Review

Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea

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Little doubt is left that climate change is underway, strongly affecting the Earth's biodiversity. Some of the greatest challenges ahead concern the marine realm, but it is unclear to what extent changes will affect marine ecosystems. The Mediterranean Sea could give us some of the answers. Data recovered from its shores and depths have shown that sea temperatures are steadily increasing, extreme climatic events and related disease outbreaks are becoming more frequent, faunas are shifting, and invasive species are spreading. This miniature ocean can serve as a giant mesocosm of the world's oceans, with various sources of disturbances interacting synergistically and therefore providing an insight into a major unknown: how resilient are marine ecosystems, and how will their current functioning be modified?

The Mediterranean: a miniature model of the world's oceans

The Mediterranean is a peculiar sea, a product of a tormented geological history, where continents collide and water masses come and go, a crossroads of biogeographical influences between cold temperate biota and subtropical species (see Box 1). During the Mesozoic, it also united the Atlantic and Pacific realms through a large ocean known as the Tethys. The legacy of the Tethys and later geological events have produced a marine life that is unusually diverse for such a small enclosed sea; it is now considered a 'biodiversity hotspot' [1,2] and a 'miniature ocean' by physical oceanographers [3].

However, the Mediterranean is a sea under siege. Today it is a place where urbanisation of the littoral zone, the most productive part of the sea, is reaching a climax on the northwestern shores. On the southern and eastern shores, runaway population growth is producing an unprecedented anthropic pressure on marine ecosystems (pollution, overfishing, habitat destruction and species introductions). These major disturbances, in addition to species introductions, severely impact the natural balance of ecosystems and have resulted in the extensive loss of biodiversity [4]. Climatic models [5] further predict that the Mediterranean basin will be one of the regions most affected by the ongoing warming trend and by an increase in extreme events. This makes the Mediterranean a potential model of more global patterns to occur in the world's marine biota, and a natural focus of interest for research. There are reasons to believe that the Mediterranean is already one of the most impacted seas in the world, since climate change interacts synergistically with many other disturbances.

Here, we will focus on the effects of climate change on the Mediterranean biota. As well as considering the effects of climate alterations *per se*, particularly rising temperatures, we will also look at two phenomena mechanically related to temperature: the emergence of pathogens and biological invasions. The evidence gathered here points towards complex interactions and synergies between the various disturbance factors at play. Whereas the different forcings are now well documented, major unknowns remain as to how they will ultimately affect the functioning of ecosystems through cascade effects.

Physical evidence of changes in the Mediterranean

The Mediterranean Sea displays a specific hydrology, with well-identified water masses in each sub-basin (Figure 1) and at different depths. One peculiarity is a homogeneous deep-water layer below ~250 m that does not get colder than 12–13 °C. The general thermohaline circulation of the Mediterranean is determined by the flux of incoming Atlantic water by the Gibraltar Straits and by the sinking of waters formed at the three coldest areas of the sea: the Gulf of Lions, the northern Adriatic and the North Aegean Sea. Over the past three decades, this general pattern has been disrupted in several ways.

The first definite signs of changes in sea temperature came from Mediterranean deep waters. A 30-year time-series (1959–1989) of deep-water temperatures acquired in the northwestern Mediterranean (NWM) demonstrated a general warming trend of ~0.12 °C (~0.004 °C per year), a possible result of human-induced global warming [6]. Later data have confirmed this trend [7,8]. Some unexpected effects on thermohaline circulation have been documented from 1987 through the 1990s; these changes have been

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Box 1. The Mediterranean: A hotspot of species diversity

The Mediterranean Sea is a remnant of the east–west oriented Tethys Ocean which, ~200 million years ago (mya), separated two supercontinents: Laurasia in the North and Gondwana in the South. Communication with the Indian Ocean permanently ceased 12–13 mya, and since then the Mediterranean has been a nearly enclosed sea, with a degree of enclosure of over 99% (calculation according to Ref. [87]). During the Miocene (5.6–5.3 mya), the communication between the Mediterranean and the Atlantic Ocean was interrupted on several occasions in events known as the 'Messinian Salinity Crisis'. These interruptions had a deep impact on the Mediterranean biota: the sea more or less dried up and was then repopulated by species of Atlantic origin.

Although the Mediterranean only consists of 0.82% of the world ocean area and 0.3% of its volume, marine organisms which dwell in this sea represent 4–18% of the world marine species, depending on the phylum taken into consideration [1] (e.g. macrophytes in Figure I).

Why are there so many species in the Mediterranean Sea? One reason is its tormented geological history, which has led to high rates of environmental change and speciation. Another reason is the variety of climatic and hydrologic situations to be found in this sea, leading to the co-occurrence of cold, temperate and subtropical biota [1]. Finally, the rate of endemism is relatively high, averaging more than one-quarter of the whole Mediterranean biota.

The Mediterranean is sometimes considered a factory designed to produce endemics. During the Pleistocene climatic glacial cycles, North-Atlantic species periodically shifted their latitudinal ranges allowing individuals to enter the Mediterranean via the Gibraltar Straits. Once in the Mediterranean, because of reduced opportunities for North–South migration in response to changing sea temperatures, these populations were subject to higher evolutionary pressures. In addition, the Alboran basin, at the entrance to the Mediterranean, acts as a buffer reducing gene flow, and the 46 000 km of Mediterranean coasts are highly compartmentalised into fairly isolated sectors [88]. As coined by C. N. Bianchi [89], the Mediterranean has functioned as a 'diversity pump' from the Atlantic.

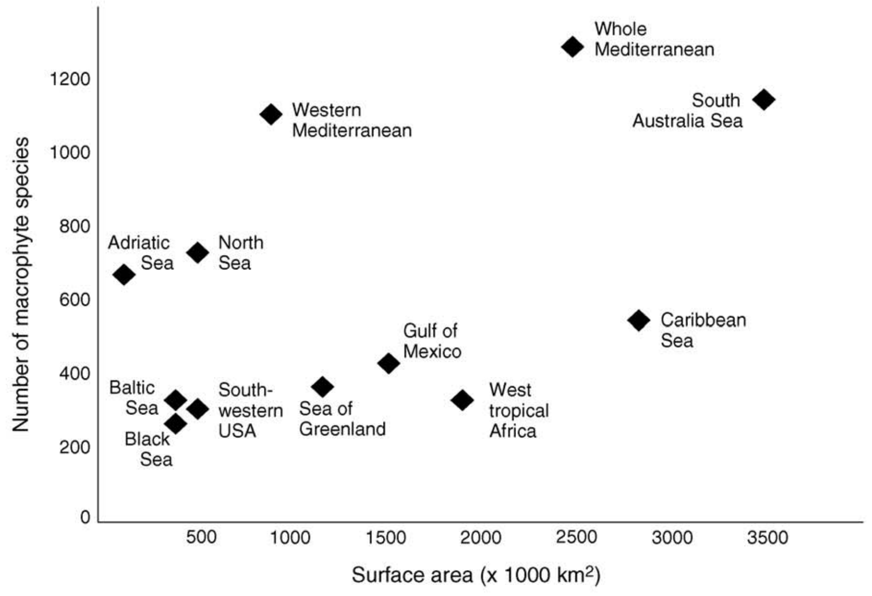

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Figure I. A plot of macrophyte species number against sea surface area for a selection of marine biogeographical provinces. The Mediterranean is clearly a hotspot of species diversity. This is not an artefact linked to the pressure of investigation: the Gulf of Mexico and the Caribbean Sea are far from being understudied areas. (Modified with permission from [88]).

termed the Eastern Mediterranean Transient (EMT). Strong anomalies in temperature and rainfall are believed to be involved in triggering the EMT, which has dramatically changed the hydrology of the deep eastern Mediterranean [9]. Temperature, salinity, stratification and circulation of water masses have been affected. Through the alteration of the carbon and nitrogen cycles, the deep-sea biota has also been negatively impacted [10]. Observations made between 2004 and 2006 have indicated that the EMT signal has propagated to the western basin and has disrupted previous thermohaline patterns there also [11].

Whether deepwater events eventually affect coastal waters is still uncertain, but at shallow depths two types of climate-driven effects have been observed: a warming trend and an increase in the frequency of exceptional events. A ~30-year data set (1974–2005) from the Spanish Catalan coast first demonstrated the warming of the littoral zone at four different depths from the surface to 80 m [8,12]. These data show a clear trend at all depths, with an impressive warming of 1.4 °C at 20 m. Other data sets (same period, other parts of the NWM) have been recovered and analysed, all showing similar trends of +0.8–1 °C over the last 30 years [13–15]. Interestingly, a century-long data set from the Marseille tide gauge displays a warming trend of 0.7–0.8 °C from 1885 to 1967 [16]. This is a slower rate than that documented in the more recent, shorter series, which indicate a faster rate of increase during the last 3–4 decades due in part to the superimposition of this trend with the Atlantic Multidecadal Oscillation (AMO) [15,17], and to the exceptionally warm 1990s coinciding with a maximum positive phase of the North Atlantic Oscillation (NAO) index [8] (Box 2). Comparable data are not available for the eastern Mediterranean or for the southern shores. However, satellite sea surface temperature data from the last ~20 years appear to show a significant (~1 °C) warming trend in the Aegean Sea as well [18].

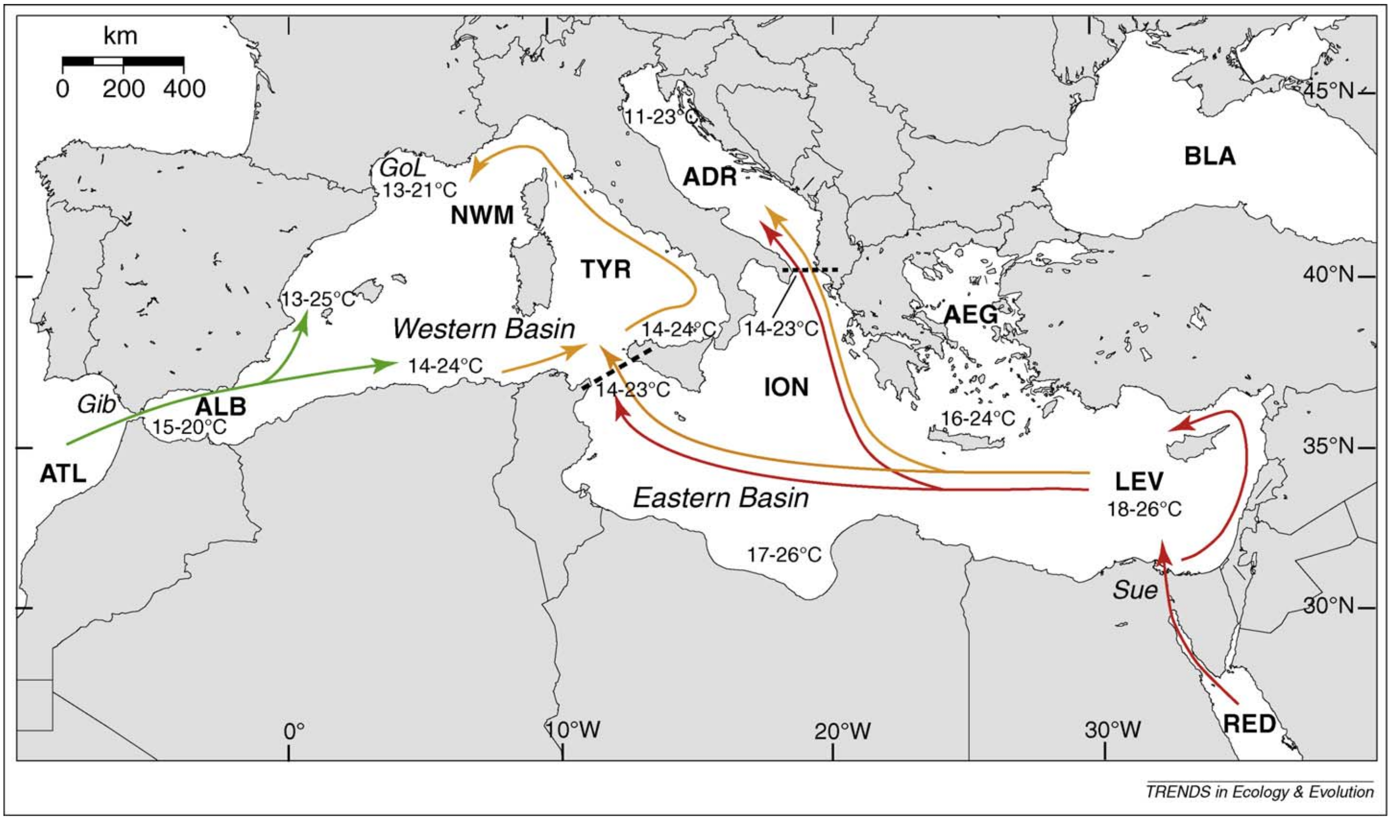

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Figure 1. Geography of the Mediterranean Sea with the main routes of species range expansion. Bold capital abbreviations correspond to the main Mediterranean subregions (ALB: Alboran Sea; NWM: North Western Mediterranean; TYR: Tyrrhenian Sea; ADR: Adriatic Sea; ION: Ionian Sea; AEG: Aegean Sea; LEV: Levantine Basin) and adjacent seas (ATL: Atlantic Ocean; BLA: Black Sea; RED: Red Sea). Italic abbreviations correspond to some remarkable Mediterranean locations (*Gib*: Gibraltar Straits; *GoL*: Gulf of Lions; *Sue*: Suez Canal). Reported temperatures correspond to winter–summer mean sea-surface temperatures. Arrows represent main routes of species range expansion according to their origin: Mediterranean natives (orange), Atlantic migrants (green) and Lessepsian migrants (red).

Since the late 1990s there has been increased awareness of the importance of acquiring time-series data to monitor changes in the Mediterranean [19–21]. This data has allowed for the documentation of the increased frequency of extreme events [22–25]. Reported temperature anomalies may in part be correlated with positive NAOs [26] (Box 2). Temperature is convenient to monitor, but associated changes in sea level or ocean chemistry, particularly acidification, must also be kept in mind [27–29].

Towards homogenisation of the Mediterranean biota?

The Mediterranean marine biota has historically been divided into three biogeographical provinces (the western and eastern basins, and the Adriatic Sea; Figure 1), each subdivided along latitudinal patterns [30]. Species of subtropical origin are therefore more abundant in southern parts of these provinces whereas temperate species dominate the northern parts (Box 1). Climate change, through long-term temperature increase and a higher frequency of short-term extreme events, is undoubtedly affecting the biology and ecology of the organisms in the sea. Most visible changes impact life cycle, reproductive effort and demography, but generally result from subtle adaptive responses (such as physiological adjustments and microevolutionary processes).

A direct consequence of warming is a simultaneous increase in the abundance of thermotolerant species and the disappearance or rarefaction of ‘cold’ stenothermal species. Such changes occur as shifts in distribution ranges and/or population dynamics, and were detected as early as the 1980s [31]. Although seawater warming probably affects the entire Mediterranean [15,17], range shifts have mainly been reported in NWM taxa; this is either due to the higher proportion of cold stenotherm species in the NWM or to observation bias, or a mixture of both. Considering the NWM only, one of the coldest areas in the Mediterranean, tens of significant range expansions of species of warm-water affinity have been recorded, two-thirds of which correspond to mobile species [14]. Striking examples are those of the ornate wrasse *Thalassoma pavo*, a typical Mediterranean thermophilic fish, and of the warm stenotherm orange coral *Astroides calycularis.* Both are very common in the eastern and southern shores and have seen their distribution recently shift northwestwards [31–33]. Many other species display a similar pattern, although it is also known that multidecadal events such as the AMO or NAO influence their distributions [34–36] (Box 2).

The eastern Mediterranean is an important source of thermophilic species expanding their ranges in the NWM and the Adriatic. In addition to native Mediterranean species, a particular case of distribution range expansion is that of introduced species. An introduced species is defined here as a species that (a) colonises a new area, (b) displays a geographical discontinuity with its native area, (c) has human activities as a primary vector of range extension, and (d) can reproduce *in situ* without human

Box 2. Disentangling the ups and downs of temperature

Current climate warming, though anthropogenically-driven, is superimposed over natural phenomena, some of which are cyclic. During the Last Glacial Maximum (LGM), ~23 000 to 19 000 years ago, the Mediterranean sea surface temperature was 2 °C lower than today in the eastern basin, and up to 8 °C lower in the northwestern basin [90]. After the LGM, climate warmed again and has since been punctuated by cooling events recurring roughly every 1500 ± 500 years [91–93]. The last such cold episode is the so-called Little Ice Age (LIA), which had three cold peaks (14–15th, 16–17th and 19th centuries) [94,95]. Post-LIA warming, in the late 19th through the early 20th century, is of natural origin. In contrast, since the late 20th century, anthropogenic forcings have enhanced, or are responsible for, the current global warming [96,97].

This overall warming trend may be clouded or accentuated by shorter term events, themselves cyclic or not, such as the Atlantic Multidecadal Oscillation (AMO) and the North Atlantic Oscillation (NAO). The AMO is a 50–70-year climatic oscillation between cool and warm episodes. Its influence reaches the Mediterranean where relatively warm episodes occurred in the 1870–1890s, 1930–1940s and since the 1990s [16,17,98]. The AMO is similar to the Pacific Decadal Oscillation (PDO) [99]. The NAO is a non-cyclic climatic phenomenon. A positive NAO index corresponds to a northward shift of the northern Atlantic storm track and to a significant increase of storminess in northern Europe, while dry conditions and mild winters prevail in southern Europe, the Mediterranean and North Africa. In contrast, when the NAO index is negative, impacts are more or less opposite and the Mediterranean receives increased rainfall [100]. The prevalence of positive NAO phases since the late 1970s has obviously contributed to the observed warming of the northern hemisphere. In the Mediterranean, reported temperature anomalies often locally translating into disruption of the wind regime, of the water mass stratification and of the thermocline depth, could in part be correlated with positive NAO [26].

assistance. It is termed invasive when it acts as key or engineer species within the recipient ecosystem. The Mediterranean is one of the areas worldwide most severely hit, with about 600 introduced species [37,38]. Their number has more or less doubled every 20 years since the beginning of the 20th century [38,39], but this increase does not seem to be related to climate change.

Most of the introduced biota in the Mediterranean originates from the Red Sea (i.e. Lessepsian migrants; ~67%), with an additional set of species (~7%) from other tropical areas. All in all, the bulk of the species introduced into the Mediterranean are of tropical origin. They have long been confined to the easternmost Levantine shores, but the warming of the Mediterranean favours their spread [40]. They are now rapidly progressing westwards and northwards, through the whole eastern basin, with some now reaching the Adriatic and the western basin (Figure 1). Although it is difficult to disentangle natural range expansion through time from climate-induced effects, particularly in regions lacking systematic field monitoring and temperature records, it seems that the last 20 years have seen an accelerated rate of westward migration of Lessepsian species [41]. A good example of this is the westward spreading of the rabbitfish *Siganus luridus* (Figure 2), recently reaching the Gulf of Lions [42].

Marine invertebrates and fish are not the only species concerned by such expansions. The last decade has seen increasing reports of toxic dinobionts in coastal areas, with possible consequences on human pathology. In some cases, they are exotic species favoured by environmental changes occurring in the Mediterranean [43]. *Gambierdiscus toxicus*, the main causative agent of ciguatera poisoning, normally has a tropical or subtropical distribution. *Gambierdiscus* sp. have, however, recently been reported from Crete [44]. Until now cases of ciguatera poisoning in the Mediterranean remain unascertained [45]. Simultaneously, range expansion of the palytoxin-producing dinobiont *Ostreopsis ovata* in the Mediterranean has been documented, with definite consequences on human health (irritation, cough, fever and respiratory problems) [46,47]. Each time, increased temperatures are thought to trigger proliferation of these harmful algae.

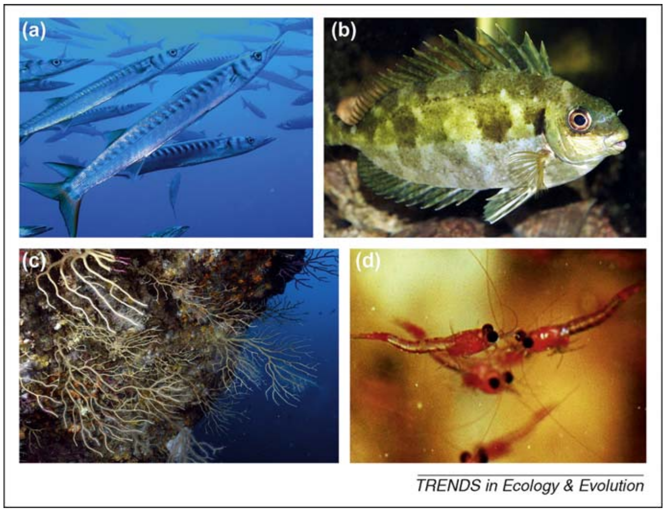

Figure 2. Representative examples of marine species responding to climate change in the Mediterranean. **(a)** The barracuda *Sphyraena viridensis* greatly increased its natural distribution range over the last 30 years; **(b)** the Lessepsian herbivorous rabbitfish *Siganus rivulatus* is affecting the eastern Mediterranean ecosystems, and is increasing its introduced range area. It was found in 2008 in the Gulf of Lions (Carry-le-Rouet, France); **(c)** a seascape of dead seafans *Paramuricea clavata* after the 2003 thermal anomaly in the NWM; **(d)** the crustacean mysids *Hemimysis* spp. are a classical example of a species shift in relation to climate change. Photographs (reproduced with permission) by T. Pérez **(a)**, J.G. Harmelin **(b)** and R. Graille **(c, d)**.

Fisheries records are a precious source of biological information. A 50-year-long record of *Sardinella aurita*, abundant in the tropical Atlantic has revealed a positive correlation between long-term temperature increase along the Spanish coast and both its northward expansion and reproductive success. Maximum annual catch varies with April mean sea surface temperature of the previous year [48]. Quantitative data on landings related to the warming trend of the Mediterranean are still rare, but several other new species are currently entering Mediterranean fisheries [14]. Warm-water top predators such as barracudas (*Sphyraena* spp.; Figure 2) and dolphinfish (*Coryphaena hippurus*) are now frequently sold in NWM fish markets. Whereas obvious changes have been reported for such prominent pelagic fishes, more subtle changes could also influence benthic and benthopelagic fish, such as bathymetric or latitudinal shifts [20].

Changes in life cycle and behaviour are more difficult to document, and their impacts more difficult to predict. Big pelagic fish, such as purplish amberjack *Seriola dumerilii* and bluefin tuna *Thunnus thynnus* now remain for longer periods in the western basin, which although beneficial for local fisheries in the short term [49], might endanger their stocks in the longer term. Conversely, large stocks of 'cold-water' species, such as the anchovy *Engraulis encrasicolus*, dramatically collapsed during the positive NAOs of the 1980s due to modifications in the trophic web, affecting eggs and larvae [49,50]. Cold stenotherm species could serve as useful sentinels for the coming changes. One of the best-documented examples is that of a sudden species shift between two congeneric marine cave mysid crustaceans [51] (Figure 2). Following repeated temperature anomalies, particularly in 1999, swarms of the endemic cave-dwelling *Hemimysis speluncola*, abundant till the late 1990s, collapsed and disappeared from many different caves of the NWM, leading to a drastic distribution range contraction. It was replaced by *Hemimysis margalefi*, uncommon until then. Subsequent studies confirmed a higher thermotolerance for the newly dominant *H. margalefi* compared to the cold stenothermal *H. speluncola*, unable to move north and now restricted to the cold regions of the Gulf of Lions and the northern Adriatic [51].

Particular sources of concern are the synergistic effects of the warming trend with extreme events on the temperate component of the Mediterranean biota. Many of these species are endemic and include poorly dispersive species. The particular geographical context of the Mediterranean Sea makes it impossible for shallow-water temperate species already trapped in the northernmost, coldest parts of the different basins to migrate or disperse northwards to mitigate temperature changes. Potential refuges for such species might be found at depth but this hypothesis remains to be tested and not all taxa will find suitable habitats by moving deeper. In contrast, species considered as indicators of the warmer, southern, parts of the Mediterranean, are gradually becoming more frequent and widespread in the colder, northern parts. As a result of warming, one expectation could be a homogenisation of the Mediterranean biota, disrupting present biogeographical entities. But if global warming is to impact all parts of the Mediterranean equally, current temperature gradients would have to be maintained as mean temperatures increase. Under this scenario, homogenisation of the Mediterranean biota would be unlikely. Rather, the southern parts would become increasingly colonised by sub-tropical species (e.g. species coming from the sub-tropical Atlantic mixed with Lessepsian migrants from the Red Sea) while the northern parts would be populated by warm-water native species currently abundant in the southern and eastern Mediterranean. Such a scenario has already been suggested, with some authors proposing that the Mediterranean Sea is heading towards 'tropicalisation' [52]. The use of this term might appear exaggerated in view of the data currently available, but a 'meridionalisation' of the Mediterranean (a definite augmentation of the proportion of thermophilic species in the Mediterranean biota) seems a more realistic description of changes to come.

Recurrence of diseases leads to increased stress levels

Heat stress is recognised to trigger diseases at sea, with the frequency of these events clearly increasing over the last two decades [53,54]. Recent extreme temperature events are likely to have disturbed the normal functioning of biological systems. Species present a 'natural' range of thermal tolerance and respond to natural temperature fluctuations by physiological, biochemical and molecular adaptations. Acute physiological stress, leading to diseases and mass mortality, appears when tolerance thresholds are exceeded and when escape towards more favourable conditions is impossible. The general lack of thermotolerance data on Mediterranean temperate sessile invertebrates such as sponges and corals, long suspected of being particularly sensitive to temperature, made the disease outbreaks and mass mortalities of the past decade totally unexpected.

First signs of a disease are often associated with a change in colour or bleaching (similar to 'coral bleaching' in tropical coral reefs), the development of a bacterial film on the epidermis, followed by fast decomposition [24]. The taxonomic groups affected by such disease outbreaks are mostly sponges and corals (Table 1), a high proportion of which are endemic to the Mediterranean, and some commercial and key species (e.g. sea-fans; Figure 2). After being initially affected, bare skeletons become exposed following the break-up of necrosed parts which are then colonised by microorganisms and later by macroscopic pioneer taxa [22,24]. Colonised skeletons can remain attached for years, or are eventually detached by storms. This delayed effect explains the great reduction in biomass within populations affected [55]. For species having relatively slow dynamics, even high recruitment rates cannot counterbalance immediate and delayed effects of disease outbreaks, which therefore drastically transform 'seascapes' (Figure 2).

Potential early warnings of recent Mediterranean mass mortality events remained relatively unnoticed. For example, in the 1970s and 1980s, local mortalities of sea urchins and gorgonians had been attributed to positive temperature anomalies, and commercial sponge diseases coincided with a positive NAO [14,56–60]. Although not well documented, these early disease and mortality episodes should have drawn attention to the vulnerability of these systems to seawater temperature increases. The first well-documented Mediterranean multispecies mass mortality events were those of the summers 1999 and 2003. They affected at least 30–40 hard-substrate invertebrate species over several hundred kilometres of coastline between the Tyrrhenian Sea in Italy and the Gulf of Lions in France with some places in Spain also affected [22–24,55,61–65]. In both cases, analysis of meteorological data and seawater temperature records highlighted exceptional temperature patterns. Seawater temperatures of summer 2003 were the warmest in 30 years [23–25]. In 1999 and 2003, not only were temperatures high but the warm and stable conditions lasted for an unusually long time. In both years, a positive correlation was observed between mortality rates and exposure to heat stress [23]. The 1999 event was also shown to have played a significant role in well-documented species replacement and range shift [51]. Little data exist outside the NWM, although 1999 mortalities have been related to similar temperature anomalies in Tunisia and the Aegean Sea [14,24].

Since 2003, some localised mortality episodes have been observed almost every year in different parts of the NWM. The extent of these episodes has been very limited and

Table 1. Mediterranean sessile marine invertebrates affected (+) by mortality events before, during and after the two climatic anomalies of 1999 and 2003

Species names[a]	Status[b]	<1999	1999	2003	>2003	Refs
Porifera						
Agelas oroides				+	+	[14,23,24]
Aplysina cavernicola			+			[24]
Cacospongia mollior			+	+		[23,24]
Cacospongia scalaris		+	+	+		[14,22–24,58,71]
Clathrina clathrus			+			[24]
Crambe crambe				+		[23]
Hippospongia communis	(h, p)	+	+	+		[14,22–24,58,71]
Ircinia dendroides		+	+	+		[14,22,24,58,71]
Ircinia oros		+	+	+		[14,22,24,58,71]
Ircinia variabilis		+	+	+	+	[14,22,24,58,71]
Petrosia ficiformis				+	+	[14,23]
Sarcotragus muscarum		+	+			[14,24,58,71]
Spongia officinalis	(k, h, p)	+	+	+	+	[14,22–24,58,71]
Cnidaria						
Balanophyllia italica				+		[23]
Cladocora caespitosa	(k)		+	+	+	[14,23,24,61]
Corallium rubrum	(k, h, p)	+	+	+	+	[14,23,24,62]
Eunicella cavolinii	(k)	+	+	+	+	[14,22–24,56]
Eunicella singularis	(k)	+	+	+	+	[14,22–24,56,65]
Eunicella verrucosa	(k)		+	+		[23,24]
Leptogorgia sarmentosa	(k)		+	+		[23]
Oculina patagonica		+	+			[24,86]
Paramuricea clavata	(k)	+	+	+	+	[14,22–24,55,59,60]
Parazoanthus axinellae	(k)			+	+	[14,23]
Bryozoa						
Adeonella calveti	(k)		+			[24]
Myriapora truncata			+	+		[23,24]
Pentapora fascialis	(k)		+	+		[23,24]
Reteporella spp.				+		[23]
Turbicellepora avicularis			+			[24]
Mollusca						
Arca spp.			+	+		[23,24]
Lima lima			+	+		[23,24]
Lithophaga lithophaga	(k, sp)			+		[23]
Neopycnodonte cochlear			+			[24]
Ostrea edulis	(h, p)			+		[23]
Spondylus gaederopus	(k)	+		+		[14,23]
Echinodermata						
Paracentrotus lividus	(k, h)	+				[57]
Urochordata						
Halocynthia papillosa			+			[24]
Microcosmus sp.	(h)		+			[24]
Pyura dura			+			[24]

[a] Most of the species listed are Mediterranean endemics.

[b] Key species (k), harvested species (h), protected species (p) or strictly protected species (sp) according to the Berne Convention on the conservation of European wildlife and natural habitats (see: www.coe.int/biodiversity).

although the impacted species usually belong to the same group of sensitive stenothermal gorgonians, sponges and others, none has been of greater intensity than those seen in 1999 or 2003. These events have triggered the growing interest of the scientific community in thermotolerance research [12,21,51,66,67], which is the first step towards developing predictive tools. However, despite the growing number of marine disease outbreaks and mass mortality throughout the oceans, and the potential influence of climate warming on this trend [68], very little is yet known about how infectious agents take advantage of environmental changes in the Mediterranean. Contrary to sponges, corals and gorgonians from coral reefs [54,69,70], the role of potential pathogens has been invoked in the literature but rarely fully demonstrated in the Mediterranean. This was the case for the 1980s commercial sponge disease which resulted from an attack of unidentified bacteria on the sponge skeleton [58,71]. In the 1999 mortality event, although opportunistic microorganisms colonising weak or dying organisms were first suspected [22], several *Vibrio* strains isolated from necrosed gorgonian tissues were finally proven to induce tissue necrosis in experimental conditions at a rather high temperature [72,73]. After the 2003 mass mortality, a dominant strain affecting the Mediterranean gorgonian *Paramuricea clavata* was identified as *Vibrio coralliilyticus*, a thermo-dependent pathogen of tropical scleractinians [73].

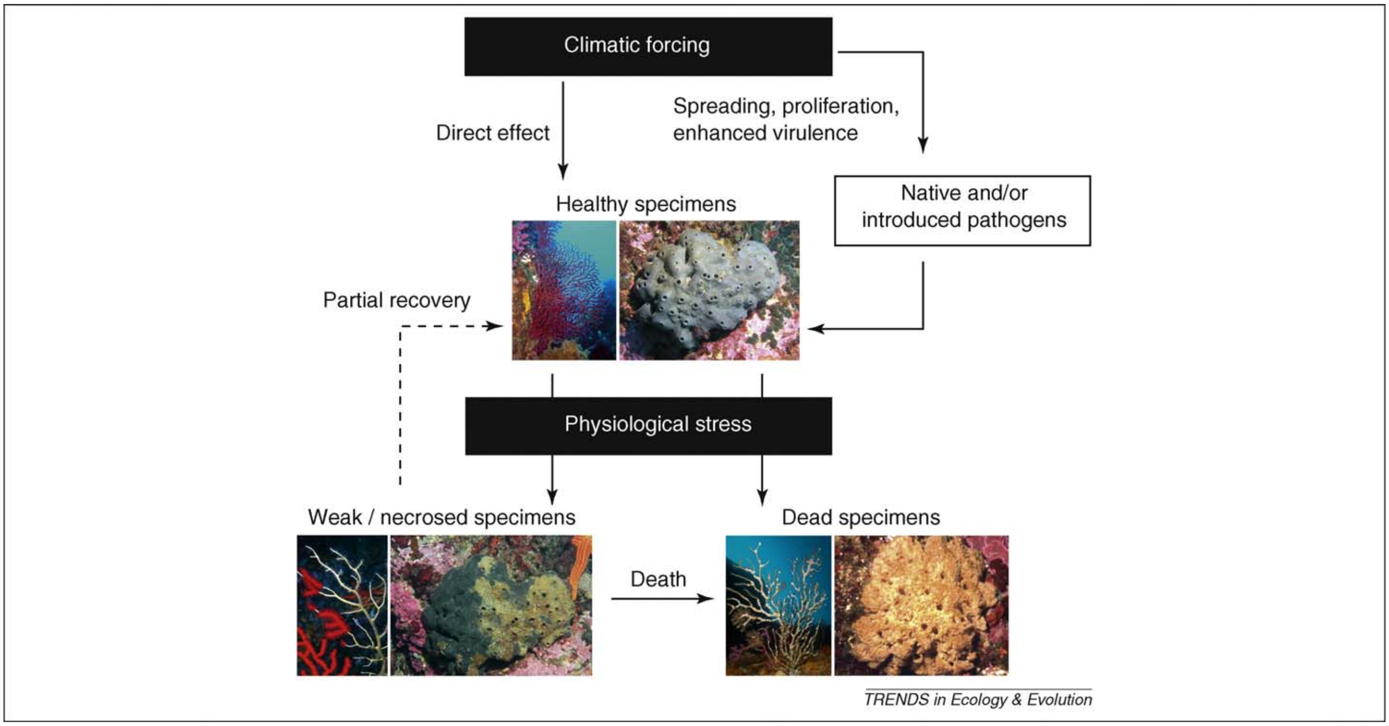

Figure 3. Synthetic view of the combined action of climate forcing and pathogens on the stress levels and disease symptoms of Mediterranean benthic invertebrates. Gorgonians *Paramuricea clavata* (left) and bath sponges *Spongia officinalis* (right) affected at different stages are illustrated. Photographs (reproduced with permission) by J.G. Harmelin, R. Graille and T. Pérez.

As illustrated in increased mortality rates of the starfish *Astropecten jonstoni* along the Sardinian coast [74], the introduction, spread and increased virulence of various pathogenic *Vibrio* strains might have been promoted by climate warming [73]. However, at this point, it is not clear whether we are witnessing the real emergence of pathogens in the Mediterranean, or a growing interest in such epidemiological studies. Further research should be aimed at investigating the causal relationships between heat stress, effect on metabolism, effect of putative pathogens and disease symptoms (Figure 3).

The repetition of disease outbreaks and mass mortality events is also driving major seascape changes and could thus cause important alterations in Mediterranean biodiversity and ecosystem functioning patterns. The eastern Mediterranean, where temperatures are even higher, and where most sensitive species are absent or distributed deeper in cooler waters, provides a putative picture of what the western basin might look like in the near future. Disease outbreaks and mass mortality events, combined with current patterns of species and ecosystem distribution shifts, might thus contribute to some degree to the homogenisation of Mediterranean biota.

Effects of climate change on ecosystem functioning

Adaptive responses to large-scale perturbations such as climate change affect all biological levels. They initially take place at the individual levels but are integrated and translated to upper levels [75]. Environmental parameters, individual organism responses and species interactions, constitute the framework of the ecosystem's dynamic equilibrium. Any change in these parameters must have functional consequences, especially when they involve structuring, key and/or engineer species. However, these types of impacts are poorly documented in the Mediterranean.

Since the Mediterranean is markedly oligotrophic, benthic littoral ecosystems are under strong nutritional forcing. For some benthic suspension feeders, seasonality in food uptake is characterised by summer dormancy due to low food availability [76]. Late summer is also the time when most mass-mortality events have been reported, hence mainly affecting species experiencing summer energy shortage, which includes many structuring species (e.g. anthozoans and sponges) [76]. The combination of thermal stress and food shortage results in mass mortality events likely to disrupt benthic–pelagic coupling.

Cascading effects induce changes in fluxes of matter and energy in trophic webs. They are a potential major mechanism of climate-induced functional change. For instance, planktonic communities, especially copepod assemblages, have a strong influence on pelagic ecosystem fluxes having the role of a biological carbon pump to deeper waters. They have a very strong impact on fish recruitment. Planktonic communities are themselves controlled by gelatinous species, through the predation of copepods, fish eggs and larvae. As a result of repeated positive NAOs in the period 1966–1993, assemblages of the two dominant copepods of the NWM, *Centropages typicus* and *Temora stylifera*, have undergone phenological changes in abundance and composition. In particular, *T. stylifera* displayed a delayed abundance peak and a two-fold reduction in abundance [77]. Positive NAOs also resulted in a shift towards non-siliceous phytoplankton, the preferred food of *C. typicus*, following the disappearance of diatom-dominated seasonal blooms [26,78]. In addition, the positive NAOs of the 1980s seem to have promoted jellyfish blooms resulting in increased predation on planktonic communities [26].

Climatic forcing considerably modified both bottom–up and top–down interactions. Changes in plankton can therefore impact higher trophic compartments such as small pelagic fishes (e.g. anchovy and sardine) whose stocks have been considerably modified over recent decades.

The high productivity of coastal ecosystems (and associated fisheries) depends on terrestrial organic inputs from rivers, which in Europe are linked to NAO variations. In the 1990s, catches of the common sole *Solea solea* in the Gulf of Lions [79] have been correlated to floods of the Rhône River with a time lag of five years. The main prey of sole was found to fluctuate with the Rhône river flow and the 1994 centennial flood induced a threefold increase in polychaetes off the Rhône delta for four years [79,80]. Trophodynamic linkage between climatic anomalies and coastal fishery yields are thus extremely strong and illustrate how climatic forcing could influence the dynamics of ecosystem functioning in the short-term and long-term.

In the deep sea, organic matter input from the photic zone is essential. However, the consequences of climatic forcing on deep-sea ecosystem functioning are still poorly documented, although the eastern Mediterranean is known to be event-driven (e.g. the EMT [10]). For example in the 1990s, the EMT uplifted nutrient-rich waters, resulting in enhanced primary productivity in the euphotic zone, therefore increasing organic matter flux to the seabed, which impacted the deep-sea biota through cascading effects. The density, activity and biomass of bacteria and meiofauna were dramatically reduced, converting the eastern Mediterranean deep seafloor into a 'monoculture' of opportunistic species such as the polychaete *Myriochele fragilis* [10,81].

Mediterranean marine ecosystems are certainly heading towards a climate-induced revolution in their functioning. Their resilience to such changes remains to be determined since other disturbances (biotic and abiotic) combine and interact. For example, the arrival of new species in these ecosystems (through natural range shifts or human-induced introductions) might be a major disruptive force for ecosystem functioning. The arrival of new key species, sometimes acting as ecosystem engineers, could alter competition patterns between native species, and/or transform current ecosystems into new ones. Mediterranean subtidal ecosystems are characterised by low levels of herbivory, low levels of chemical defences, and small pressures from top predators. The arrival of Red Sea macroherbivores in the eastern Mediterranean, such as the rabbitfishes *Siganus luridus* and *S. rivulatus* [82,83], has been shown to disrupt native ecosystems. Another potential key species, the cornetfish *Fistularia commersonii*, a Red Sea top predator, has been observed to very rapidly spread through the Mediterranean. Finally, in the NWM, *Caulerpa taxifolia*, *C. cylindracea* and other unpalatable invasive macrophytes outcompete native ecosystem engineers [84,85]; they have become the dominant species along entire stretches of coast, resulting in dramatically reduced ecosystem diversity, uniform seascapes and a shift towards detritus food webs. Invasive species therefore already play a key role in the 'revolution' underway in the Mediterranean.

Conclusions

The spectacular alterations described above will drive the Mediterranean into uncharted territory, and human interactions with marine life will probably be severely affected. The effects that climate change will have on this region should serve as an example of what could happen globally. We must take the opportunity of an increasing awareness on all sides of this miniature ocean to establish a solid network of observatories that will serve a global purpose, beyond the Mediterranean. Regional action plans, which are a priority, must focus on networking initiatives. National governments seem to have recognised that global change is underway, and will have tremendous ecological, societal and economic impacts. Hopefully, scientific initiatives will serve as useful guidelines to policy makers along the Mediterranean shores, but will also have to address many questions still pending.

Among the uncertainties, it is not known whether all parts of the Mediterranean will be equally affected by global change. Different climatic conditions are involved in the Mediterranean basin, so responses are expected to vary. Answers might come from current efforts to ensure that several eastern and southern Mediterranean stations begin continuous records of temperature and of some indicator species. In addition, initiating new baseline studies and improving existing ones will be an essential step towards understanding the changes happening, shedding light on the way Mediterranean species will cope with ongoing changes.

The most difficult task will be to understand how numerous biotic and abiotic factors interact. Newcomers (whether natural or introduced) can trigger major changes in ecosystem functioning. But the same ecosystems are increasingly exposed to pollution, overfishing, and to alterations in the normal patterns of temperature and several other physical–chemical factors associated with temperature, such as sea level changes and acidification. For example, the combination of elevated temperature and acidification has been shown to be detrimental to the calcification of major bioconstructing coralline algae, not these factors considered alone [29]. If pollution, mass mortalities and biological invasions are also taken into account, the effects on ecosystem functioning are likely to be dramatic. Only a multidisciplinary approach can tackle such a complex problem: linking functional ecology with invasion biology and macrophysiology.

The Mediterranean is a biodiversity hotspot under intense pressure from anthropogenic impacts. Here, we have focused on climate change, but many other pressures are also having enormous effects. Studies on the Mediterranean can hopefully bring new insights on how these interact and how they could eventually lead marine ecosystems to shift significantly. Such an understanding will hopefully provide us with solutions to prevent similar biodiversity decline and ecosystem alteration at the scale of the world's oceans.

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