

Marine biodiversity warming vs. biological invasions and overfishing in the Mediterranean Sea: Take care, 'One Train can hide another'

Abstract

Biodiversity means the variety of life, encompassing levels of complexity from within species to across ecosystems. Biodiversity therefore includes several dimensions: evolutionary scale (genetic, species, higher taxonomic levels and phylogenetic diversity), functional scale, organizational scale (patch, ecosystem, landscape/seascape diversity), spatial scale (from sample to local, regional and global richness) and heterogeneity diversity. Biodiversity can therefore be measured in different and complementary ways, thus involving the use of at least 200 different metrics, which can suggest different and contrasting conclusions. It is worth emphasizing that species richness may be the least appropriate metric, despite its popular acceptance. There is a growing tendency for stakeholders, managers, government officials, environmentalists, scientists, politicians and the media to focus, as concerns threats to biodiversity, on species richness and climate change. However, focusing on climate warming can mask other stressors that, today, and perhaps for decades to come, may have more impact on ecosystems than global warming. In the Mediterranean Sea, the overall impact of Non-Indigenous Species (NISs) and overfishing on species diversity, ecosystem diversity and ecosystem functioning exceeds to a greater or lesser degree the direct impact of warming. Drastically altered functioning patterns, and even new ecosystems are spreading throughout the Mediterranean Sea. This trend is likely to become more pronounced over the next decades. Ecosystem goods and services are also being profoundly altered, generally towards a decline, as illustrated by the overgrazed barren grounds of the eastern basin, which no longer support fisheries, by the impact of the *Caulerpa* meadows on the scuba diving business and the economic value of the fisheries of the western basin, by the brackish lagoon ecosystems and by the blooms of the introduced comb jelly *Mnemiopsis leidyi* in the Black Sea, before the arrival of its predator *Beroe ovata*. Here, we draw attention to the fact that, at this moment and probably also in the future, the huge flow of NISs and overfishing constitute worrying issues, although largely ignored by stakeholders and political authorities. Take care: Un train peut en cacher un autre (one train can hide another; i.e. one danger may hide other unsuspected dangers), that is to say the impact of warming may contribute to hiding other effects, of at least equal gravity, such as biological invasions and overfishing.

Keywords: biodiversity, biological invasions, global warming, mediterranean sea, overfishing, stakeholders

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Charles F Boudouresque,¹ Aurelie Blanfune,¹ Catherine Fernandez,² Christophe Lejeune,^{3,4} Thierry Perez,² Sandrine Ruitton,¹ Delphine Thibault,¹ Thierry Thibaut,¹ Marc Verlaque¹

¹Aix-Marseille University and Toulon University, Mediterranean Institute of Oceanography France

²Institut Méditerranéen de Biodiversité et d'Écologie marine et continentale (IMBE), Avignon Université, France

³Sorbonne Universités, station Biologique de Roscoff, France

⁴Station Biologique de Roscoff, France

Correspondence: Charles F Boudouresque, Aix-Marseille University and Toulon University, OSU Pytheas, Mediterranean Institute of Oceanography (MIO), CNRS, IRD, Campus of Luminy, 13288 Marseille cedex 9, France, Email Charles.boudouresque@mio.osupytheas.fr

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Introduction

Global change is often considered erroneously as a nomenclatural equivalent to global warming. In fact, it refers to the interactions between natural changes in the Earth's physical and biological structure and the broader effects of human activities. Therefore, global change has natural and anthropogenic components. Global change encompasses biological invasions, modifications in biological diversity (species, ecosystems, etc.), ecosystem functioning, biogeochemical cycles, pollution, changes in land use and land cover, in addition to changes in climate and the distribution pattern of climatic zones, most of these parameters being in interaction (Figure 1 Board of Environmental Studies and Toxicology, 2000).^{1,191} Biodiversity is too often considered as a nomenclature equivalent to species richness, which actually represents a rather limited part of the biodiversity concept,² In fact, biodiversity is a multidimensional concept, involving the use of hundreds of metrics. Species richness is perhaps the least appropriate metric to choose for describing biodiversity, while it is too often favoured by managers, the political authorities and even by some scientists unfamiliar with the concepts of modern ecology (see

below). Here, we attempt to show that global warming, both natural and human-driven through the increase in greenhouse gas emissions, although favoured as a research focus by some scientists (seeking funding?), could in fact represent a limited part of the expected global change, at least in the Mediterranean Sea.

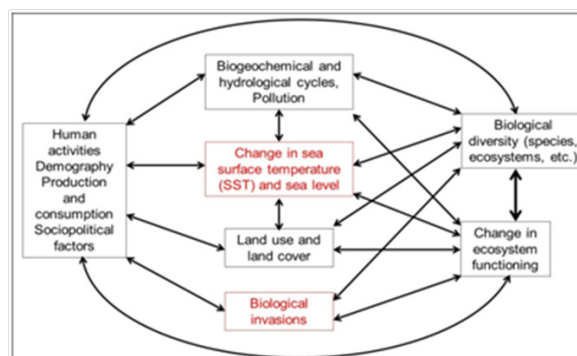


Figure 1 Conceptual model of global change due to human activities. From Board on Environmental Studies and Toxicology (2000) and Verlaque and Boudouresque (2004), modified, updated and redrawn.

The modern concept of biodiversity

'Biodiversity' is today a term that has gained popular currency, widely used not only by scientists, but also by political leaders, government officials, conservationists, environmentalists ('greens') and the public at large. Although scientists have long defended the need for the adoption of the biodiversity concept by end-users, as an essential good for human societies, it is not yet accepted that it actually encompasses a wide spectrum of concepts, sometimes worlds away from its popular definition.² The term 'biological diversity' was first used by Dasmann.³ Thomas Lovejoy, in the foreword to the book 'Conservation Biology' (Soulé and Wilcox, 1980 [214]), introduced the term to the scientific community. The term's contracted form, 'biodiversity', was coined by Wilson⁴ in the proceedings of the National Forum on Biological Diversity. It gained in popularity after the 'United Nations Conference on Environment and Development' (UNCED), also known as the Rio Summit, Rio Conference and Earth Summit, held in Rio de Janeiro (Brazil) from June 3 to 14, 1992.⁵ Since then, both the term and the concept of biodiversity have achieved widespread use among biologists, conservationists, political leaders and the general public. The term is often used to reflect a concern for the natural environment, nature conservation and species extinctions. In the course of their more than 40-year lifespan, the meaning of the terms 'biological diversity' and 'biodiversity' has greatly evolved. The way their meaning has shifted in the environmentalist's jargon is quite different from changes of meaning within the scientific community. As a result, misunderstandings between environmentalists and scientists are all too frequent. Misunderstanding also occurs within the scientific community, between those who refer to biodiversity as it was originally defined and those who refer to it under its current definition, or one of its current definitions, or more exactly the suite of concepts they cover. Biodiversity means the variety of life, encompassing levels of complexity from within species to across ecosystems. For taxonomy concepts, see Boudouresque¹⁹³ and Boudouresque et al.⁷ Biodiversity therefore includes several dimensions (Figure 2).⁵

Evolutionary scale, i.e. diversity within species (genetic diversity), diversity between species, diversity between taxa higher than species (genera, families, orders, classes, phyla, kingdoms, etc.) and phylogenetic diversity (mean phylogenetic distance between taxa; Faith⁹).

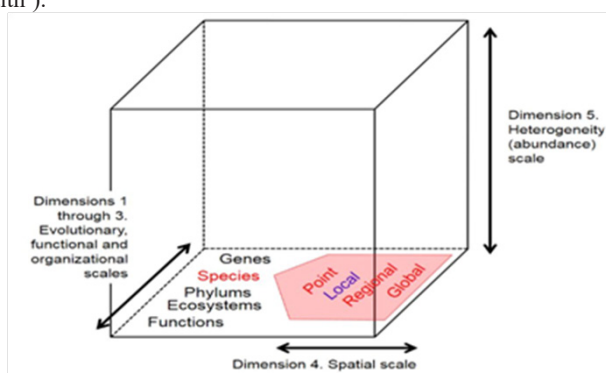


Figure 2 Biodiversity is a multidimensional concept. Dimensions 1 through 3: from genes to ecosystems, landscapes/seascapes and functions. Within each evolutionary, functional and organizational level (e.g. species), dimension 4 (spatial scale), from point to global. Within each spatial level (e.g. local), dimension 5 (proportional distribution), from e.g. very rare to dominant. From Boudouresque, 2014 (modified).

Functional scale, i.e. diversity in the functional role of species, functional groups and guilds within ecosystems, e.g. photosynthetic

or chemosynthetic primary producers, diazotrophic species, filter-feeders, suspension-feeders.

Organizational scale, i.e. diversity between patches, communities, ecosystems, landscapes/seascapes, including beta-diversity.^{10,2}

Spatial scale, from local and regional to global.¹⁰⁻¹² As far as the species diversity is concerned (evolutionary scale), it can be considered at the scale of a sample (point diversity), of an ecosystem within a region (alpha-diversity), of all the ecosystems of a region (gamma-diversity) and of all the ecosystems of a large biogeographic province (epsilon-diversity). The spatial (geographic) scale matters a great deal for biodiversity estimates Boudouresque.^{2,13-15}

In addition, biodiversity includes the proportional distribution of the individuals among the species, the so-called heterogeneity diversity, abundance diversity or evenness.¹²

The concept of biodiversity integrates not a single but a multitude of meanings: it is par excellence a multidimensional concept. The choice with regard to the meaning (qualitative or quantitative, compositional or functional, scale, etc.) depends primarily on one's goals and interests. Biodiversity can therefore be measured in different and complementary ways and thus involves the use of at least 200 different metrics (Sala and Knowlton, 2006; Boudouresque, 2014). This complexity of meanings, scale and units makes it impossible to assess the state of biodiversity using a single measure.

Species diversity (= species richness) means the taxonomic diversity at the level of the species (generally sensu the Linnaean system of classification), i.e. the number of species at a given scale of space (sample, habitat, ecosystem, landscape/seascape, region, Earth). Species diversity squares with the most popular perception of the concept of biodiversity.²¹ Most studies dealing with biodiversity report this simple measure of biodiversity. Although species diversity may be relevant (as long as the spatial scale is provided) for comparisons between ecosystems, or within ecosystems over time, and therefore represent a prerequisite, it may not constitute a good measure of the structure, function and degree of disturbance of the ecosystems. Moreover, different measures can suggest different and/or contrasting conclusions.^{15,10,2} A naïve approach to the biodiversity concept could lead to regarding such conclusions as diametrically opposed. It is worth emphasizing that species richness maybe the least appropriate metric, despite its popular acceptance, often inducing bias in ecological reasoning, within global change science. Obviously, the taxonomic knowledge (including the species level) is of paramount importance in biodiversity studies and cannot be omitted; however, this cannot justify the kind of 'species richness dictatorship' found in most biodiversity studies.

The Mediterranean: a biodiversity hotspot

The Mediterranean Sea is a hotspot of marine epsilon species diversity; it harbours at least 17 000 taxa.^{16,17,2,18,198} While it represents only 0.3 and 0.8 % of the volume and the surface area of the world ocean, respectively, it harbours 6.4 % of the world marine taxa, with species diversity of sponges (Porifera; kingdom Opisthokonta) and brown algae (Phaeophyceae; kingdom Stramenopiles) of up to 10 % and 17 % of the known species worldwide, respectively.^{19,26,194,198} The Mediterranean is one of the few regions harbouring a species diversity hotspot in both the marine and continental realms.^{18,23-25} Why are there so many species in the Mediterranean Sea? According to Lejeune et al.,²⁶ a first reason is its tormented geological history, which has led to high rates of environmental changes with successive extinctions, re-colonisations and speciation. A second reason is the

wide range of climatic and hydrological situations which can be found in this sea, resulting in the co-occurrence of cold, temperate and subtropical biota. Finally, the rate of endemism is relatively high in the Mediterranean Sea, reaching at least 25 % of the whole biota. The sea has been considered as a factory designed to produce endemics. During the Pleistocene climatic glacial cycles, North-Atlantic species periodically shifted their latitudinal ranges, allowing populations to enter the Mediterranean via the Strait of Gibraltar. Once within this new environment, populations were subject to higher evolutionary pressures, in relation with wide variations in sea level, temperature and salinity. In addition, the Alboran basin, to the east of Gibraltar, might act as a buffer reducing gene flow, and highly compartmentalised coasts (total length 46 000 km) further increase isolation between already isolated sectors.^{26,192} As pointed out by Bianchi,¹⁸⁹ the Mediterranean functions as a 'diversity pump' from the Atlantic Ocean. Moreover, the presence of paleo-endemic species (e.g. the sea grass *Posidonia oceanica*) attests that the region also acted as a refuge for Tethyan relicts.^{27,28,205} The Mediterranean Sea also harbours a wide range of ecosystems, some of them being unique, in terms of their structure and functioning,^{20,26,5} such as the mediolittoral *Lithophyllum byssoides* rims,^{29–32} the shallow vermetid platforms,^{30,31} the *Posidonia oceanica* sea grass meadow,^{8,33} the *Cystoseira* seaweed forest,^{29,34–40} the coralligenous assemblages^{30,31,41,42,101,188} and the dark submarine caves.^{43–45}

The Mediterranean: a hotspot of biological invasions

The Mediterranean is the area that is worldwide the most severely hit by biological invasions, with ~1000 Non-Indigenous Species (NIS) recorded so far.^{46–49,200,211} This is in contradiction (at least within the marine realm) with the old paradigm of Elton (1958),⁸⁰ who claimed that species diversity was a factor of resistance to invasions.⁸⁰ In fact, in the marine realm, it frequently occurs that the higher the species richness is, the more vulnerable the habitat; this may concern point diversity, alpha diversity, gamma diversity and/or epsilon diversity; the reason partly lies in the fact that species-rich habitats are favourable for the life of organisms, regardless of their native or exotic status^{52–54} (see Fridley et al.,⁵⁵ for the 'invasion paradox'). What matters is also the presence of a vector⁸⁰ such as the Suez Canal^{22,56,61} and aquaculture facilities.^{58,59}

The main vector of introduction of new species into the Mediterranean Sea is the Suez Canal, which was opened in 1869 and connects the Red Sea and the Eastern Mediterranean Basin. Since then, it has been enlarged and deepened several times, the last such operation having been conducted in 2015.^{133,201} The flow of tropical Red Sea species entering the Mediterranean, the so-called Lessepsian species, was first concentrated within the Levantine Basin, but these species have been steadily spreading westwards and northwards.^{22,26,56,61,62} The second most important vector is shellfish farming (reared species escaping from the farms and species accompanying shellfish transfers), with warm and cold areas of the North Pacific Ocean as donor regions.^{59,63,65,196,212} Other vectors include fouling and clinging on ship hulls, ballast waters, aquarium trade, fishing baits and waterways crossing watersheds.^{67–70,72–74,199,213}

Invisibility relies first upon the occurrence of a vector, and then on the propagule pressure.^{76–80} The invasion success also depends on a number of factors,⁸⁰ such as the release from enemies (ERH, Enemy Release Hypothesis; Ivanov et al.,²⁰⁴ MacLeold et al.,²⁰⁶, the availability of unused resources, a community becoming more susceptible to invasion whenever there is an increase in the amount of unused resources, because there is either more resource supply

or less resource uptake (FRAT, Fluctuation in Resource Availability Theory^{81,82}), reallocation of resources from chemical defence towards growth and reproduction, made possible through the release from enemies (EICA, Evolution of Increased Competitive Ability;^{83,84}), the possession of toxic biochemical compounds ('allelochemical weapons') unknown to native species in the recipient area (NWH, Novel Weapon Hypothesis;^{71,85,86}) and the naïveté of native species, which do not recognize as an enemy the introduced predator and hence do not escape.⁸⁷ In contrast, warming is not a direct factor favouring habitat/ecosystem invisibility or species invasiveness;²¹² but see⁸⁸. Warming can advantage thermophilic introduced species; however, at the same time, it can disadvantage cold water introduced species. The overall amount of new introduced species and the dominance of introduced species might therefore be unchanged. The alleged 'aggressiveness' of tropical introduced species, such as *Caulerpa taxifolia* and *C. cylindracea* (Chlorobionta; kingdom Archaeplastida) in the Mediterranean Sea, is due to the fact that they have been considered as of tropical origin,⁸⁹ while they are actually from temperate seas.^{90,26,210} Their success in the Mediterranean, a mostly temperate sea, is therefore in no way unexpected. Some of the most invasive species, such as *Caulerpa* spp., *Sargassum muticum* (Phaeophyceae, kingdom Stramenopiles) and the comb jelly *Mnemiopsis leidyi* (ctenophores, Metazoa, kingdom Opisthokonta), are not of tropical origin, but of temperate or even of cold water origin. This highlights the leading role of vectors that by far outweighs that of warming.⁸⁰

The overwhelming impact of biological invasions on Mediterranean species and ecosystems

NISs can be non-established (no sexual or asexual reproduction in the wild), casual (non-lasting reproduction), introduced (i.e. established, naturalized; reproduction in the wild without human assistance), invasive (high impact on native species and on the ecosystem functioning, and/or an economic impact, and/or an impact on human health) or transformers (ecosystem engineer of a new ecosystem)^{47,60,80,91,92} Macrophyte NISs are widespread in the Mediterranean ecosystems of the infralittoral and circalittoral zones⁹³ from sea level down to 30–40m depth and from 30–40 m depth down to the lower limit of photosynthetic organisms, respectively. Disturbance regimes do not matter: NIS prevalence, NIS species richness and NIS cover and biomass generally do not differ between disturbed and pristine areas, such as Marine Protected Areas (MPAs)^{53,80,94,195} but see.⁹⁵ This contradicts the old paradigm of Elton,⁵⁰ who claimed that disturbances enhance ecosystem invasibility. Undisturbed Mediterranean benthic ecosystems are characterized by a low level of herbivory; the sea urchin *Paracentrotus lividus* and the teleost *Sarpa salpa* are the most conspicuous macro-herbivores.^{96,39,97–99} As a result, the food web is driven by the detritus-feeders rather than by the herbivores. In addition, most Mediterranean Multicellular Photosynthetic Organisms (MPOs) have not developed chemical defences against herbivores (Figure 3).^{8,33,100,103}

In the north-western Mediterranean, the dramatic arrival of strongly defended and poorly palatable invasive species, such as *Caulerpa taxifolia* (Chlorobionta), *Asparagopsis armata*, *Lophocladia lallemandii* and *Womersleyella setacea* (Rhodobionta; kingdom Archaeplastida), has profoundly changed the functioning of the ecosystems, with a further decrease of the flow running through the herbivores being expected (Figure 4).^{71,86,100,104–107} In contrast, in the eastern Mediterranean, the arrival of voracious herbivorous teleosts (*Siganus luridus* and *S. rivulatus*) from the Red Sea, via the Suez Canal, has strongly intensified the herbivore pressure (Figure 5).¹⁰⁰

107–111,202 The recent arrival in the Levantine Basin of the voracious sea urchin, *Diadema setosum*, will further enhance the herbivore compartment.^{57,112} This has resulted in an impressive regime shift, from ecosystems dominated by canopy-forming primary producers and under bottom-up control, such as *Cystoseira* spp. and *Sargassum* spp. (Phaeophyceae; kingdom Stramenopiles), to an Alternative Stable State (ASS) dominated by encrusting calcified corallines (Rhodobionta) and sometimes characterized also by sea urchin overgrazing, called 'barren ground', with top-down control.^{113,96,40,114} Finally, in coastal lagoons harbouring shellfish farm facilities, on natural and artificial hard substrates, the dominance (species richness, cover, biomass) of MPOs introduced from the cold-temperate northern Pacific Ocean is overwhelming. In Thau Lagoon (Southern France), they represent 32% of the gamma species diversity, 97–99% and 48–95% of the spring and autumn biomass, respectively, and 100% of the cover (Figures 6) (Figure 7). Similar observations have been reported in other Mediterranean lagoons, e.g. the Venice Lagoon (northern Adriatic Sea, Italy).^{115–117}

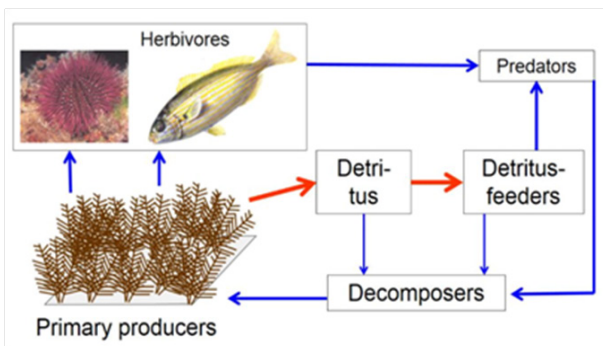


Figure 3 A simplified sketch of food-webs in undisturbed Mediterranean marine benthic ecosystems. Here, a *Cystoseira* forest. Herbivores are the sea urchin *Paracentrotus lividus* and the teleost *Sarpa salpa*. The intensity of the flow is proportional to the width of the arrow between functional compartments (in red, the main path). From Boudouresque et al. (2005) and Boudouresque (2015b), modified.

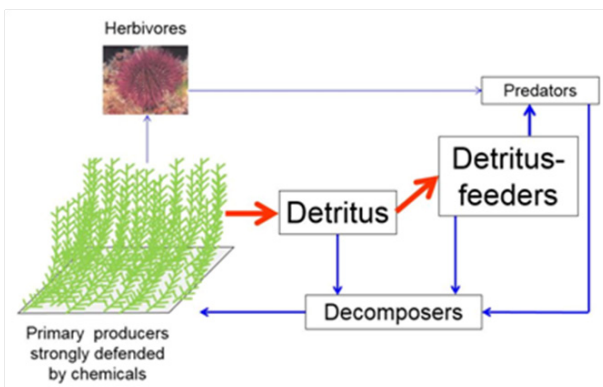


Figure 4 A simplified sketch of a food-web in a Mediterranean benthic ecosystem, in the presence of non-palatable primary producers, here *Caulerpa taxifolia*. The possible increase in the DOC (Dissolved Organic Carbon) release towards the pelagic ecosystem is not considered here. The herbivore is *Paracentrotus lividus*. The intensity of the flow is proportional to the width of the arrow between functional compartments (in red, the main path). From Boudouresque et al. (2005) and Boudouresque (2015b), modified.

At Kos Island (Greece, eastern Mediterranean), Bianchi et al.¹¹⁸ compared benthic data collected in 1981 and in 2013, by the same persons with the same method. During this 30+ year period, increases in Sea Surface Temperature (SST, +1–2°C), human pressure (resorts and hotels, 15 to 163 beds/km²), and NISs (e.g. rabbitfish *Siganus*

rivulatus and *S. luridus*) were observed. Huge changes occurred in rocky reef habitats; the once flourishing *Cystoseira* and *Sargassum* forests have disappeared in favour of sponges and wide bare substratum areas (Figure 8).

These changes can be seen as a synergistic action between biological invasions, SST warming and human impacts. More realistically, they evidence the supremacy of NISs (especially overgrazing rabbitfish), over the other stressors, including warming. Open ocean and coastal lagoon pelagic ecosystems are also widely impacted by NISs. The textbook case is the introduction in 1982 of one of the top 100 worst invasive species, according to IUCN, the ctenophore *Mnemiopsis leidyi* in the Black Sea through ballast waters. The introduction of this strong predator, native to the Gulf of Mexico,^{119,120} coincided with the collapse of local fisheries. Whether the introduction of this ctenophore is the reason for the collapse or just a collateral event that made things worse is still not clear. Nevertheless, the intentional introduction in 1997 of *Beroe ovata* (ctenophore), which feeds almost exclusively on *M. leidyi* in its native habitat, resulted in impressive changes in the pelagic ecosystem.^{121–126} *M. leidyi* has been spreading through the Mediterranean Sea, possibly following currents, but other vectors must also be involved, especially in the case of coastal lagoons with very little connection with the patterns of circulation of main currents (Jasper et al., unpublished data). High abundance in some coastal lagoons, such as the Berre, Bages-Sigean, Salses-Leucate and Biguglia lagoons along the French coasts, have been observed for ~10 years.^{127,128}

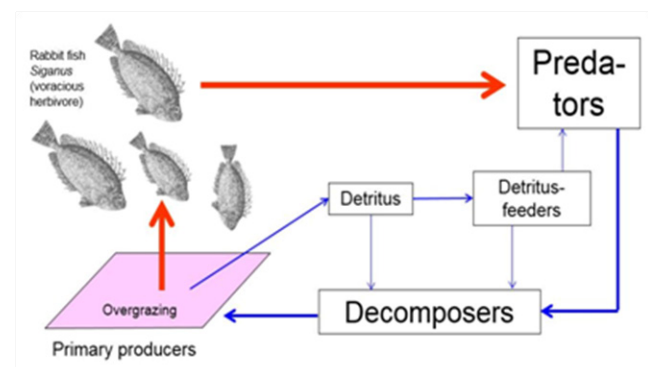


Figure 5 A simplified sketch of a food-web in a Mediterranean benthic ecosystem, in the presence of herbivorous fish of the genus *Siganus* (eastern Mediterranean), here, a barren-ground. The intensity of the flow is proportional to the width of the arrow between functional compartments. In red, the main path. From Boudouresque et al. (2005) and Boudouresque (2015b), modified.

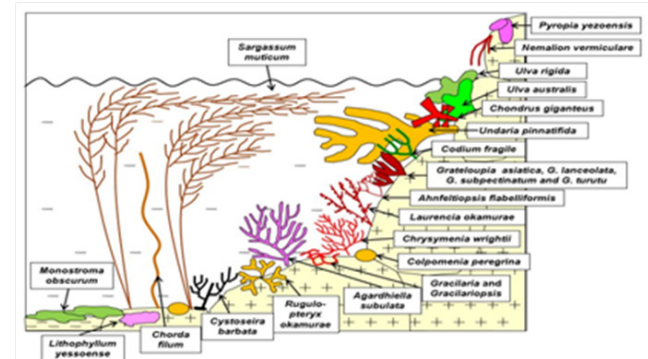


Figure 6 A sketch of the dominant MPOs on shallow (down to 1 m depth) rocky substrates of the Thau Lagoon (southern France) in spring. Most of these taxa are native to Japan, Korea and the northwestern Pacific Ocean (see Figure 7). From Boudouresque et al., 2011, modified.

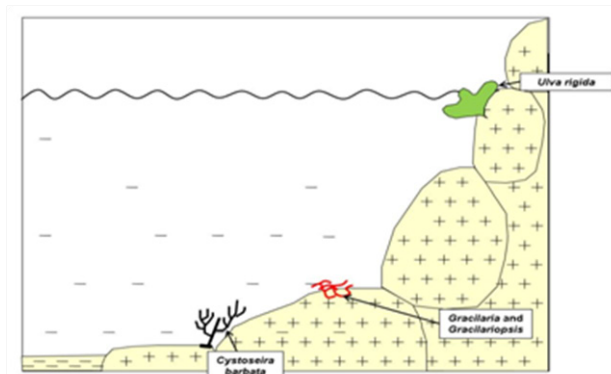


Figure 7 The same sketch as that of figure 6, after the removal of the species native to the northwestern Pacific Ocean. The only native taxa are *Cystoseira barbata*, *Gracilaria* sp. and *Gracilariopsis* sp. *Ulva rigida* is probably a cryptogenic species (sensu Carlton, 1996). Drawn from data in Boudouresque et al. (2011).

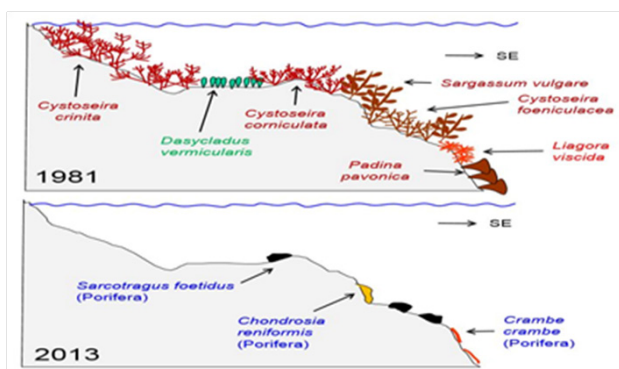


Figure 8 Schematic profile of a reef slope down to about 7 m depth at Kos Island (Greece), illustrating the impressive change between 1981 (top) and 2003 (bottom). Brown algae (Phaeophyceae) are in brown and red-brown, green algae (Chlorobionta) are in green, red algae (Rhodobionta) in red and sponges (Porifera, Metazoa) in blue. From Bianchi et al. (2014), redrawn.

The Levantine Basin has hosted first the Lessepsian species, among which several conspicuous jellyfish *Rhopilema nomadica*, *Phyllorhiza punctata* and *Cassiopea andromeda* have been reported. Most large jellyfish are well known for feeding upon eggs and larvae of fish and crustaceans, but also for interacting strongly with human activities such as clogging fishing nets, damaging boat and power plant intakes and fishing gear and causing the closure of productive areas to fishing activities. *Rhopilema nomadica*, native to the Red Sea, has a bell diameter of up to 90 cm and can constitute dense rafts of up to dozen kilometres in length, drifting with the alongshore currents.^{129–133} The jellyfish is spreading autochthonically as current-borne adults, reaching Maltese waters in 2004,¹³⁴ and then the Tunisian coasts in 2008,¹³² where the species has established a reproducing population. *Phyllorhiza punctata*, another pelagic species known previously only from Australia, the Philippines and Japan entered the Mediterranean Sea either through the Gibraltar strait or the Suez Canal via vessels, and most likely as sessile polyp stages attached to ship hulls or drilling rigs.¹³⁵ *Cassiopea andromeda* is an atypical jellyfish, living upside down on the seafloor in shallow waters, and dispersion is mainly done through juvenile stages (ephyrae), so of limited extension within the oriental basin, even more so in the western basin. But it was observed in Turkey in 2000,¹³⁶ and then in 2010 further west in the central Mediterranean, around the Maltese Islands.¹³⁷ It is suggested therefore that the most likely vector responsible for transporting this species is shipping (ballast waters, hull-fouling).^{135,138}

The impact of overfishing

Overfishing is ubiquitous in the Mediterranean Sea, as in most of the world ocean.^{139–141} Both benthic and pelagic ecosystems are concerned. Some fishing techniques, such as artisanal fishing gear, target specific prey (see e.g. Leleu et al.¹⁴²), while others, such as trawling, capture non-targeted species and have a strong mechanical impact upon benthic ecosystems.^{143–146} Due to overfishing, most benthic ecosystems are strongly depleted in teleosts (fish), especially in invertivores (consumers of invertebrates) and top predator fish, with a dramatic decrease in mean size and in number of individuals.^{64,147–149} Only a very few Marine Protected Areas (MPAs), such as the Port-Cros National Park (Provence, France), the Stait of Bunifaziu Natural Reserve, the Scandola Natural Reserve (Corsica) and the Cabrera National Park (Balearic Islands), are free of this impact.^{40,149,150} As a result, there is often an increase in the pressure of herbivorous species, such as the sea urchin *Paracentrotus lividus* and the teleost *Sarpa salpa*, which are released from predation by top predators^{96,151} (but see¹⁵²). This results in overgrazing, the decline or the collapse of marine forests (*Cystoseira* spp. and *Sargassum* spp.) and the phase shift to 'barren grounds' dominated by encrusting corallines (red algae, Rhodobionta), turf MPOs and sea urchins (*Paracentrotus lividus*, *Arbacia lixula*) (Figure 9). These barren grounds constitute an Alternative Stable State (ASS) of the previous forest state; even a small number of sea urchins, where the overfishing of their predators is reduced, can prevent the shift back towards the forest state.^{153–155} The effects of other fishing techniques, such as uprooting by fishing nets, can also contribute to the extirpation of *Cystoseira* spp. and *Sargassum* spp.⁶⁶ Barren grounds nowadays occupy extensive, ever-increasing surface areas of infralittoral Mediterranean benthic habitats.¹⁵⁶



Figure 9 A barren ground dominated by sea urchins, encrusting corallines and turf MPOs. 5-6 m depth, Bay of Kotor, Montenegro. Photo © Thierry Thibaut.

The formerly canopy-forming species, *Cystoseira* spp. and *Sargassum* spp., are locally or functionally extinct in many Mediterranean regions.^{34,102,157} This is particularly worrying if one considers that these long-lived (perhaps more than one century) species grow slowly and often disseminate at only very short distances, so that recolonization of lost habitats may be unlikely at the human timescale.

In pelagic ecosystems, the proliferation of gelatinous planktonic organisms drives a regime shift from ecosystems dominated by top predators to ecosystems dominated by jellyfish^{158–160} (but see¹⁶¹). The collapse of shark species, in the Mediterranean Sea, is particularly conspicuous; some species, such as hammerhead (*Sphyrna* spp.), blue (*Prionace glauca*), thresher (*Alopias vulpinus*) and shortfin mako sharks (*Isurus oxyrinchus*) have declined by between 96 and 99.99 % since the late 19th century or the mid-20th century (Ferretti et al., 2008).¹⁴⁸

The direct impact of the sea surface temperature warming

The warming of the Mediterranean Sea (SST) began at the end of the Last Glacial Maximum (LGM), ~20 ka ago. The mean annual SST was then between 8°C and 2°C lower than today, in the north western and the eastern basins, respectively.¹⁶² Fucoids (Phaeophyceae; kingdom Stramenopiles) currently restricted to the North Atlantic Ocean, e.g. *Fucus vesiculosus*, were probably present in the NW Mediterranean Sea and in the Adriatic Sea, not only during the LGM, but must have remained until 6000 years ago.¹⁶³ The distribution of species and ecosystems 20ka ago was probably radically different from today, although this is partly speculative. The post-LGM natural reorganization of the Mediterranean biota could be still incomplete, as calcified remains of the thermophilic scleractinian *Astroides calycularis*, dating back to previous interglacial periods, have been discovered far north of their current distribution range.⁸⁹ The current warming of the Mediterranean Sea water triggers the northwards and eastwards range extension of warm water native species, such as the teleosts *Coryphaena hippurus*, *Sardinella aurita*, *Sparisoma cretense*, *Sphyrena sphyrena* and *Thalassoma pavo*, the sea urchin *Arbacia lixula*, the molluscs *Erosaria spurca*, *Luria lurida* and *Stramonita haemastoma*, the seagrass *Cymodocea nodosa* and the Chlorobionta *Caulerpa prolifera*.^{26,89,164–167} and unpublished data]. This trend should become more pronounced by the end of the 21st century [168,169]. Cold water native species, such as the teleost *Sprattus sprattus sprattus*, the echinoderm *Marthasterias glacialis*, the seagrass *Zostera marina*, the Rhodobionta *Calliblepharis jubata* and *Gymnogongrus crenulatus* and the Phaeophyceae *Fucus virsoides*, which are trapped in the northern Mediterranean, and cannot escape via the northwards shift of their range area, could therefore be threatened with local extinction. Recurrent mass mortality events among sponges, gorgonians (cnidarians) and other sessile metazoa, during high temperature anomalies, have dramatically illustrated this issue.^{26,170–177,209} Possible effects of the increase in temperature and/or pCO₂ on a Rhodobionta which plays a role in the coralliferous bioconstructions, *Lithophyllum cabiochae*, have been suggested by Martin and Gattuso.²⁰⁷

In contrast to the above mentioned examples, the direct impact of the warming on habitat-forming MPOs could be weaker. Parravicini et al.¹⁷⁸ show that the increase in temperature may be more complex than the simple prediction of species modifying their distribution range according to their thermal limit, near their boundary, with even a decrease in their cover on shallow rocky reefs. The worrying regression of *Cystoseira* and *Sargassum* forests, with several species locally and/or functionally extinct, seems to be related to overfishing (resulting in overgrazing by herbivores; see above), uprooting by fishing nets and coastal development, in addition to invasive NISs, rather than to sea water warming,^{34,66,102,157,179,180} but see.¹⁶⁶ As far as the *Posidonia oceanica* seagrass meadows are concerned, a negative effect of warming is unclear; it can shrink its range near its warm limit (e.g. in south-eastern Turkey) and favour its expansion near its cold limit (e.g. northern Adriatic and Gulf of Lions),^{51,145,181} but see.^{182,183} Conversely, the increasingly rapid rise of the sea level will result in a significant withdrawal of the lower *P. oceanica* limit, whenever it is beyond the compensation depth.¹⁴⁵

Finally, one of the most important effects of sea water warming could be to enhance the range area progression of Red Sea (Lessepsian) invasive species, such as the rabbit-fish *Siganus* spp., and the lion-fish *Pterois miles*,¹⁸⁴ with a potentially overwhelming impact.

Conclusion

There is a growing tendency for stakeholders, managers,

government officials, environmentalists, scientists, political leaders and media reports to focus, as concerns threats to biodiversity, on species richness and climate change. They can hardly be blamed, as climate change obviously constitutes a major threat to species diversity, ecosystem diversity, ecosystem functioning, and to human lifestyles. However, the 'species richness lobby' and focusing on climate warming can mask other stressors that, today, and perhaps for decades to come, may have more impact on ecosystems than global warming^{185–195} It would be beyond the scope of the present paper to discuss the reasons why most scientists, stakeholders and political leaders prefer to focus on global warming and its direct impact, such as the acidification of seawater.

In the Mediterranean Sea, the overall impact of NISs and overfishing on species diversity, ecosystem diversity and ecosystem functioning exceeds to a greater or lesser degree the direct impact of warming. Drastically altered functioning patterns and even new ecosystems are spreading throughout the Mediterranean Sea. This trend is likely to become more pronounced over the next decades. Ecosystem goods and services are also being profoundly altered, generally towards a decline, as illustrated by the overgrazed barren grounds of the eastern basin, which no longer support fisheries,⁴⁰ by the impact of the *Caulerpa* meadows on the scuba diving business and the economic value of the fisheries of the western basin^{186,187} and by the blooms of the introduced comb jelly *Mnemiopsis leidyi* in the Black Sea, before the arrival of its predator *Beroe ovata*.

In addition to direct impacts, which are far from negligible, warming not only boosts the expansion of the range of NISs but also triggers the rise of the sea-level; it therefore increases the huge impact of NISs and contributes to the submersion and death of the *Lithophyllum byssoides* algal rim, in the lower part of the mediolittoral zone¹⁹⁰ and to the withdrawal of *Posidonia oceanica* meadows at their lower depth limit.

Mediterranean coastal lagoons, such as Thau Lagoon and Venice Lagoon, and rocky reefs at Kos Island, Greece, may unfortunately be the harbingers of future Mediterranean seascapes. Here, we draw attention to the fact that, at this moment and probably also in the future, the huge flow of Non-Indigenous Species and overfishing constitute worrying issues, although largely ignored by stakeholders, managers, government officials and political leaders. Take care: Un train peut en cacher un autre (one train can hide another; i.e. there may be other, unsuspected dangers), that is to say the effects of the warming may contribute to hiding other effects, of at least equal importance, such as biological invasions and overfishing. The synergistic effects of the cocktail constituted by biological invasions, overfishing and global warming in the coming decades require, as a matter of urgency, a major effort at global scale in order to better assess the putative impact on Mediterranean marine ecosystems, and the goods and services they provide for the benefit of human society.

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Conflicts of interest

The authors declare there is no conflict of interests.

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