection for tuna, sharks, rays, sturgeons, common bass, sea bream and hake on Roman and Greek tables led to a large increase in their exploitation. Bluefin tuna fishery was coastal, subsistence and small scale for millennia. Industrial overexploitation probably started around 1950 with open water purse seining substituting coastal trap fisheries. Today the Atlantic-Mediterranean bluefin tuna stock is considered overfished. Similar fate touched the swordfish and the demersal high-level predator *Merluccius merluccius*. Common dentex (*Dentex dentex*) and common Pandora (*Pagellus erythrinus*) are today considered depleted and the dusky grouper (*Epinephelus marginatus*) may be locally extinct [10]. Lotze's results show that large predators and consumers >1 m in length were reduced to 11% of former abundance, a far more drastic reduction than smaller macrofauna (47%), especially in the last century.

As a result, a process of trophic downgrading [18] was observed in the Adriatic [10], with diversity shifting towards smaller, lower trophic level species. Increased exploitation and functional extinctions have altered and largely simplified food webs by changing the proportions of top predators, intermediate consumers and basal species.

Sharks, rays and chimaeras, are by far the most endangered group of marine fish in the Mediterranean Sea, with 31 species (40% of all) critically endangered, endangered or vulnerable [60]. Another detailed historical reconstruction concerned large predatory sharks in the Northwestern Mediterranean Sea, using a diverse set of historical records dating back to the early nineteenth and twentieth centuries [61]. Records from the 1920s–1930s showed that the Mediterranean Sea sustained abundant populations of large sharks, regularly targeted by many coastal fisheries. The analysed species, mackerel sharks (*I. oxyrinchus* and *Lamna nasus*), requiem shark (*Prionace glauca*), hammerhead shark (*Sphyrna zygaena*), and thresher shark (*Alopias vulpinus*), showed rates of decline up to 99.99%, levels at which they can be considered functionally extinct in coastal and pelagic waters of the Northwestern Mediterranean Sea. Trends of biomass data also showed a significant reduction in mean size over time, which is the lowest in the world [62].

In addition to large predatory sharks and bony fishes, other top predators like cetaceans and the monk seal underwent extreme declines due to a variety of human impacts [63,64].

A concluding remark could be that wherever high-level predators have been extirpated, ecosystems have consequently become degraded and simplified [65]. It is then plausible to assume that a return of high-level carnivores to a system will allow degraded systems to recover [16]. A tempting question is whether conservation of these predators could restore biodiversity and ecological functioning [16]. The science of marine reserves can give insights on this potential.

3. Recovery of high-level predators and biodiversity within marine protected areas

3.1 Data from the world

Several studies have demonstrated that marine reserves are an effective tool for the recovery of large piscivorous fish and upper trophic levels (direct effects), but have also shown a large variability of effects in terms of triggered trophic cascades (indirect effects). In fact, while in some temperate ecosystems it was possible to demonstrate that recovery of high-level predators (sea otters, snappers, spiny lobster, sea bream) can lead to the re-establishment of lost trophic interactions (e.g. sea urchins and macroalgae) [66,67], in more diverse ecosystems like coral reefs a more variable response is observed, depending on conditions such as duration of protection, taxonomic resolution of the study (species or functional group) and possible compensation effects due to functional redundancy [67–76].

Recent meta-analytical studies give a useful global overview of marine reserve protection effects in terms of recovery of upper trophic levels and trophic changes.

A global meta-analysis based on data from 124 reserves demonstrated that protection yielded significant average increases of density, biomass, average organism size and species richness of the communities within reserves [77]. Differential responses were observed among taxonomic groups, with large fish and invertebrates targeted by fishing showing significant increases in density and biomass overall, while algal cover increased in temperate reserves and decreased in tropical reefs, due to the recovery of exploited large herbivores.

Through the analysis of long term time series of ecological data in and out of marine reserves from several regions, it was demonstrated that positive effects on target predatory fish and lobsters occurred rapidly after reserve establishment but continued to increase, in some cases up to 25–40 years after protection (respectively Serranide and Lutjaniae in the Apo islands and triggerfish in Kenyan reserves) [78]. This analysis showed that the ecosystems were still generally far away from their carrying capacity in terms of high-level predators. Large herbivorous fish showed decadal increases in abundance too. Indirect effects through trophic cascades were common especially in terms of sea urchin reductions, but showed conspicuous time lags (average 13 years after protection) with respect to direct effects, probably due to behavioural mechanisms of predation risk reduction [78].

Similar conclusions on the magnitude and timing of protection effects were drawn from a meta-analysis of data from several temperate and tropical locations [79]. The authors observed clear trophic changes in protected ecosystems due to a time lasting build-up of biomass and abundance of upper trophic levels. Indirect negative effects were also evident for low mobility, small sized, and non-target fish species.

Other meta-analytical studies revealed that commercial species including many top predatory fish were observed to increase in density in many southern Europe MPAs [80,81]. Response of commercial exploited fishes to protection depended on species maximum body size, with large species showing the strongest increase in MPAs. Moreover the response of large species increased with time of protection. Commercial exploited fish with a benthic habitat responded positively to protection, while exploited fish with a bentho-pelagic habitat did not show a demonstrable response to protection. For non-commercial unexploited fish with a benthic habitat, densities were higher inside the reserve, probably because positive effects in habitat changes were more important than possible negative trophic cascade effects [80,81]. On the other hand, densities were higher outside the reserve for bentho-pelagic non-exploited species, suggesting possible trophic cascade effects due to predator increases.

A crucial question is whether MPAs are able to protect and restore species performing key ecological functions, but remarkably few studies have evaluated functional recovery after habitat degradation [82]. An interesting study in this regard reported that recovery of species richness and diversity in marine reserves coincided with increases in functional richness and diversity of fish assemblages [83]. Species recovery in reserves resulted in increased representation across different functional categories, particularly key groups like large carnivores and herbivores.

Thus reserves reveal initial trajectories towards recovery, but if compared with the few studied pristine ecosystems, it appears clear that the levels of piscivore biomass observed in recent marine reserves across the world are well below what the ecosystems could sustain. Moreover, for indirect changes to occur in marine reserves an absolute increase in abundance, mean size or biomass of target species, i.e. a restoration or build up to some (unknown) former level, is necessary [78,84]. Management of marine reserves should thus acknowledge that the potential for recovery of ecosystem functioning through protection is high, but will likely require long time frames [76,78,84]. In this context long-term monitoring is necessary and needs to be carried out for long enough lapses of time to have the chance to detect indirect effects. Special attention should be paid to variations in high-level predator biomass, a variable that can yield useful information on the state of recovery of a system following protection.

3.2 Mediterranean marine protected areas

Mediterranean MPAs, when well enforced [85], have shown to be very effective in leading to increases in the biomass and diversity of large piscivorous and invertebrate feeding fish, especially for serranids, sciaenids, sparids, and the larger labrids [50,58,84, 86–96], as also reviewed in [97].

Due to Mediterranean food web complexity the indirect effects of predator recovery are often masked by many factors, such as local conditions of oceanography, habitat topography and complexity (presence of refuges for prey species) and intensity of fishing outside the reserve. As in the rest of world, moreover, indirect effects can occur with considerable time lags with respect to direct effects [98].

Variable results have been drawn from the observation of indirect protection effects. In the Scandola Marine Reserve lower abundance and species richness of macrozoobenthos were observed [99] where predators attained higher abundance compared to nearby unprotected sites [88]. At the Ustica Marine Reserve, increases in piscivores (groupers) coincided with a decrease of small size microcarnivorous fish [58,100] and a seasonal increase of abundance and species richness of polychaetes and gasteropods [101,102]. Even with regard to the strong trophic interaction sea breams – sea urchin – algae [82], somewhat contradictory results have resulted on the potential for recovery of algal beds in MPAs through sea bream protection [49,92,98]. In fact, densities of fish need to reach a critical threshold in order to reduce sea urchins and drive the transition [50]. It has been demonstrated that when a protected area has the proper physical and biological characteristics (appropriate habitat for sea breams, as well as dimension and duration of protection encompassing their mobility and life cycle) to trigger changes at population and/or community levels, it allows the recovery of the predatory sea bream population, and the re-establishment of predatory control upon sea urchins, as happened in the Torre Guaceto MPA [92]. In the protected zone of Torre Guaceto, moreover, coralline barrens were less extended whereas turf forming and erect-branched algae showed an opposite pattern.

Due to the absence of pristine sites left in the Mediterranean and the few quantitative historical data to set a baseline against which to compare the health of current ecosystems and set precise conservation targets, comparisons among marine protected areas of different age, or between MPAs and fished sites (space for time substitutions) have shown to be useful in setting some reference points.

A recent large-scale study covering several MPAs and fished sites across the Mediterranean revealed a trajectory of degradation and recovery, with high-level predator biomass being significantly larger at protected than at non protected sites [96]. A gradient of 31-fold range increase in fish biomass was observed, reaching a maximum of 115-fold. This is the largest fish biomass gradient ever reported for reef fish assemblages and is probably indicative of the large impact of historical and current fishing pressure in the Mediterranean [96]. Continuous increase of high-level predators (particularly groupers) at the Medes islands, where they reached 49% of fish biomass after 27 years of protection, show that the potential for recovery in Mediterranean MPAs is comparable to other parts of the world and that aiming at achieving fish biomass values similar to those observed in the pristine tropical systems is possible. The authors finally suggest how the marine reserves with highest fish biomass are a useful current baseline against which managers can compare recovery trends for fish assemblages in rocky habitats across the Mediterranean. No clear pattern in the structure of benthic community was associated with the gradient on fish biomass, but three alternative community states were revealed in the trajectory of recovery: large fish biomass and reef dominated by non-canopy algae, lower fish biomass but abundant algal canopies and suspension feeders, and low fish biomass and extensive barrens.

The functional approach is still rare in the Mediterranean. Spanish marine protected areas were shown to support higher functional diversity than adjacent unprotected sites, due to a difference in the trophic structure rather than in species diversity [103]. High-level predators contributed the most to the dissimilarity between protected and unprotected sites. Coupling a functional approach with food web modelling it was also found that protected areas support higher trophic levels and are characterized by more complex food webs than exploited areas [104]. Finally it was demonstrated that the Lavezzi Islands Reserve significantly protects functional originality ('original' species are species that support unique and essential processes) and diversity, with the most original species being the large predator *Seriola dumerili* [105]. Protection of these species is an insurance against functional diversity erosion and a prerequisite to sustain coastal goods and services derived from ecosystem functioning [81,105].

4. Food web modelling in the Mediterranean

The complexity of species interactions in Mediterranean ecosystems together with the long history of exploitation and the variety and intensity of anthropogenic stressors (fishing, pollution, aquaculture, etc.) that differentially impact them, has prompted the need for a holistic approach to the comprehension of this ecosystem and the management of its marine resources. Thus, in the context of an ecosystem-based management of marine resources [106,107], food web modelling, already largely applied across the world especially through the software Ecopath with Ecosym [108–110], has gained growing recognition also in the Mediterranean. As already recently reviewed [110], food web modelling in the Mediterranean has allowed the unification of a large amount of sparse ecological information in order to identify keystone species and disentangle species interactions in different ecosystems, as well as quantify structural and functional ecosystem traits, assess the impacts of human activities and analyse management options for marine resources. While the majority of models in the Mediterranean have described fished ecosystems to assess fishing impact, models applied to marine protected areas are scarce, yet they delivered interesting results. The management of the Port Cros MPA in France was shown to be succeeding in protecting top trophic level groups, and the model released interesting information on dusky grouper export from the MPA [111]. A model built on the Bonifacio Strait natural reserve of Corsica, analysed high-level predator sensitivity to increased artisanal and recreational fishing effort and examined management options for recreational fisheries [112]. Ecosystem effects of protection were analysed by comparing the Miramare Reserve in the Adriatic with an industrially exploited area, revealing higher mean trophic level of the community, higher food web complexity, and higher fish/invertebrates and pelagic/demersal ratios in the MPA [104].

A meta-analysis conducted on results from 39 Ecopath models from the Mediterranean allowed the determination of the main keystone species or functional group from different Mediterranean ecosystems. High-level predators such as marine mammals, seabirds and large fishes ranked high in several models and a higher proportion of keystone groups appeared in non-fished or slightly fished ecosystems with respect to exploited ecosystems [110].

Trophic modelling coupled with historical data allowed assessment of the structural degradation of two food webs in the Mediterranean (the North-Central Adriatic and the South Catalan Sea) from the 1970s to the 1990s, largely consequent to top predator depletion. Clear reductions in the mean and maximum trophic level of the community, decreasing fraction and percentage biomass of top predators, together with reductions in indexes of food web complexity were a clear sign of the degradation due to the overexploitation of higher trophic levels and to food web simplification. The Mediterranean resulted more degraded and less robust to species loss than other non-Mediterranean systems [113].

A previously mentioned study that interestingly analysed palaeontological, archaeological, fisheries and ecological data through food web modelling, delivered dramatic results on the historical degradation of the Adriatic ecosystem [10] and through simulations of species losses showed that today's ecosystems are probably less robust to species extinctions than in the past.

5. Conclusions

Similarly to what happened in terrestrial ecosystems [16,18], we are nowadays witnessing the far reaching impacts of high-level predator depletion in marine ecosystems, impacts that are far more striking when ecological observations are available from a time previous to predator depletion. In these cases we have seen how extirpation of predators may cause prominent ecosystem shifts. Kelp forests were replaced by barren grounds in the Aleutian Islands, and corals were outcompeted by macroalgae on coral reefs, with consequent reductions in species and functional diversity. Moreover, on long time scales, superficially less evident but not less dramatic changes occurred in some ecosystems, like the shift towards the poorly diverse and macroinvertebrate-dominated kelp forests of Canada coastal zones.

The few pristine ecosystems existing in the world show an ecosystem shape with surprisingly high biomass levels at the top of the trophic pyramid, setting new baselines and targets for MPA management.

Nevertheless, for many ecosystems, information on their state prior to the beginning of exploitation does not exist. Most of our knowledge on the state of Mediterranean ecosystems originates from field studies in the last 30 years [96]. At this time, when the first marine protected areas were created (Port Cros, 1963; Scandola, 1975; Medes Islands, 1983) the ecosystem structure of the Mediterranean had already been largely affected by many centuries of exploitation, in some cases dating back to prehistory [56]. Large predators such as sharks, monk seal and large piscivores that were once very common had already been actively fished or hunted. As has been shown for other ecosystems in the world, the communities we observe today in the Mediterranean, with sea breams being the key benthic predators causing habitat shift, are probably not representative of the past and of the natural conditions of this ecosystem. In fact, it was suggested that if recent changes in the abundance of medium-sized predators have caused trophic cascades in coastal communities leading to ecosystem shifts, it is plausible to hypothesize that the dramatic changes in the size and abundance of once common large fish must have caused significant changes in food web structure over historical periods, as this has been shown for marine food webs worldwide [2,17].

With this background, a crucial question is unavoidable: how would Mediterranean marine ecosystems look in the presence of large predators?

We have seen how historical reconstruction of the abundances and sizes of large animals in the last century is scant in the Mediterranean [61], but may help setting up appropriate conservation and fisheries management goals and targets for assessing the recovery of endangered species, food webs and whole communities [50].

To answer our questions, we have highlighted that marine protected areas across the world and in the Mediterranean are significantly leading to a slow recovery of high-level predators, but even the oldest MPAs have not yet reached their carrying capacity. We have reviewed how these predators can have a major role in strongly shaping communities and modifying ecosystem functions and that they can be a good indicator of the state of recovery of an MPA.

We have seen that for highly complex food webs like the Mediterranean ones, it is difficult to ascertain information on the food web consequences of high-level predator recovery from empirical ecological studies [41]. Food web modelling is largely considered a very useful tool to unravel trophic interactions, describe ecosystem structural traits, derive maturity indexes for comparisons [104,109,114] and also assess the potential for recovery of high-level predators [115], but model applications in marine protected areas are still few, especially in the Mediterranean. This scarcity is largely due to the large amount of data needed to get reliable models and the associated uncertainties on data precision. Nevertheless, if reliable ecosystem models could be built in a cost effective way, they could provide useful information for the research and management of marine protected areas.

If the fundamental role of high-level predators in marine ecosystems is finally acknowledged [18], as well as their leading position in MPA recovery, their monitoring should then be a fundamental point in the design and management plan of MPAs.

Nevertheless the pre-existing disturbance of millennia of exploitation undergone by the Mediterranean Sea, which led to the ecological extinction of large top predators such as many species of sharks and marine mammals, must be acknowledged by MPA management, which should define realistic targets of recovery and conservation thereafter. For some of these wide ranging large animals, recovery is a challenging task, but can be enhanced by comprehensive MPA networks that in order to be effective, should be built on sound scientific data and with the help of advanced scientific tools like predictive habitat modelling and spatial mapping, integrated with life history and behavioural data [116,117]. We have seen that the recovery of high-level predators like large predatory fish in MPAs is an important and realistic target, but their monitoring is not an easy task. A challenging objective for both research and management could be the development and implementation of consistent field monitoring methods to assess the abundance of the entire fish assemblage, from the smallest cryptobenthic species to the large highly motile predatory fish. In this way reliable relative values of high-level predator increase could be obtained. Complementing historical reconstruction, ecosystem modelling and effective long term monitoring of high-level predators in the field could help us to effectively assess the recovery of marine coastal ecosystems.

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