Mediterranean Sea biodiversity between the legacy from the past and a future of change

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Chapter 1

MEDITERRANEAN SEA BIODIVERSITY BETWEEN THE LEGACY FROM THE PAST AND A FUTURE OF CHANGE

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ABSTRACT

The Mediterranean Sea is a biodiversity hotspot containing between 15,000 and 20,000 marine species, nearly a quarter of which are endemic. The causes of the high Mediterranean biodiversity lie primarily in the turbulent geological history of the basin during the Tertiary and in the dramatic climatic fluctuations of the Quaternary. Both induced a rate of environmental change, and hence species occurrence, which acted as a ‘biodiversity pump’. As a result, species with different biogeographic origins and affinities are found in the basin. A background of warm-temperate Atlantic-Mediterranean species, representing half of the biota, and the endemics are flanked by both boreal and subtropical species. Although the Mediterranean Sea as a whole constitutes a distinctive province of the Atlantic-Mediterranean biogeographic region, a great variety of climatic and hydrologic situations is found in its fairly isolated sub-basins. Thus, a dozen different biogeographic sectors can be recognized: 1) Alboran Sea; 2) Algeria and north Tunisia coasts; 3) Tyrrhenian Sea; 4) Balearic Sea to Sardinia Sea; 5) Gulf of Lions and Ligurian Sea; 6) northern Adriatic Sea; 7) central Adriatic Sea; 8) southern Adriatic Sea; 9) Ionian Sea; 10) Levant Sea; 11) southern Aegean Sea; 12) northern Aegean Sea; the micro-sector of the Straits of Messina can be added. The high Mediterranean biodiversity is presently threatened by the combined action of anthropogenic impacts, introduction of alien species, and climate change. Mediterranean Sea ecosystems are modified at increasingly fast rate, which constitutes an unprecedented phenomenon because of the overwhelming influence of humans, a driver of change not present in the geological past. Humans are modifying the climate through increased carbon dioxide emission, which also causes sea water acidification, and directly altering biodiversity through the deliberate or involuntary introduction of alien species. The present-day Mediterranean is a primary stage for the Anthropocene, the dynamics of human populations being a major factor in the future of its biodiversity. Mediterranean ecosystems must become closely managed ‘new commons’, where natural and socio-economic components are integrated. A complex scenario is emerging, both undetermined and unpredictable. Changes that occurred in the past, before the Anthropocene, are of little help in understanding the future of Mediterranean biodiversity. Three tools, combined, can help to predict and manage change: MPA networks, adoption of field models, and long-term monitoring.

Historia magistra vitae (= history is the teacher of life)
Cicero, *De Oratore* 2.36

INTRODUCTION

Mediterranean marine biodiversity has received only a fraction of the attention accorded to its terrestrial counterpart, despite the great cultural and economic importance that the sea has had for the Mediterranean countries (Costello et al., 2006; Blondel and Médail, 2009).

Attempts to provide estimates of the number of marine species living in the Mediterranean are comparatively recent (Fredj et al., 1992; Bianchi and Morri, 2000; Boudouresque, 2004; Coll et al., 2010), and indicated a number of macroscopic marine species ranging from 8,500 to 17,000. Even the knowledge about conspicuous and popular taxa cannot be considered exhaustive. Fish, for instance, should be the best known inhabitants of the sea, yet the estimated number of fish species living in the Mediterranean passed from 562 to 650 (an increase of more than 15 %!) in the last three decades (Coll et al., 2010). Even larger increments in the numbers of species may be expected from the study of inconspicuous and little known taxa or undersampled habitats such as submarine caves or deep waters (Bianchi and Morri, 2002). If knowledge about macroscopic organisms is still deficient, that of bacteria, archaea, protists and fungi is almost non-existent (Coll et al., 2010). Mediterranean protists and fungi would comprise approximately 4,400 and 3,500 - 4,000 species, respectively, while the number of bacterial and archaeal species can hardly be guessed at, although several recent studies (e.g., Feingersch et al., 2010) are revealing the microbial diversity within the Mediterranean. In all, the Mediterranean Sea is possibly inhabited by somewhere between 15,000 and 20,000 marine species. The present high rate of introduction of exotic species into the Mediterranean Sea (Zenetos et al., 2005, 2008; Galil, 2008, 2009) is likely to make this number keep on growing in the near future.

Focusing on macroscopic organisms, for which our knowledge is comparatively better, the Mediterranean Sea harbours somewhere between 4 and 18 % of the world’s marine species, with large differences according to the phylum taken into account. These figures are remarkable if one considers that the Mediterranean Sea is only 0.82 % in surface area and 0.32 % in volume of the world ocean (Bianchi and Morri, 2000). Endemism, i. e. the number of species living exclusively in the Mediterranean, is also high, averaging nearly one quarter of the whole Mediterranean biota (Tortonese, 1985; Fredj et al., 1992; Giaccone, 1999), and peaking at nearly one-half of the Mediterranean species in the case of some animal groups such as sponges (Voultsiadou, 2009) and amphipods (Bellan-Santini, 1990).

High specific richness, coupled with an important proportion of endemics, makes the Mediterranean Sea one of the world’s ‘biodiversity hotspots’ (Lejeusne et al., 2010). This hotspot, however, is also one of the most threatened (Cuttelod et al., 2009). Present-day

Mediterranean biodiversity is undergoing rapid alteration, but protection measures, for either species or ecosystems, are still inadequate. Numerous national, regional and international actions have been put in place to enhance the conservation of Mediterranean biodiversity, but their concern is only with marine mammals, sea turtles, some fish and a minority of ‘popular’ invertebrates and plants (Bianchi, 2002a). In total, about 200 Mediterranean marine species are listed as in need of some form of protection (Relini, 2000), that is about 1 % of the total species richness of the Mediterranean. European Union directives encourage ecosystem-based management, and most marine ecosystems of the Mediterranean are presently in danger (Bellan-Santini et al., 1994). Although the designation of marine protected areas (MPAs) is generally believed to be the most effective means of protecting them, the goal of protecting at least 10 % of the Mediterranean Sea by 2012, as envisaged at the Word Sustainable Development Summit in Johannesburg in 2002, is still far out of reach (Figure 1). Coastal Mediterranean MPAs cover only 9,910 km², which is 0.4 % of the total surface area of the Mediterranean Sea; adding the great extent (87,500 km²) of the high-seas international whale sanctuary ‘Pelagos’ leads to a total of 97,410 km², approximately 4 % of the Mediterranean (Abdulla et al., 2009). Cumulative no-take area amounts to 202 km², or 0.01 % of the total surface of the Mediterranean. No MPA has been designed to date to encompass deep sea habitats. In addition, the southern and eastern sectors of the Mediterranean Sea are insufficiently protected (Cuttelod et al., 2009), and even in the north-west many MPAs are just ‘paper parks’ - under-developed and/or insufficiently enforced (Francour et al., 2001; Montefalcone et al., 2009).

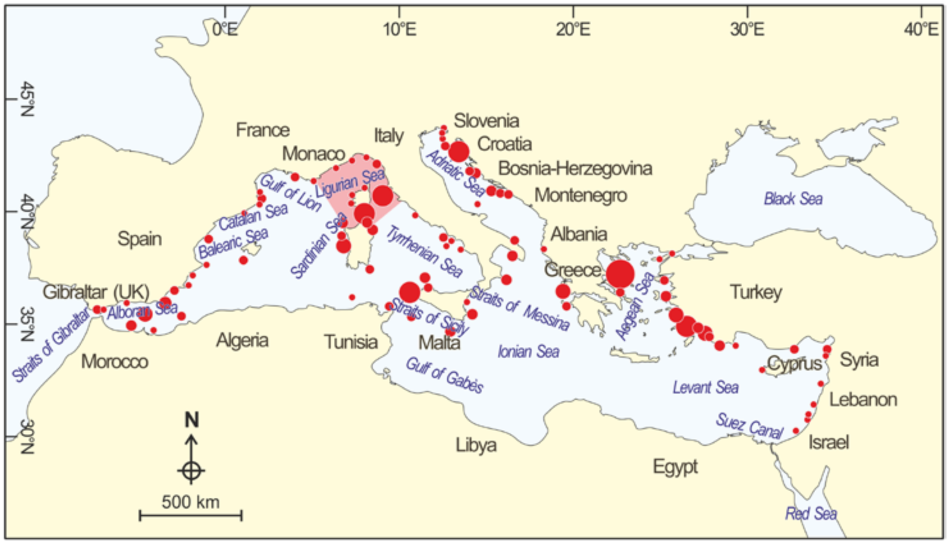

Figure 1. Geographical setting of the Mediterranean Sea. Red circles indicate coastal Marine Protected Areas, their diameter being roughly proportional to the surface protected. The pink triangle is the international whale sanctuary ‘Pelagos’.

Present conservation efforts seem to fade into insignificance in the face of the rapid change that Mediterranean Sea biodiversity is presently experiencing under the combined influence of anthropogenic impacts, introduction of alien species, and climate change. While human impacts and rapid spreading of aliens are unprecedented drivers of alteration, climate fluctuations have been the rule in the geological past. With the help of geological and fossil records and the reconstruction of Mediterranean paleoclimatology, the results of past climate fluctuations can be recognized in the present-day situation. What cannot be easily inferred, however, is which particular mechanisms acted in the past to drive the biota to be as we see it today. How species did expand or contract their range? Were former residents killed by the new climatic conditions or did competition with the newcomers play a major role? Was the penetration and subsequent diffusion of these newcomers a gradual conquest or a sudden flood? How important was the role of refuges, such as the intertidal, submarine caves or the depths? Nowadays, it is possible to observe these mechanisms in action but we do not know, of course, what will be the final outcome. It is often said that the present is a key to the past, and perhaps the reverse is true (Precht and Miller, 2007). Combining our knowledge of the history of the Mediterranean Sea biota with the analysis of the present patterns and trends might help evaluate how likely it is that the same drivers we observe at work today acted similarly in the past and might depict possible scenarios for the future. This would be an essential step for the management and protection of Mediterranean Sea biodiversity.

After summarizing the origin and causes of Mediterranean Sea biodiversity, this chapter will describe the present situation and try to identify the drivers of the on-going modifications.

THE ORIGIN OF MEDITERRANEAN SEA BIODIVERSITY

The causes of the high Mediterranean biodiversity have always intrigued marine biogeographers and ecologists, and still continue to be the subject of much research. Recent syntheses have been provided by Boudouresque (2004), Coll et al. (2010) and Lejeusne et al. (2010), who followed Bianchi and Morri (2000) in arguing that the high biodiversity of the Mediterranean Sea may be explained by historical, paleogeographic, and ecological reasons. By historical reasons, we allude to the fact that the Mediterranean has been intensively studied since antiquity, its exceptionally long tradition of marine research dating back further than for almost any other sea. Aristotle, the first and in many ways the greatest of all naturalists (Briggs, 1974), was already describing the marine life of the Aegean in the 4th century BC (Voultsiadou and Vafidis, 2007). In the 1st century AD Plinius summarized in his *Historia naturalis liber IX* the existing knowledge on the biota of the '*mare nostrum*' (= our sea, as Romans used to call the Mediterranean). During the Renaissance (15th-16th centuries), Italian and French naturalists were attracted to the biota of the Mediterranean Sea (Fantini, 1989), and many Mediterranean marine species were among those described by Carl von Linné in the 18th century. Modern marine biology was born in the 19th century on the Mediterranean shore, where the Stazione Zoologica di Napoli, the oldest of the major marine biological institutions, was established (Riedl, 1980). It might thus be concluded that a larger volume of accumulated knowledge is the prime factor responsible for the higher species richness of the Mediterranean when compared to other seas. However, based on the comparison of marine flora richness and sea surface area for a number of marine biogeographical provinces, Lejeusne et al. (2010) demonstrated that the high Mediterranean species richness is not an artefact of intense investigation: Mediterranean macrophyte species largely outnumber those of other warm-temperate and even tropical provinces, such as the

Gulf of Mexico and the Caribbean Sea, two areas far from being understudied. To this, it may be added the paradox that in one of the alleged best-known seas of the world there are many areas that remain insufficiently studied, such as the north African coast (especially Libya and Egypt), the SE Adriatic, the Aegean and the Levant Sea (Morri et al., 1999, 2009; Logan et al., 2002).

Paleogeographic reasons are probably more important, as the whole basin has experienced a turbulent geological history (Bianchi and Morri, 2000), which has led to an enhanced rate of environmental change, and hence species occurrence, with few equals in the world.

The Late Tethys and the Mediterranean Paleoendemics

The Mediterranean Sea is frequently, although rather imprecisely, considered to be the right heir of the ancient Tethys Sea (Figure 2). The Tethys was a once-extensive, wedge-shaped, eastward-opening equatorial ocean that indented Pangea in the Mesozoic (Suess, 1893). Towards the end of the Mesozoic, in the Cretaceous, the Tethys came to separate the two supercontinents of Laurasia to the north and Gondwana to the south. The expansion of the Tethys became the Mesogea, a sea stretching between the two supercontinents (Douvillé, 1900). After the opening of the Atlantic Ocean, the Mesogea was connecting, through an uninterrupted equatorial belt (the so-called Tethyan seaway), the newly born ocean to the older Indo-Pacific Ocean (the ancestral Panthalassa).

According to geological reconstruction, the ultimate fate of the Tethys has been sealed by plate tectonics. Today’s configuration of the Tethys is the formation of remnant and successor seas, including the Gulf of Mexico, the Caribbean, the Mediterranean, the Red Sea and the intertropical zone of the Indian Ocean. A significant portion of the former Tethys, however, uplifted during the Cenozoic geodynamic evolution marked by the Alpine orogeny, which practically ended in the Oligocene (Mather, 2009). The formation of the Alps, Carpathians, Dinarides, Taurus and Elburz mountains separated the main body of the Tethys, to the south, from the Paratethys, to the north (Figure 3). The Paratethys was a large shallow sea that spread over a large area from Central Europe to western Asia. The Black Sea, the Caspian Sea and the Aral Sea are all that is left of that once vast inland sea (Rögl, 1999).

The overall convergence of Africa and Eurasia, which involved several successive local rifting processes and collisions during the Tertiary, led to the shrinkage of the Tethys in the Oligocene. The consequent diminution of its warming influence in the world oceans produced cold water conditions elsewhere. This may have resulted in higher extinction rates outside the Tethys and the Indo-west Pacific than within these regions. At that time, the Tethys was harbouring a highly diverse warm-water biota. Throughout most of its geological history, Tethys had been the global centre of marine biodiversity - a role assumed today by the area between the Philippines and Indonesia (Briggs, 1974). Can the high biodiversity of the present-day Mediterranean Sea be directly linked to that of its Mesozoic ancestors? The answer is probably no.

Up to the Burdigalian, in the Miocene (Table 1), the connection between the shrunken Mesogean Tethys, which in a sense could be considered as the first sketch of the Mediterranean, and the Indopacific to the east and the Atlantic to the west was maintained. However, the westerly flowing tropical current drastically slackened and biotic exchange between the Atlantic and the Indian oceans was curtailed: this marked the beginning of the distinction between the Indo-West Pacific and the Caribbean-East Pacific biogeographic regions (Crame, 2004).

The connection that previously existed between the proto-Mediterranean and the Indian Ocean in the area of the Mesopotamian trough (Harzhauser et al. 2007) ceased when the Isthmus of Suez was raised during the Miocene orogeny (Figure 3). Marine interconnections only remained in the west, leaving the Atlantic as the only biological reservoir for the adjacent proto-Mediterranean. The marine biota of the Tethys was typically tropical. Coral reefs, built especially by *Porites*, were present up to the Tortonian (Pérès, 1985).

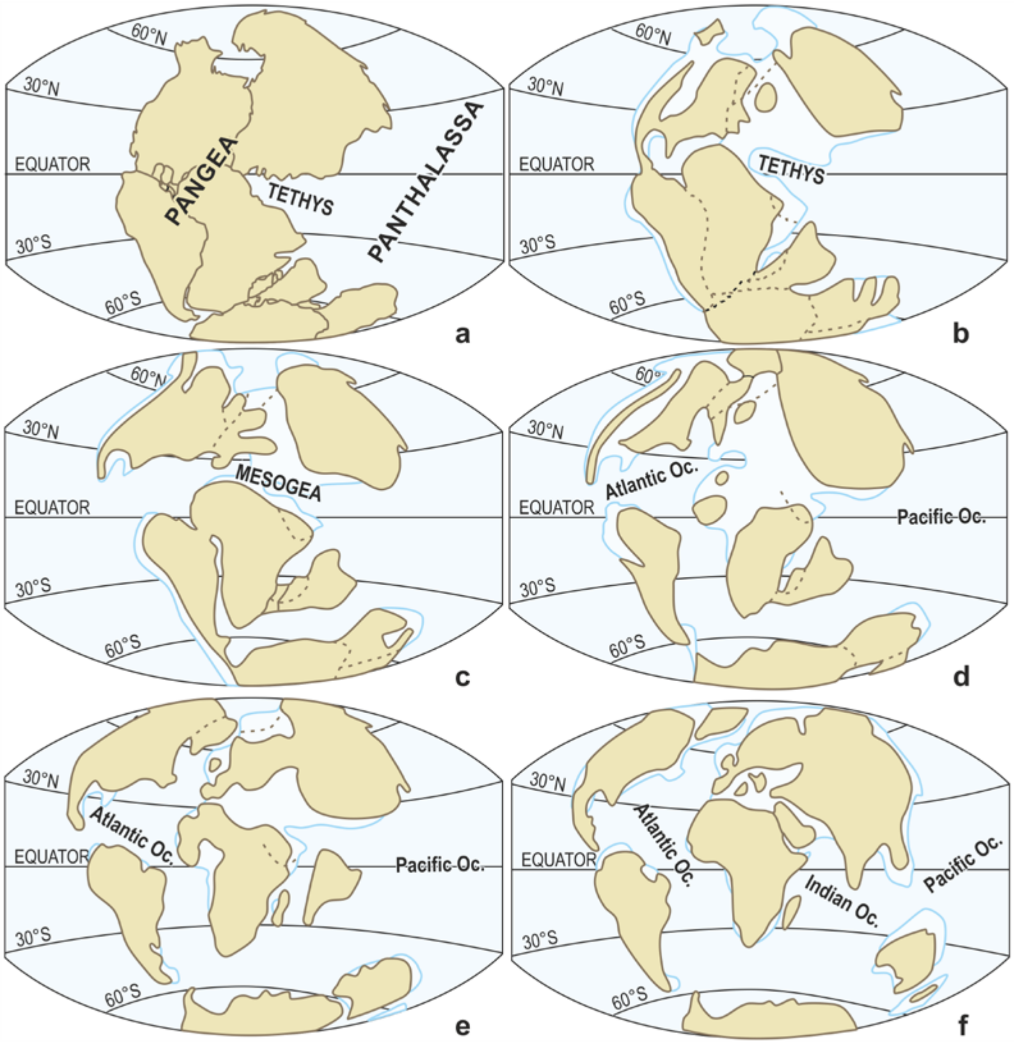

Figure 2. Evolution of the Tethys: a) Jurassic, 200 million years ago; b) Late Jurassic, 140 mya; c) Middle Cretaceous, 105 mya; d) Late Cretaceous, 75 mya; e) Upper Eocene, 50 mya; f) Miocene, 20 mya.

Towards the end of the Miocene, the connection with the Atlantic was also interrupted on several occasions, and the Mediterranean became a virtually isolated sea, with a degree of enclosure of over 99 % (Lejeusne et al., 2010). The segregation of the Mediterranean basin from the Atlantic took place because of the closure of the Betic and Rif straits, roughly in the same region as today's Gibraltar. The negative water balance should have nearly desiccated the Mediterranean (Figure 3), which was probably transformed into a series of large evaporitic lakes during the so-called 'salinity crisis' at the end of the Messinian age (Hsü et al., 1977).

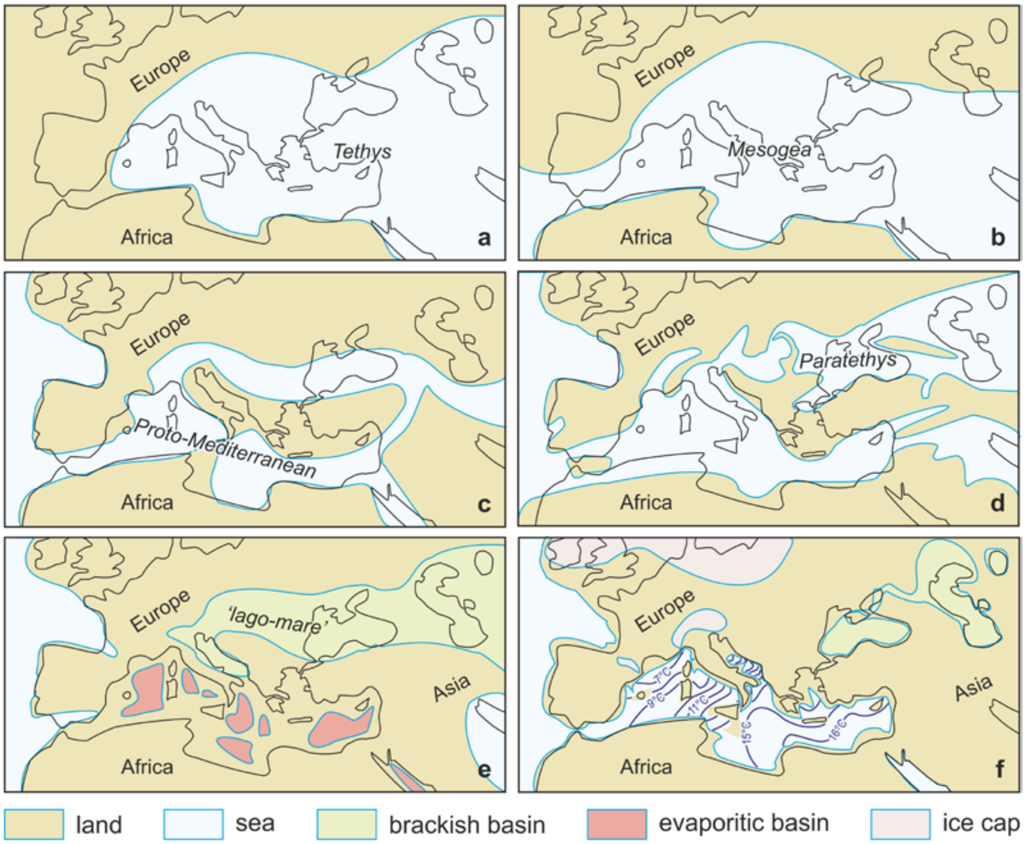

Figure 3. Major phases in the geological evolution of the Mediterranean Sea (plate movement is omitted to represent land masses in their relative position of today): a) the Tethys in the Triassic, 220 million years ago; b) the Mesogea in the Cretaceous, 120 mya; c) the proto-Mediterranean in the Oligocene, 30 mya; d) isolation from the Indian Ocean in the middle Miocene, 10 mya; e) the Messinian salinity crisis in the late Miocene, 5.6 mya; f) the last glacial maximum (Würm glacial) in the late Pleistocene, 20 000 years ago, with winter surface isotherms.

The reconstruction of the series of events that accompanied the Messinian salinity crisis has been the object of many controversies and differing interpretations (Rouchy and Caruso, 2006, and references therein). Most authors, however, agree that within about six hundred thousand years the Mediterranean, which was secluded from free hydrological exchanges with the world ocean, shifted from anoxic pre-evaporitic to evaporitic hyperhaline, then to hypohaline conditions. After the main phase of massive evaporite precipitation, the ending of the Messinian salinity crisis was characterized by the so-called '*Lago Mare* (= Lake Sea) event', i.e. the progressive and generalized establishment of brackish to freshwater aquatic environments throughout the Mediterranean, possibly linked to the flow of the brackish waters of Paratethys into the dry basins (Roveri et al., 2008).

The peculiar hydrological conditions of the isolated Mediterranean during the Messinian salinity crisis should have produced dramatic effects on the biota of ancient Tethyan origin. Again, there is no consensus about what happened (Hsü, 1986). Some authors believe that the biota was completely annihilated, others consider that at least part of it may have survived through the Neogene (Por and Dimentman, 1985). Survival of Tethyan biota should have been possible in fully marine refuges that may have persisted from permanent links with the Atlantic via the Betic portal or in satellite basins within the western Mediterranean, possibly in southern Spain (Por, 2009). The existence of seaways between the eastern Mediterranean and some oceans at that time has also been postulated (Rouchy and Caruso, 2006). Possibly, it is from the remnants of the Tethyan biota that what are today called the Mediterranean paleoendemics should have evolved (Tortonese, 1985). Alleged Mediterranean paleoendemics are known in invertebrate groups (Bellan-Santini, 1990; Rosso and Di Geronimo, 1997) and have especially been described among macrophytes (Basso et al., 1996; Giaccone and Di Martino, 1997).

According to the highly influential opinion of Por (2009), the idea that during the Messinian high salinity crisis all the marine life of the Mediterranean was exterminated is not correct. He firmly maintains that marine life, with many documented examples especially in echinoderms and fishes, survived into the Pliocene in near-shore environments. The classical Tethyan relic, a Messinian survivor (Pérès and Picard, 1964), is the endemic Mediterranean seagrass *Posidonia oceanica* (Figure 4), which however did not leave any fossil evidence in the Mediterranean basin prior to the lower Pleistocene (Di Geronimo, 1984). In a provocative paper, Taviani (2002) opposed the idea of Tethyan relics, arguing that the evidence of biological catastrophe during the Messinian salinity crisis is strong and supported by many independent data. The Tethyan affinity of a given taxon presently found in the Mediterranean Sea must therefore be explained in a different way, such as its survival outside the Mediterranean and subsequent re-introduction into the basin. Taviani (2002) used the emblematic case of *Posidonia oceanica* to critically address the problem of the Tethyan relics. He said that the present disjunct occurrence of the bi-temperate genus *Posidonia*, with one species endemic to the Mediterranean and eight to South Australia (Den Hartog, 1970), represents a real puzzle for biogeographers (Figure 4). He also argued that first one must explain how *P. oceanica*, a temperate seagrass known today to be restricted to the Mediterranean Sea, could have escaped unharmed the substantial temperature modifications transforming the Mediterranean basin from Neogene tropical to Pleistocene boreal conditions. If the species is so adaptable, why is its range so restricted at present? Although there is no strong evidence to identify the seagrass species inhabiting the Mediterranean during the late Neogene, it is likely that they were warm taxa of tropical-subtropical affinity, not related to the temperate *Posidonia* of today. An additional problem is the possibility that the Messinian salinity crisis would have left the stenoecious *P. oceanica* untouched. An alternative view is that *P. oceanica* may be a secondary endemic. Its ancestor was inhabiting the eastern Atlantic and only in relatively recent times (middle-late Pliocene?) was

Table 1. Most significant steps in the history of Mediterranean Sea biota. Mya = million years ago.

Mya	Era	Period		Epoch	Age	Standard Stages	Paleogeography	Paleobiogeography
0.012	Cenozoic	Quaternary		Holocene				Present day biota
0.08				Pleistocene	Tarantian		Alternate warm and cold phases, currents reversal at Gibraltar	
0.126						Tyrrhenian		Main penetration of subtropical (Senegalian) biota
0.781					Ionian			
1.22					Calabrian	Sicilian		Main penetration of boreal (Celtic) element
1.5						Emilian		
1.8						Santernian		
2.6					Gelasian		Progressive cooling	Mass extinction of subtropical Atlantic biota
3.6		Tertiary	Neogene	Pliocene	Piacenzian			Subtropical Atlantic biota
5.3					Zanclean		Atlantic flood	Repopulation of the Mediterranean. Subtropical Atlantic biota
7.2				Miocene	Messinian		Salinity crisis	Mass extinction of the paleomediterranean biota
11.6					Tortonian		Definitive closure Suez Isthmus	Tropical biota, Atlantic affinity. Paleomediterranean element
13.8					Serravallian		Tethys (Mesogea)	Tropical biota, Indo-west Pacific affinity
16.0					Langhian			
20.4					Burdigalian			
23.0					Aquitanian			
33.9			Paleogene	Oligocene				
55.8				Eocene				
65.5				Paleocene				
145.5	Mesozoic	Cretaceous						

its range confined to the Mediterranean basin only. The reason for such restriction still needs to be investigated in depth. Considering the poor preservation potential of non-calcareous plants, the historical record of seagrass could be only tracked through the record of fossil remains (rhizomes, leaves, fruits). Seagrass remnants interpreted as *Posidonia* date back to the Eocene of the Paris basin (Fritel, 1909) and the Paleocene of Belgium (Stockmans, 1932), amongst others. Admittedly, the *Posidonia oceanica* problem is an open issue, and according to Taviani (2002), it is not a strong argument to anchor the concept of true Tethyan relics.

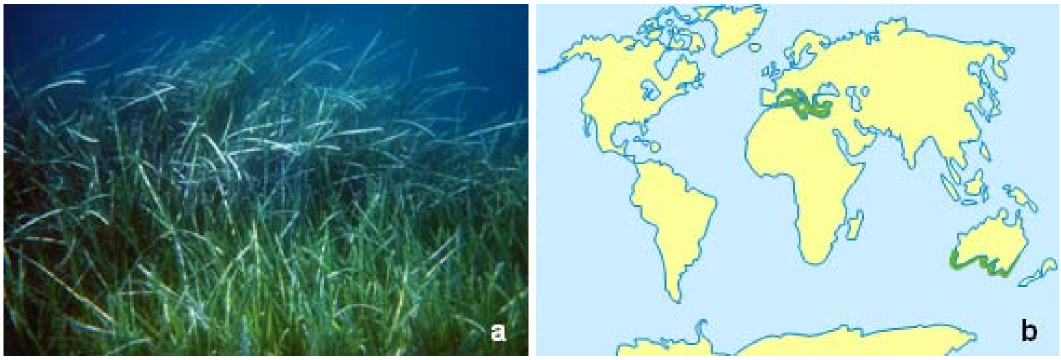

Figure 4. The seagrass *Posidonia oceanica* (a) and the disjunct range of the genus *Posidonia* (b): *P. oceanica* is endemic to the Mediterranean Sea, whereas *P. angustifolia*, *P. australis*, *P. coriacea*, *P. denhartogii*, *P. kirkmanii*, *P. ostenfeldii*, *P. robertsonae* and *P. sinuosa* are restricted to South Australia.

The situation is different with those paleoendemics that possibly are relics of the Paratethys, rather than of the Tethys. As the Paratethys evolved in a brackish water basin, these relics must be comprised of euryhaline species: examples are known in fish and invertebrates (Bianchi et al., 2004). A peculiar case is that of *Marifugia cavatica*, the only freshwater serpulid species in the world (Bianchi, 1981). It lives in karstic caves in a region of approximately 50,000 km^2 that reaches Monfalcone and Trieste to the NW and includes Dalmatia, Croatia and Slovenia (Figure 5). Some stations of Slovenia and Croatia belong to the Danube basin, all the others to water courses draining into the Adriatic Sea. *M. cavatica* thrives on the walls of karstic cavities where it can build large and crumbly masses of tubes (to several tens of m^2 circa 1 m thick). It can survive the summer drying that sometimes occurs in underground water courses, exploiting the high humidity of these environments and the condensation of water. It is thought that the extreme hardness of karstic waters favoured the possibility of survival in fresh water of a species of marine origin (Sacchi and Testard, 1971). Many inhabitants of continental underground waters are derived from marine phyletic lineages (Riedl and Ozretic, 1969): small-sized species originate in the interstitial environment and penetrated into karstic regions through the net of fissures existing in the karst rock; conversely, large-sized species should have penetrate through the so-called ‘marginal caves’, which form at the transition between marine caves and continental caves. *Marifugia* is taxonomically close to *Ficopomatus*, a brackish-water genus (Pillai, 2008; Kupriyanova et al., 2009): its affinities and present geographic distribution indicate its Paratethian origin (Bianchi and Sanfilippo, 2003).

Marine caves provide further elements to the controversy about the origin of Mediterranean paleoendemics. Logan et al. (2004) discussed the case of *Tethyrhynchia mediterranea*, a small brachiopod that has not been recorded from the Atlantic and exhibits enigmatic taxonomic affinities, being the only species of the genus and belonging to the separate family Tethyrhynchidae. The species probably evolved by neoteny and, at present, is only known from the dark parts of submarine caves (Logan and Zibrowius, 1994). There is little, if any, evidence of recent speciation in Mediterranean submarine caves (Bianchi et al., 1996): they commonly harbour preadapted species derived from cryptic or deep habitats (Balduzzi et al., 1989) but may also act as refuges for archaic forms of Tethyan origin (Harmelin et al., 1985). Larval brooding and development of *T. mediterranea* indicate low dispersal ability, mitigating against recent colonization and suggesting that its present biogeography may represent relict populations of a wider distribution in the Mesozoic Tethys (Logan et al., 2004). Further searching for this species from cryptic and deep habitats within and outside the Mediterranean, and its possible ancestors in Cenozoic rocks in the region, will help clarify its origin.

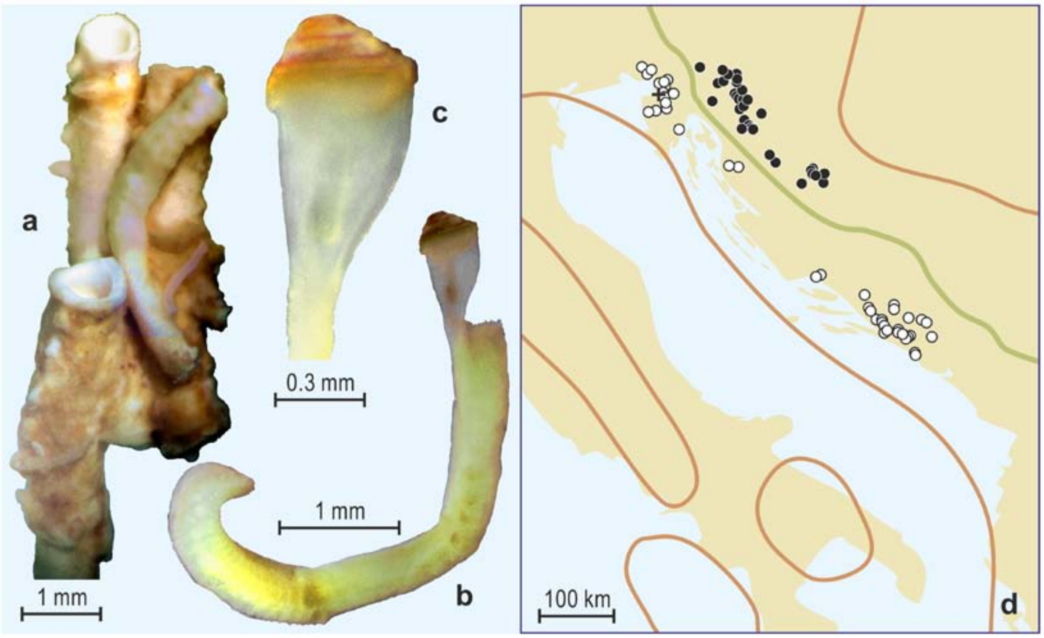

Figure 5. The troglobitic fresh water serpulid *Marifugia cavatica*, supposedly of Paratethyan origin: a) tubes; b) worm extracted from its tube; c) operculum; d) present geographical distribution with respect to the Miocene coastline (thick brown line): open circles represent localities that drain toward the Adriatic Sea, black circles localities that are drained toward the Danube and hence the Black Sea, the thick yellow line representing the water divide. Cross shows the locality where fossil tubes of *Marifugia* were found.
d) Redrawn and modified from Bianchi and Sanfilippo (2003) and Kupriyanova et al. (2009).

The Pliocene Recolonization and the Origin of the Neoendemics

Whoever is right in the controversy about the alleged sterilization of the Mediterranean during the Messinian salinity crisis, there is no doubt that the once high biodiversity of the Mediterranean was severely reduced because of the abnormal hydrological regime. Full marine conditions through the whole basin were restored only when the flow of Atlantic waters re-entered the Mediterranean through the newly formed Gibraltar portal at the dawn of the Pliocene, in the Zanclean. The flood resulting from this catastrophic event was extremely abrupt: it has been estimated that is was three orders of magnitude larger than the present Amazon River, implying a sea level rise in the Mediterranean of more than ten metres per day (Garcia-Castellanos et al., 2009). The once-desiccated basin was thus refilled in an extremely short period (Figure 6).

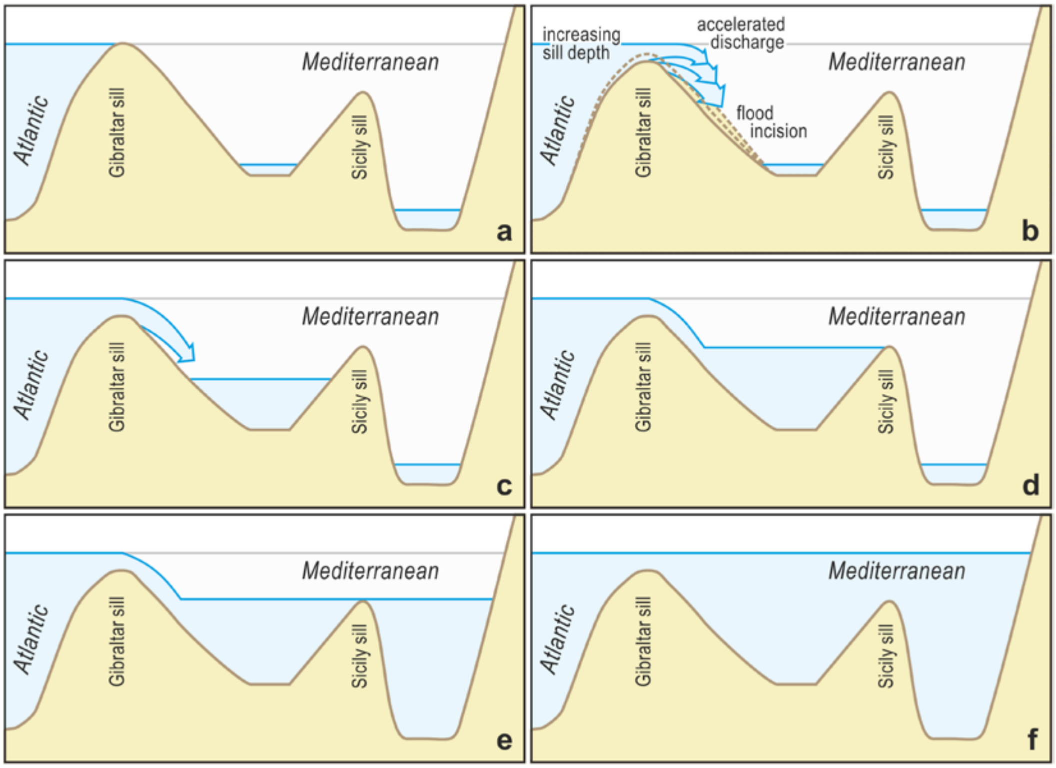

Figure 6. Phases of the Zanclean flood at the end of the Messinian salinity crisis: a) initial time; b) Atlantic water floods into the Mediterranean, progressively eroding the Gibraltar sill; c) time of maximum incision rate; d) western Mediterranean level reaches the Sicily Sill; e) eastern basin level reaches the Sicily Sill; f) the Mediterranean becomes full.
Redrawn and modified from Garcia-Castellanos et al. (2009).

With the water came the biota, so that the Mediterranean Sea was repopulated by species of Atlantic origin. The Atlantic passive margins adjacent to the Mediterranean have a modest record of Tertiary-to-Quaternary successions, and appear especially poor in marine examples, due to the lack of any important uplift. This hampers a full evaluation of the origin, migration, extinction and evolution of marine taxa. However, most authors maintain that the present

Mediterranean marine biogeography is inherited from the post-Miocene recolonization from the Atlantic, with all its evolutionary implications (Pérès, 1985; Sarà, 1985). The claim of a Pliocene interconnection between the Mediterranean and the Red Sea is considered unsubstantiated by any solid evidence (Taviani, 2002).

Through the Early to Middle Pliocene (Table 1), the Mediterranean biota maintained a subtropical character. In the Late Pliocene, the climate turned to temperate, although the temperature was 4 °C warmer than at present (Combourieu-Nebout et al., 2000). At the beginning of the Pleistocene, the climatic deterioration led to the so-called 'Gelasian crisis', i.e. extinction pulses that affected the warm stenothermal biota (Por, 2009). Once again, much of the pre-existing biota went lost, while among the survivors originated the Mediterranean neoendemics (Fredj et al., 1992). Emblematic neoendemic species, possibly of Pliocene origin, include several gorgonian seafans (Morri et al., 2008), such as *Paramuricea clavata* (Figure 7). The genus *Eunicella* includes the Atlantic-Mediterranean species *E. verrucosa* and

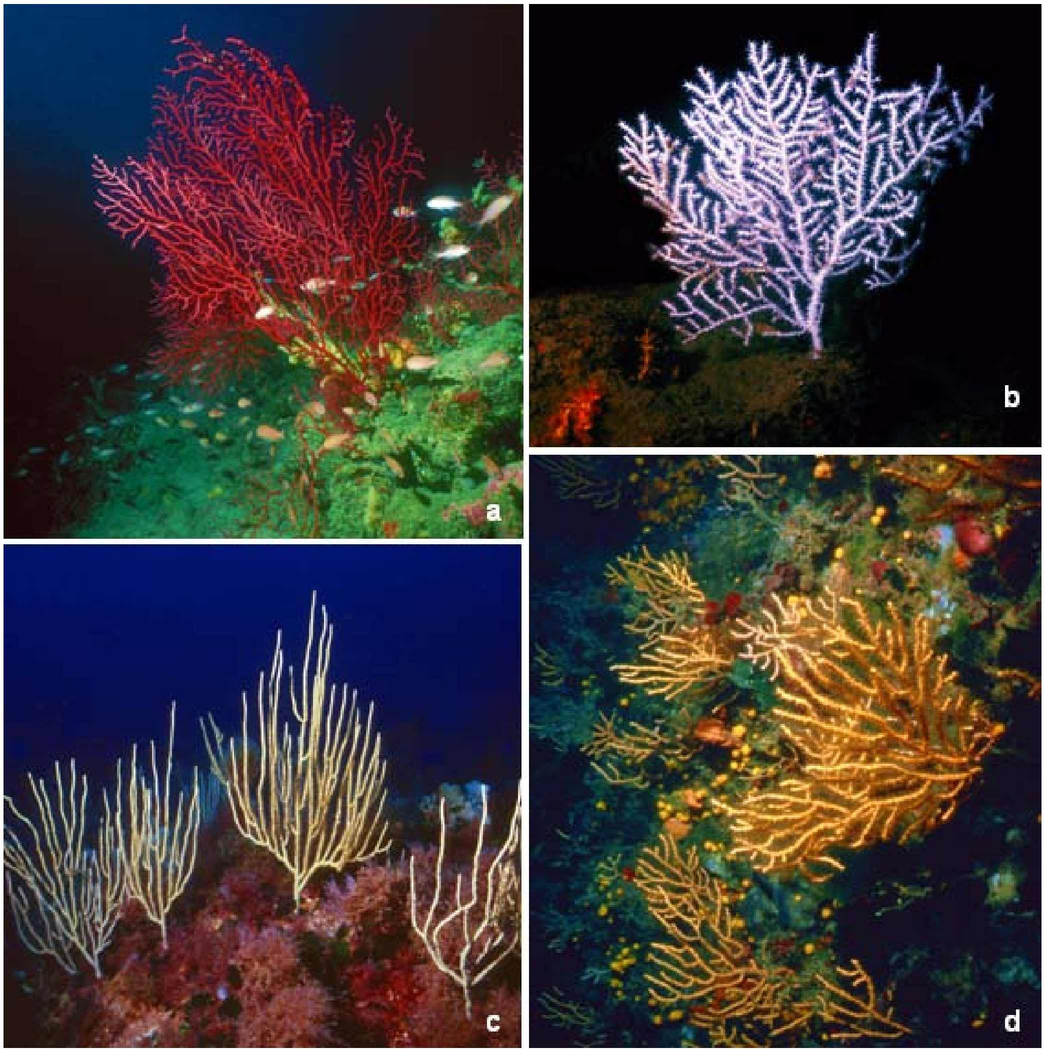

Figure 7. Common Mediterranean gorgonians: a) *Paramuricea clavata*; b) *Eunicella verrucosa*; c) *Eunicella singularis*; d) *Eunicella cavolini*.

the two Mediterranean endemics *E. singularis* and *E. cavolini*: the three species are strictly related taxonomically but occupy different habitats in the Mediterranean (Grasshoff, 1992), which might indicate recent sympatric speciation by ecological isolation. A fourth species, *E. filiformis*, which is only distantly related to the previous three, is restricted to the Eastern Atlantic, and has been found in the Mediterranean Sea only in close vicinity of Gibraltar.

The Quaternary and the Shaping of the Modern Biota

The Early Pleistocene witnessed the onset of astronomically-driven paroxysmal glacial-interglacial cyclicity (Shackleton et al., 1990). The cool climatic mode was predominant, warm intervals being confined to short-lasting interglacials: out of the approximately 100,000 years representing a glacial-interglacial cycle, only one-tenth was marked by warm temperate conditions. The alternation between glacials and interglacials caused sea level fluctuations worldwide (Figure 8) and implied the penetration into the Mediterranean Sea of species with boreo-arctic affinities (the so-called Celtic biota) or with (sub)tropical affinities (the so-called Senegalian biota), respectively (Table 1). These different immigration waves concerned especially the shallow-water biota, which exhibited alternating cold- and warm-temperate affinities (Pérès, 1985). The deep-water fauna suffered significant extinction rates because of the onset of homothermic conditions (Taviani, 2002).

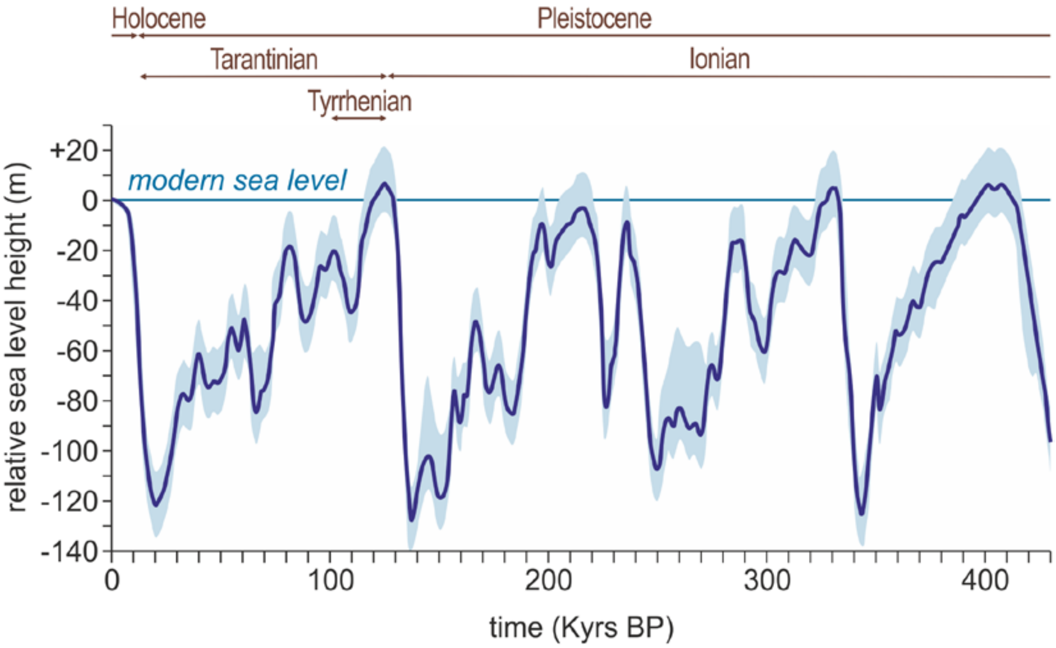

Figure 8. Eustatic sea-level curve (bold black line), with associated confidence intervals (grey area), for the late Quaternary.

Redrawn and modified from Rovere et al. (2010), based on data kindly provided by C. Waelboreck (Gif-sur-Yvette, FR).

The alternating entries of boreal and southern invaders were probably related to the current system in the Straits of Gibraltar, itself controlled by the input of meteoric and continental waters that this basin received. The hypothesis of current reversal through the Straits of Gibraltar has been summarized by Pérès (1985). In the conditions of a characteristic interglacial period, the Mediterranean region had a warm and arid climate and a deficient water balance (Figure 9). There was, therefore, an important penetration of Atlantic surface water into the Mediterranean through the Straits of Gibraltar. The Atlantic itself was in a period in which warm temperature waters extended considerably further towards the north (thus modifying the biogeographical provinces). All the conditions were therefore present that would allow both the introduction and maintenance of a (sub)tropical littoral biota in the Mediterranean. The temperature of the homothermal deep layer was higher than in present times, because the temperature of the surface waters during the coldest months of the year (which determine the temperature of the deep water) was also higher. Such conditions were, therefore, inimical to the survival of previous boreal forms. During a glacial period, eustatic regression would reduce the water level everywhere, including at the Straits of Gibraltar. Further, the displacement of the arid zone towards the south implies that the humid temperate and cool zone would come to occupy the Mediterranean regions. Under these conditions, precipitation and run-off would increase, so that the water balance would be reversed, and a surface current of Mediterranean water would pass outwards towards the Atlantic, while a bottom countercurrent of Atlantic water would be directed inwards, towards the Mediterranean. The hypothesis of currents reversal explains well the successive waves of shallow-water immigrant biota during interglacial periods, less so those of deep-water fauna during glacial periods. In the lower Pleistocene and, more recently, in the last glacial period (Würm) much deep-water fauna of Atlantic origin, such as that associated to the so-called ‘white corals’ *Lophelia pertusa* and *Madrepora oculata* (Mastrototaro et al., 2010) thrived through the Mediterranean. While the entry of Atlantic species with teleplanic larvae can be easily envisaged, that of species with short-living larval stages can be explained only by accepting the idea that the Gibraltar sill was much lower than the present 350 m depth (Di Geronimo, 1990).

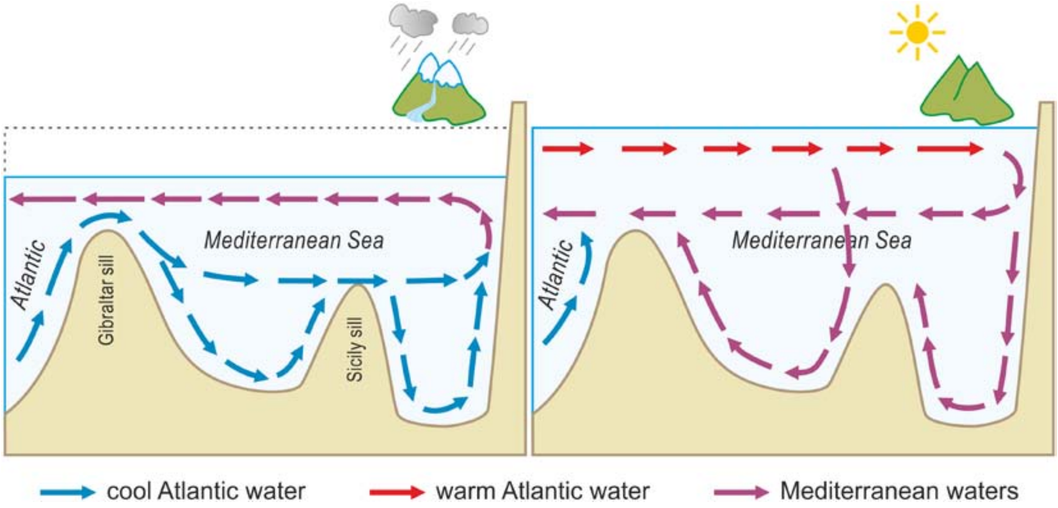

Figure 9. Current reversal at Gibraltar during the Quaternary: left panel, glacial phase; right panel, interglacial phase.

Much of the biota that penetrated into the Mediterranean during the alternating cold and warm periods became extinct when the climatic conditions reversed: among the best know examples are two molluscs, the bivalve *Arctica* (= *Cyprina*) *islandica* (a Celtic element) and the gastropod *Strombus bubonius* (a Senegalian element). Some species took refuge in the depths. Many boreal forms live deeper on average in the Mediterranean than in the North Atlantic: examples include the gorgonian *Swiftia dubia* (Grasshoff, 1992) and the Norway lobster *Nephrops norvegicus* (Wirtz and Debelius, 2003). The temperature of 12-13 °C in the homothermal Mediterranean deep water is probably the upper limit of tolerance for these cold water species. Yet, the depths below the summer thermocline have paradoxically been a refuge also for some species of warm-water origin, such as the sea urchin *Centrostephanus longispinus* (Francour, 1991): for this warm stenothermal species, adapting to a comparatively lower but constant temperature has probably been easier than tolerating fluctuations between 12-13 °C and 25 °C or more in shallow water.

Other survivors of these climate-driven extinction waves possibly resulted in further examples of neoendemics, which often exhibit peculiar distributions in the Mediterranean Sea: for instance, the brachiopod *Lacazella mediterranea*, whose closest relative is the sub-tropical western Atlantic species *L. caribbeanensis*, is restricted to the southwestern area of the Mediterranean, along the main path of the incoming Atlantic current (Logan et al., 2004). The Alboran basin, at the entrance to the Mediterranean, acts as a buffer, reducing gene flow (Boudouresque, 2004), so that it is in many cases possible to recognize couples of vicariant species, one endemic to the Mediterranean and the other distributed in the nearest Atlantic, either in colder or warmer waters (Figure 10). For example, the shore crab *Carcinus maenas*,

Figure 10. Examples of Atlantic-Mediterranean vicariant pairs in crabs and fishes: a) *Carcinus maenas* (Atlantic) and b) *C. aestuari* (Mediterranean); c) *Chromis limbata* (Atlantic) and d) *C. chromis* (Mediterranean).

Figure 11. Atlantic-Mediterranean seastars: a) the nominal taxon *Astropecten irregularis*, from the Atlantic, is represented by the subspecies *pentacanthus* in the Mediterranean; b) *Marthasterias glacialis* has a latitudinally wide distribution in the eastern Atlantic, Mediterranean included.

ranging from Iceland, Northern Norway and Faeroes to Mauritania, penetrates just into the westernmost Mediterranean, being replaced in the major part of the basin by the vicariant *C. aestuari*, which is also found in the Canary Islands (Wirtz and Debelius, 2003). The pomacentrid fish *Chromis limbata*, ranging from the islands of Macaronesia (Azores, Madeira, Canaries) to the Gulf of Guinea, is replaced in the Mediterranean, Black Sea and southern Portugal by *C. chromis* (Debelius, 1997). Of course, the present-day Straits of Gibraltar is not an absolute barrier, and many Mediterranean endemics can spread to the nearest Atlantic coast, such as of Morocco or the Gulf of Cadiz, while many Atlantic species penetrate into the Alboran Sea (Tortonese, 1978). In some instances, vicariance is expressed at subspecific, rather than specific, level: this is the case for the starfish *Astropecten irregularis* (Figure 11), represented by the subspecies *pentacanthus* in the Mediterranean (Tortonese, 1965). Further examples are known in other invertebrates and fish (Bianchi et al., 2004): in the barnacle *Chthamalus montagui* the Atlantic and Mediterranean forms are separated (Dando and Southward, 1981), and the Atlantic flounder *Platichthys flesus flesus* is replaced in the Mediterranean by the subspecies *italicus* (Galleguillos and Ward, 1982). Endemism at subspecific level may be considered as comparatively recent.

Current reversal at Gibraltar was not the expression of distinct glacial and interglacial maxima, but can be interpreted as successive modifications of smaller amplitude. Of course, the maximum effects would more or less coincide with the maxima of the glacial or interglacial periods. The secondary oscillations would, nevertheless, have had marked influences. There were also retarding processes, the most evident of which is associated with the melting of the glacial mass during a period of deglaciation and which would have been prolonged in the Mediterranean during a part of the subsequent eustatic transgression. At each phase, the biota that had entered the basin during the previous phase was subject to high evolutionary pressures, which may have been cause of either extinction or speciation; Lejeusne et al. (2010) defined the Mediterranean as a factory designed to produce endemics. Without fossils or molecular clock analyses it would be unwise to state when a specific neoendemic taxon was born. The major moments were probably the Late Pliocene for warm-water taxa and the Early Pleistocene for cold-water taxa, later moments in the Quaternary having possibly been less effective. The last introductions of warm-water species before modern times have been too recent to produce endemics. Instead, they originated disjunct Atlantic-Levantine distributions, such as in the case of the parrot fish *Sparisoma cretense* and the sea anemone *Telmatactis cricoides* (Figure 12); other well known Atlantic-Levantine examples include the ghost crab *Ocypode cursor* (Wirtz and Debelius, 2003), and the selachians *Carcharhinus brevipinnis* and *Taeniura grabata* (Tortonese, 1978). The (sub)tropical biota that lives today along the West African coast, reaching Macaronesia, is separated from the Gibraltar portal by the cold Canaries Current (Figure 13). During the last interglacial, there is fossil evidence that part of this biota succeeded in breaking the Canaries current barrier to spread throughout the whole Mediterranean (van Kolfschoten et al., 2003). In the subsequent glacial period, winter temperature dropped to as low as 7 °C in the Western Mediterranean, while never dropping below 16 °C in the Levant Sea (Por, 2009). Consequently, the Atlantic (sub)tropical biota became extinct in the western basin but survived in the Levantine ‘cul de sac’.

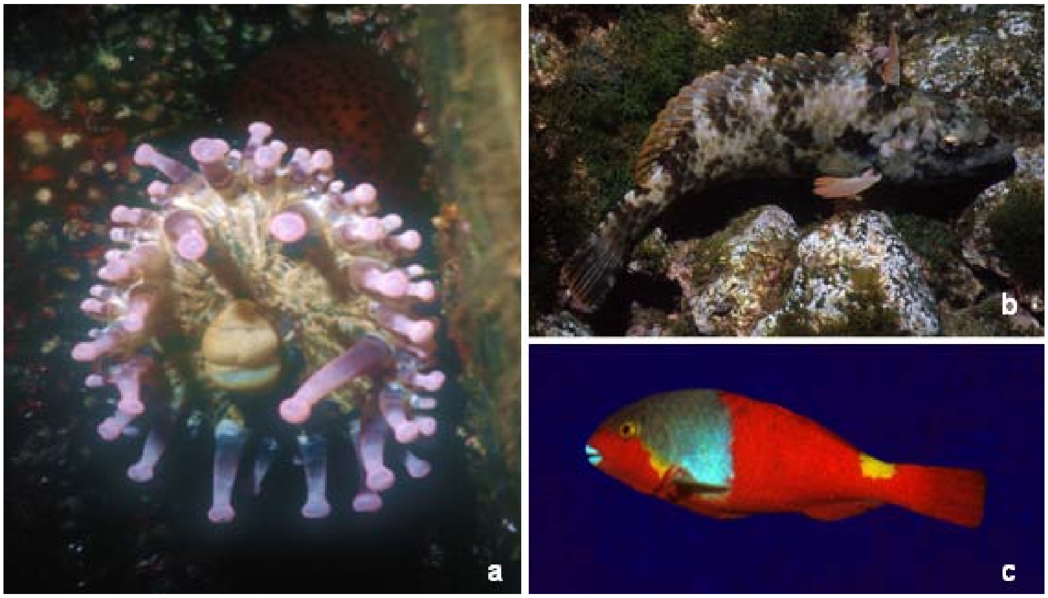

Figure 12. Atlantic-Levantine species: a) *Telmatactis cricoides*; b, c) *Sparisoma cretense*, male and female.

The Mediterranean basin has experienced major sea level change during glacial cycles, evidence for which occurs in both the geological and archaeological records, of decreasing resolution with time, throughout the last glacial cycle (Lambeck and Purcell, 2005). At the last glacial maximum (LGM), approximately 23-19 thousand years ago, the Mediterranean Sea surface dropped to 90-130 m below the present sea level (Figure 3). At that time, both the Straits of Gibraltar and the Straits of Sicily were much narrower, the island of Elba was connected to continental Italy thus reducing the exchange between the Tyrrhenian and the Ligurian seas, roughly half the present Aegean and Adriatic seas were dry, most of the present southern Ionian Sea was replaced by a 300 km wide coastal plain emergent from Tunis to Tripoli, and so was the Gulf of Lion (Rohling et al., 2009). The sea level started to rise when the climate warmed again at the beginning of the present interglacial, which has been however punctuated by cooling events recurring roughly every 1500±500 years (Lejeusne et al., 2010). The most significant cooling occurred in the Younger Dryas (YD), 12.8 to 11.5 thousand years ago (Berger, 1990). The YD saw a rapid return to glacial conditions in the Atlantic-Mediterranean region and possibly a further current reversal at Gibraltar (Huang and Stanley, 1974); at that time, Mediterranean Sea level was about 50 m below the present one (Figure 14). After YD, both sea level and temperature resumed the rapid rise to 8.2 thousand years ago (Lambeck and Bard, 2000; Sivan et al., 2001), when another sudden decrease in temperatures occurred (the so-called 8 ky event), although milder than the YD cold spell (Alley and Ágústsdóttir, 2005). The Mediterranean Sea level stabilized

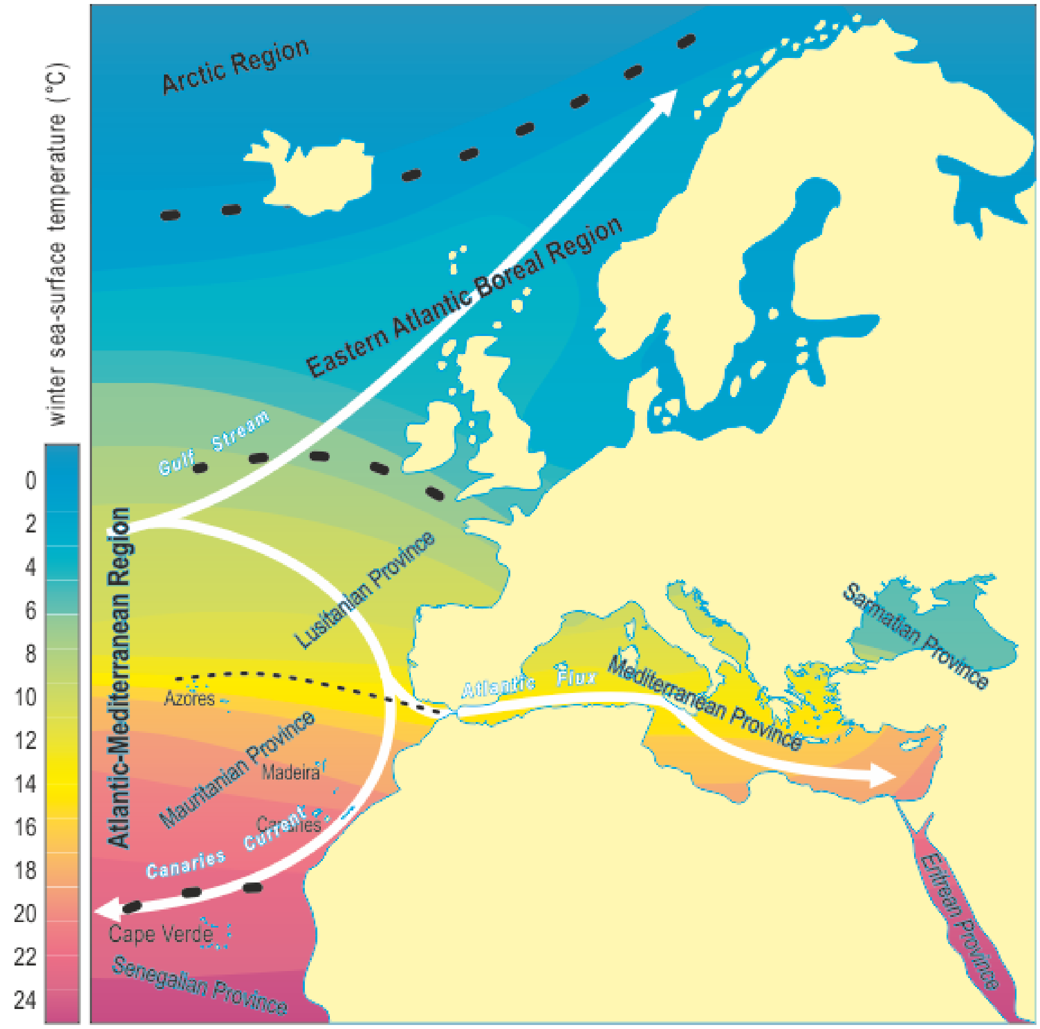

Figure 13. Boundaries and subdivisions of the Atlantic-Mediterranean Region, in relation with winter sea surface temperature pattern. Major current systems are also indicated.

around the present height by 6 thousand years ago (Rovere et al., 2010 and references therein), while temperature was higher than present for the whole period called Holocene Climate Optimum (HCO), 9 to 5 thousand years ago (Kaufman et al., 2004). The HCO was followed by a gradual decline in temperature until about 2 thousand years ago. Then the climate saw other significant fluctuations, the most notable of which are perhaps the Medieval Warm Period (MWP), roughly around the end of the first millennium of the present era, and the Little Ice Age (LIA), between the 14th and the 19th centuries (Mann et al., 2009). Sea temperature was approximately 1 °C warmer than today in the MWP and approximately 1 °C cooler than today in the LIA (Keigwin, 1996).

It is more than likely that these recent sea level and climatic fluctuations influenced the Mediterranean biota, possibly through altered water circulation, but little documentation is available about the possibility and extent of biotic exchange between the Mediterranean and the adjacent seas. Por (1971) hypothesized that during the Flandrian transgression (up to + 4 m, circa 6000 years ago) a waterway connected the Mediterranean and the Red Sea, possibly allowing Indo-west Pacific species to enter the Levant Sea. The Levant Sea was (and still is) a suitable receptacle of tropical elements because of its higher temperature and the resulting undersaturation with temperate biota. Taviani (2002) called it a ‘Godot basin’, taking the term from *En attendant Godot* by the American writer Samuel Beckett (1906-1989). Mr. Godot is the quintessence of a person expected but never arriving on the scene. Similarly, a basin in principle fully available to colonization was waiting for tropical-subtropical invaders at the peak of most interglacials, but was little supplied by the west-African reservoir because the cooler waters of the Mauritanian province and the western Mediterranean acted as a physiological barrier.

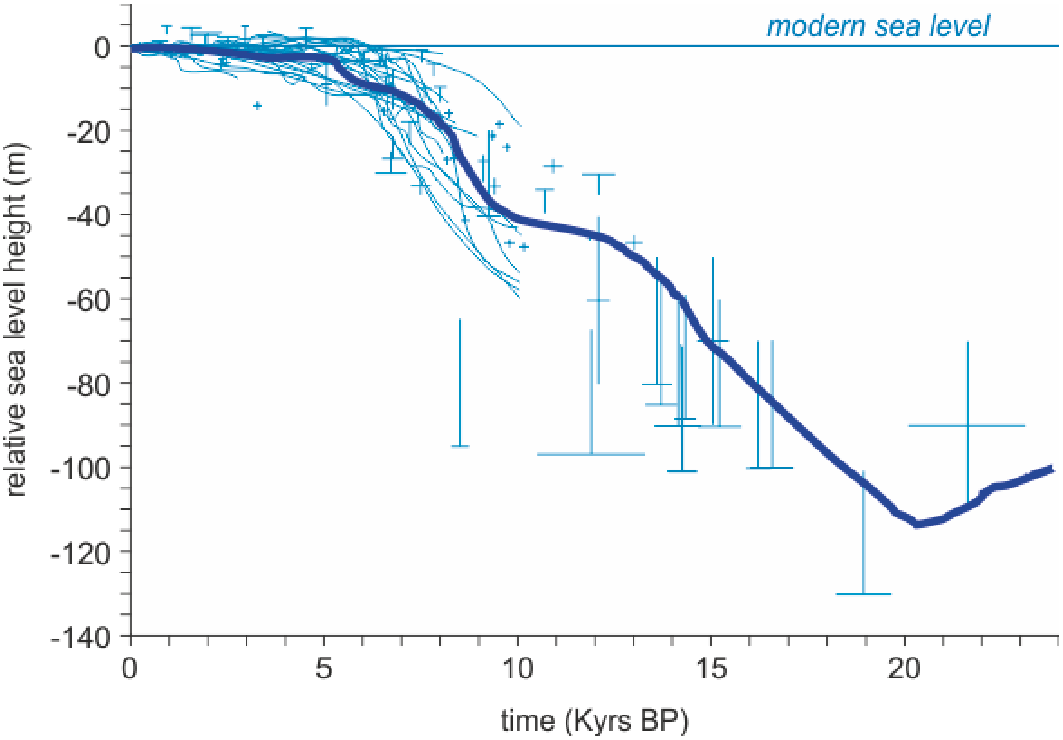

Figure 14. Sea-level rise in the Mediterranean during the Holocene.
Compiled mostly from information found in Lambeck and Bard (2000), Sivan et al. (2001) and previous papers.

Climatic and sea-level oscillations during the Quaternary have been causally linked to the deposition of sapropels, i.e. layers of dark-coloured, organic carbon-rich sediment that have been deposited in the Mediterranean basin in cycles corresponding to the Milankovian orbital perturbations (Capozzi and Negri, 2009). The sedimentation mode of sapropels is dependent on water stagnation and enhanced primary production in the photic zone related in turn to increased insolation. Sapropel deposition is accompanied by conditions of anoxia, which should have severely affected the biota in both the depths and the continental shelf. The last sapropel deposition (S1) coincided with the rapid sea-level rise after the 8 ky climatic event, and was particularly conspicuous in the eastern Mediterranean, under the influence of the enhanced intensity of the African monsoon. This may provide an additional, rather than alternative, explanation to the Godot basin hypothesis for the biotic impoverishment of the Levant Sea.

The Mediterranean Sea Biota of Today

The complex story already outlined suggests that the present-day extraordinarily rich biota of the Mediterranean Sea is mainly the outcome of the dramatic climatic events of the Quaternary, which acted as a sort of ‘biodiversity pump’ (Bianchi and Morri, 2000). Miocene and especially Pliocene events had been important for the origin of most of the endemics, while throughout the Quaternary the Mediterranean saw several waves of colonization and extinction of either temperate or tropical organisms. As a result, the present marine biota of the Mediterranean is composed of species belonging to several chorological categories (Figure 15):

i) the endemics, deriving mostly from Atlantic ancestors. Many of these species are widely distributed through the Mediterranean basin, but some occur only in a restricted area within the Mediterranean (Fredj, 1974). The latter are comparatively few but nonetheless include well-known examples, especially from the Adriatic (Gamulin-Brida and Span, 1981).

ii) a background of warm-temperate Atlantic-Mediterranean species, representing half of the total biota (Fredj et al., 1992; Koukouras et al., 2001). The great majority are found in most of the Atlantic-Mediterranean region, roughly from the English Channel (La Manche) to Macaronesia and Mauritania (Figure 13); some may stretch further north and/or south, such as the seastar *Marthasterias glacialis*, found from Norway to South Africa (Figure 11).

iii) boreal Atlantic species, to be generally interpreted as ice ages remnants that entered the Mediterranean during glacial periods (Pérès, 1985). A few are circumboreal, living also in the northern Pacific: a well known example is the seagrass *Zostera marina*.

iv) subtropical Atlantic species, a heterogeneous group that includes both the interglacial remnants, such as the Atlantic-Levantine disjunctions and other Senegalese biota, and species more widely distributed in the warm Atlantic Ocean. Some of the latter may show an amphiatlantic or transatlantic distribution, extending to the western Atlantic warm waters (Briggs, 1974).

v) widely distributed species, found in many other parts of the world ocean. We are reluctant to use the term 'cosmopolitan', which would imply an extremely wide distribution in all oceans at all latitudes; this is seldom the case: marine species considered cosmopolitan turn frequently out to be species-complexes difficult to distinguish morphologically (Bianchi et al., 2004). The term 'panoceanic' might be more appropriate. In most instances, these are circum(sub)tropical species, eurythermal enough to penetrate into (warm-)temperate waters, the Mediterranean Sea included (Briggs, 1974).

vi) Indo-Pacific species, whose occurrence in the Mediterranean Sea might suggest they are survivors of the Messinian crisis. With the exception of the recent immigrations via the Suez Canal (see below), there are very few species – if any – whose distribution encompasses the Mediterranean and the Indo-Pacific: in most cases, these are to be interpreted as circum(sub)tropical elements that disappeared from the tropical Atlantic during colder periods, or are simply not yet reported for that ocean (Pérès, 1985).

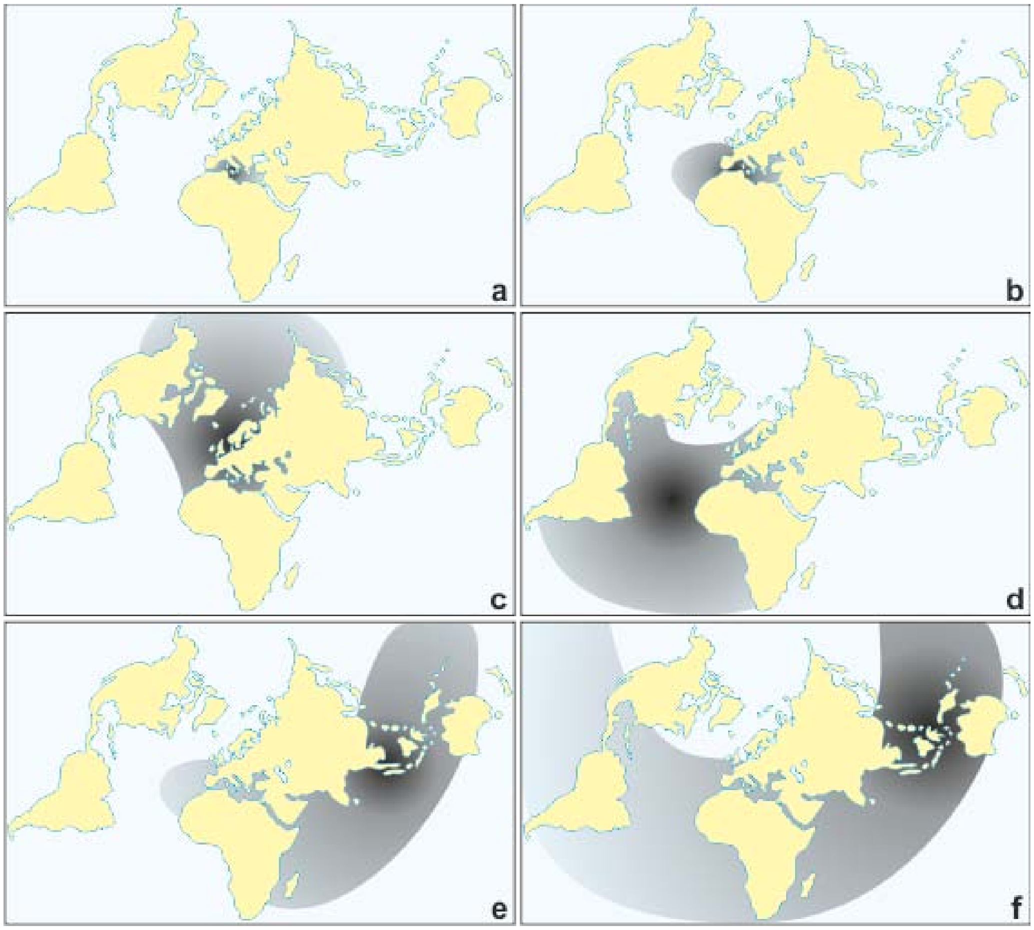

Figure 15. Main basic ranges of the Mediterranean biota: a) Mediterranean endemic; b) Atlantic-Mediterranean; c) Boreo-Atlantic; d) (sub)tropical Atlantic; e) Indo-west Pacific; f) circum-(sub)tropical.

Recent immigrants from the Eastern Atlantic (through Gibraltar) and the Red Sea (through the Suez Canal), together with species introduced by humans have been added to these native categories especially in the last decades (Galil, 2000; Bianchi, 2007).

Just One Sea? Biogeographic Subdivisions within the Mediterranean

The Mediterranean Sea as a whole constitutes a distinctive province of the warm-temperate Atlantic-Mediterranean Region (Figure 13), which according to most authors (Tortonese, 1969, and references therein) also includes a Lusitanian Province (east Atlantic from Portugal to southern Brittany), a Mauritanian Province (Atlantic Morocco to Cape Verde), and a Sarmatian Province (Black Sea). Macaronesia, the western outpost of the Mediterranean-Atlantic Region (Tortonese, 1960), is a ‘biogeographic puzzle’ rather than a biogeographic unit (Bianchi et al., 1998, 2000, and references therein). At the eastern outpost, some authors also attach to the Atlantic-Mediterranean Region the Caspian and Aral provinces, whose biota mostly includes relics from the Paratethys, some Arctic elements possibly entered through the so-called Turgai seaway (Roberts et al., 2009) in the early Tertiary (Giaccone, 1991), and few later invaders from the Mediterranean (Ekman, 1953).

The Mediterranean Province, however, is far from being homogenous biogeographically, to the point that the simple expression ‘Mediterranean species’ is not very informative (Tortonese, 1978). The 46,000 km of Mediterranean coasts are highly compartmentalized into fairly isolated sub-basins (Boudouresque, 2004), displaying a great variety of climatic and hydrologic conditions (Sarà, 1985). This implies that the above-mentioned chorological categories occur more or less abundantly in different parts of the Mediterranean. While the recent immigrants evidently tend to concentrate in the proximity of their area of penetration or first entry, it can be said as a general rule that cold-water species (the ice-ages remnants) thrive mostly in the north of the basin, warm-water species (the circumtropical eurythermics and the interglacial remnants) in the south. The most ‘typical’ Mediterranean flora and fauna are mostly found in the central parts of this sea (Pérès and Picard, 1964). Bianchi (2007) suggested that the February surface isotherms of 15° C and 14° C can be taken as the ‘divides’ between a warmer and a colder water biota within the Mediterranean. In particular, the 15° C divide would set the limit for a number of tropical Atlantic species, including those that exhibit the disjunct Atlantic-Levantine distribution; the 14° C divide, which coincides with a frontal system created by mesoscale eddies in the Algerian Basin (Millot, 2005), would represent the limit within the western Mediterranean for many ‘southern’ species, either circumtropical, Senegalian or Mediterranean endemics: the green algae *Anadyomene stellata* and *Penicillus capitatus*, the hydroid *Pennaria disticha*, the scleractinian coral *Astroides calycularis* (Figure 16), the seastar *Ophidiaster ophidianus*, the ornate wrasse *Thalassoma pavo* (Figure 16) and many others (Bianchi and Morri, 1994). On the contrary, ‘northern’ species, showing boreal affinity, thrive mostly to the north of the 14 °C divide; examples include both invertebrates (e.g., the sea anemone *Sagartia elegans*) and fish (e.g., the whiting *Merlangius merlangus*).

Generally, species richness within the Mediterranean Sea decreases from the northwest to the southeast, with some local exceptions and caution due to gaps in our knowledge of the biota along the southern and eastern rims (Coll et al., 2010). Biodiversity is generally higher in coastal areas and continental shelves, and decreases with depth (Sardà et al. 2009). The level of endemism also reduces with depth, partly due to the ample degree of eurybathy of the fauna (Fredj and Laubier, 1985). The deep homothermy of the Mediterranean Sea at 12-13°C limits the establishment of truly bathyal or abyssal groups, which are typically adapted to colder waters (Emig and Geistdoerfer, 2004). The low diversity of the Mediterranean deep fauna may also be due to the Gibraltar sill acting as a physical barrier to the colonization from the richer Atlantic deep fauna (Bouchet and Taviani, 1992). Thus, while the Mediterranean Sea is recognized as one of the most diverse regions on earth, its depths are among the poorest: it is not a coincidence that Forbes (1844) extrapolated his theory of the azoic deep ocean after working in the Mediterranean. Recent research on deep-sea meiofauna and protists (Danovaro et al. 2009a, b) contradicts the view of an impoverished deep Mediterranean in comparison with the Atlantic counterpart. Deep-sea nematodes, the richest meiofaunal group, conform to the general pattern of species richness decreasing from the northwest to the southeast (Danovaro et al., 2008). Expanding research efforts may prove that also in the case of macrofauna the depths of the Mediterranean are not so as depauperate as traditionally believed (Goren et al., 2006).

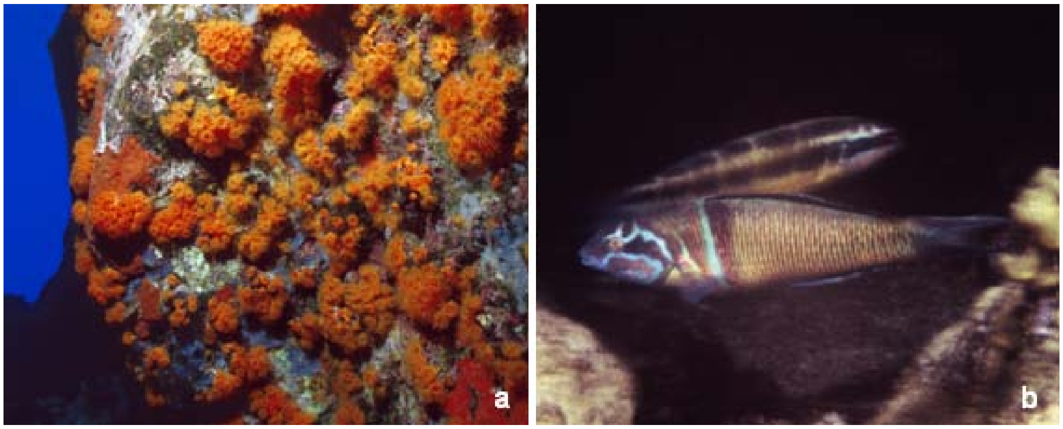

Figure 16. Warm-water species native to the Mediterranean: a) *Astroides calycularis*, endemic, and b) *Thalassoma pavo*, of the tropical east Atlantic.

While the information on deep-water biota remains too scarce for an adequate analysis of their within-basin distribution (Danovaro et al., 2010), a number of different biogeographic sectors within the Mediterranean Province can be recognized for the shallow water biota (Figure 17).

1) The Alboran Sea, situated immediately east of Gibraltar, exhibits stronger Atlantic affinities, due to the continued penetration of Atlantic flora and fauna with the incoming flux of water (Harmelin and d'Hondt, 1993). In return, most Mediterranean endemics become rare or disappear.
2) Algeria and north Tunisia coasts are similarly characterized by the occurrence of Atlantic species, although not as many as in the Alboran Sea; they progressively fade in number and abundance going from west to east, especially for species of northern origin. Mediterranean endemics are common.

3) The Tyrrhenian Sea is comparatively isolated from the rest of the western Mediterranean and is contoured by mountains preventing the input of meteorological events that strongly influence the internal conditions of the other western Mediterranean basins (Astraldi et al., 1995). These features determine an increase of the mean surface temperature, which remains higher all year round. Its biota is therefore thermophilic, with a fairly high percentage of species of subtropical affinity and a high occurrence of Mediterranean endemics.
4) Balearic Sea to Sardinia Sea, north of the 14 °C divide, is a sector that has a biota similar to that of the Tyrrhenian Sea, with the exception of certain endemics, such as *Astroides calycularis*, and a less marked subtropical affinity.
5) The Gulf of Lions and Ligurian Sea are the coldest parts of the western Mediterranean. They are characterized by a severe reduction of the thermophilic element, while some cold temperate species, not found to the south, are common (Bianchi and Morri, 1994).
6) The northern Adriatic Sea is perhaps the most peculiar sector of the whole Mediterranean. Strong winter cooling, low salinity due to significant river input, and comparatively great tidal range make it more similar to the northern Atlantic than to the rest of the Mediterranean. This is reflected in the biota, which includes disjunct Atlantic-Adriatic species, such as the periwinkle *Littorina saxatilis*. Similarly, local endemics, such as the brown alga *Fucus virsoides*, have their closest relatives in the north Atlantic, from which they may have speciated after ingression of the parent taxa during a glacial period. Both *L. saxatilis* and *F. virsoides* thrive in the intertidal, which may have acted as a refuge from competitors. Their occurrence contributes to what has been called the northern-Adriatic ‘sub-Atlanticism’ (Sacchi et al., 1985). Mediterranean endemics are scarce and the overall diversity is the lowest of the Mediterranean basin, so that the phrase ‘north-Adriatic gap’ has also been coined (Sacchi, 1983). In addition, peculiar to this sector are some taxa with Sarmatian affinity, such as the sturgeons (*Acipenser stellatus* and others) and several other fishes and invertebrates (Sacchi et al., 1985; Bianchi et al., 2004).
7) The central Adriatic is characterized by the lack of both northern-Adriatic endemics and Atlantic-Adriatic disjunctions. Mediterranean endemics and thermophilic species are still scarce, so that this sector is poorer than the Gulf of Lions and Ligurian Sea, which it resembles. However, it is significantly richer than the northern Adriatic.
8) The southern Adriatic exhibits a transitional character between the Adriatic and the rest of the eastern Mediterranean. Affinities with the western basin are strongly reduced.
9) The Ionian Sea is the least known of the Mediterranean sectors (Zenetos et al., 1997), especially as far as its southern shores are concerned. Local endemics, mostly within molluscs, have been reported for the Gulf of Gabès (Sabelli and Taviani, 1980).
10) The Levant Sea is warmer than the rest of the Mediterranean and harbours a significant number of circumtropical species. Atlantic-Mediterranean elements and Mediterranean endemics are comparatively scarce (Morri et al., 2009). Since the construction of the Suez Canal, the Levant Sea is experiencing an important influx of Red Sea species. Por (1990) defined the geographical limits to the expansion of Red Sea migrants in the Mediterranean as the ‘Antipsara line’ to the north (Antipsara being an island in the Aegean) and the Straits of Sicily to the west: these boundaries

match the 15 °C divide (Bianchi, 2007). Red Sea species naturalized in the Levant Sea have become so abundant that the latter has been proposed as a separate biogeographic province (Por, 1981).

11) The southern Aegean Sea has local endemics, but the typical Mediterranean biota is impoverished with respect to the western basin. Recent research, however, indicates that this is partly due to insufficient inventory effort (Morri et al., 1999; Koukouras et al., 2001).
12) The northern Aegean Sea lies mostly to the north of the 15 °C divide: the occurrence of warm-water species is reduced and also some typical Atlantic-Mediterranean elements are lacking.
13) The Straits of Messina is a micro-sector that harbours a wealth of biogeographic peculiarities, including Pliocene Atlantic remnants and local endemisms (Fredj and Giaccone, 1995).

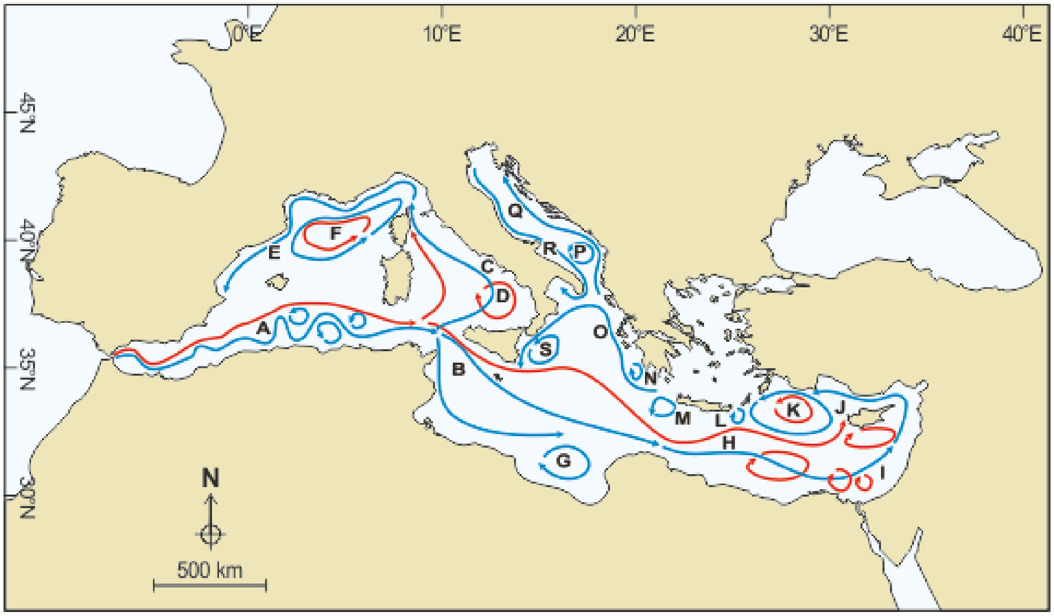

Figure 17. Major biogeographic sectors within the Mediterranean Sea: (**1**) Alboran Sea; (**2**) Algeria and north Tunisia coasts; (**3**) southern Tyrrhenian Sea; (**4**) Balearic Sea to Sardinia Sea; (**5**) Gulf of Lion and Ligurian Sea; (**6**) northern Adriatic Sea; (**7**) central Adriatic Sea; (**8**) southern Adriatic Sea; (**9**) Ionian Sea; (**10**) Levant Sea; (**11**) southern Aegean Sea; (**12**) northern Aegean Sea; (**13**) Straits of Messina. The major current and gyre systems are also indicated, together their seasonal variability. Blue line = winter circulation; red line = summer circulation. A: Algerian current and eddies; B: branches of the Ionian stream; C: Tyrrhenian cyclonic current; D: summer antyciclone in the eastern Tyrrhenian Sea; E: Ligurian-Provençal current; F: Lions gyre; G: Syrte anticyclone; H: mid-Mediterranean jet; I: Shikmona and Mersa-Matruth gyres system; J: Cilician and Asia Minor current; K: Rhodes gyre; L: Ierapetra gyre; M: western Cretan gyre; N: Pelops gyre; O: Ionian cyclonic current; P: southern Adriatic gyre; Q: eastern Adriatic coastal current; R: western Adriatic coastal current; S: western Ionian gyre.
Redrawn and modified from Bianchi (2007).

While the core-zones of these biogeographic sectors are easily identifiable, tracing their boundaries on a map is difficult. They are connected by transitional areas, rather than separated by fronts (Bianchi, 2004). Examples include the Tuscan Archipelago, where infralittoral and circalittoral biota exhibit warm (Tyrrhenian) and cold (Ligurian) affinities, respectively (Lardicci et al., 1990); and the Straits of Sicily, where western and eastern Mediterranean species meet (Bianchi, 2007) and biodiversity may be especially high (Garofalo et al., 2007). Transitional areas are expected to be the first regions where the effects of global change on marine biodiversity will be seen (Bianchi and Morri, 2003).

PATTERNS AND DRIVERS OF CHANGE

Most research on Mediterranean marine ecosystems has traditionally been directed toward identification and classification purposes, as if they were stable units (Bianchi, 1997; Bianchi and Morri, 2001). On the contrary, intensified research effort in the last decades has shown that these alleged stable units are undergoing rapid alteration (Bianchi, 2007). Distinguishing alteration due to climate change from that due to human pressure is often difficult (Bianchi and Morri, 2004); in addition, climate and humans have been shown to combine their effects on the Mediterranean marine biota (Bianchi and Morri, 2000). Por (2009) adopted the term ‘equifinality’, borrowed from geomorphology, to express the principle that both climate and human influences may lead to similar results.

An example of the difficulty of distinguishing between climatic and anthropogenic effects is offered by the large scale regression of the meadows of *Posidonia oceanica*, which are listed among priority habitats for conservation (Montefalcone et al., 2006). This degradation may be explained either by pollution or by the natural decline of the plant, which is believed to have had its climatic optimum around 6,000 - 2,750 years ago (Pérès, 1984). This period partially overlaps the HCO, and the present climatic warming has been suggested to enhance the flowering capacity of the plant (Diaz-Almela et al., 2007; Bertora et al., 2011). Den Hartog (1970) hypothesized that *P. oceanica* is a shallow-water plant surviving as a relict in deeper water owing to the last rise in sea level. Thus, regression in deeper meadows may be due to regional increases in water turbidity (Montefalcone et al., 2009) coupled with diminished plant vitality at depth. In shallow water, meadows suffer equally from local anthropogenic impacts (Montefalcone et al., 2010a) and beach morphodynamic constraints (Vacchi et al., 2010). Meadows in MPAs do not decline (González-Correa et al., 2007), if protection is enforced (Montefalcone et al., 2009) - the responsibility of natural causes for the present *P. oceanica* regression should therefore be excluded.

Several drivers of change for Mediterranean Sea biodiversity may be identified. Some are natural, some anthropogenic, most are both; many are intertwined. Arrival of alien species can be taken as natural when considering the Atlantic newcomers from the newly active Gibraltar Portal (Ben Rais Lasram et al., 2008a), but anthropogenic when considering the so-called Lessepsian immigrants, coming from the Red Sea through the Suez Canal (Galil, 2006a), or the many species actively or passively introduced by humans (Boudouresque and Ribeira, 1994; Galil, 2006b). Humans are greatly altering Mediterranean marine biodiversity in many other ways (Bianchi and Morri, 2000), including climatic change (Bianchi and Morri, 2004), which is no longer to be considered as natural because of the increased anthropogenic emission of carbon dioxide (CO_2) and other ‘greenhouse’ gases in the atmosphere. Carbon dioxide also induces acidification of sea water, which may in turn affect both organisms’ physiology and biogeochemical pathways. While Atlantic newcomers, Lessepsian immigrants and introduced species constitute the ‘raw material’ for modifying the composition of the Mediterranean biota, direct human impacts and climatic change represent the ‘mechanisms’ responsible for the modification (Figure 18).

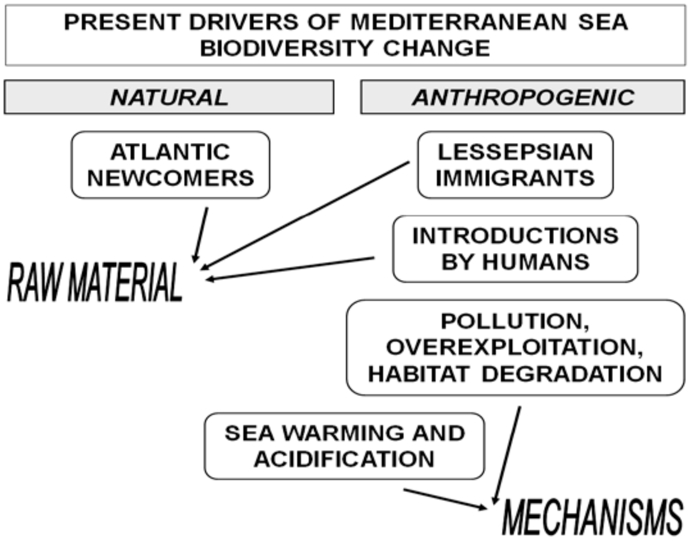

Figure 18. Scheme of the factors that are driving the change in Mediterranean Sea biodiversity.

New Inhabitants

Since the beginning of the current interglacial, at least 10,000 years ago, surface Atlantic water has been entering through the Straits of Gibraltar and, as already happened during the Quaternary, has been carrying into the Mediterranean species of prevalently (sub)tropical affinity (Bianchi et al., 2004). Many of these species became established exclusively in areas close to the Straits of Gibraltar such as the Alboran Sea and the Algerian coasts, but in recent years, many have penetrated further north and east (Bianchi, 2007). Examples include both invertebrates (Yokes and Galil, 2006; Morri et al., 2009) and fishes (Gokoglu et al., 2004; Francour and Mouine, 2008; Psomadakis et al., 2010).

The range extension of (sub)tropical Atlantic species within the Mediterranean is of secondary importance when compared to that of the Red Sea immigrants (Galil, 2009). This looks like as a contradiction when the water inflow from the ‘Atlantic river’ is compared to that from the ‘Red rivulet’ (Bianchi et al., 2004). Por (2009) explains this contradiction arguing that first, the E Atlantic tropical region is poorer than the Indo-west Pacific region; second, the interposed coasts of Mauritania and Morocco are influenced by the cold Canaries Current, a strong upwelling and low winter temperatures.

The opening of the Suez Canal in 1869 provided many Red Sea species with an opportunity to penetrate into the Mediterranean. This penetration has been called ‘Lessepsian migration' from the name of Ferdinand de Lesseps, the French engineer and diplomat who promoted the cutting of the Suez Canal. For nearly one century after the opening of the canal, Lessepsian migration remained inconspicuous, because variations in salinity along its path constituted an almost insurmountable physiological barrier: salinity was extremely high in the Bitter Lakes and reduced by the Nile plume at the northern end of the canal. Por (1971) predicted that Lessepsian migration would have been restricted to a handful of pre-adapted, highly euryhaline species. Starting from about the late 1970s, Lessepsian migration increased because of the progressive reduction of salinity of the Bitter Lakes and the diminished outflow of the Nile, caused by the building of the Aswan dam. The spreading of stenohaline Red Sea species into the eastern Mediterranean became then possible (Galil, 2006a). For a long period, the vast majority of these Lessepsian immigrants remained confined to the Levant Sea, where they now shape the coastal communities (Fishelson, 2000) and represent 37 % by weight of fishery landing (Carpentieri et al., 2008). However, many Lessepsian species have now penetrated into the western Mediterranean (Ben Rais Lasram et al., 2008b; Gambi et al., 2008; Garibaldi and Orsi Relini, 2008). Hardly a single day passes without the discovery of a further Indo-west Pacific species spread into the Mediterranean (Galil, 2009): Lessepsian migration constitutes the most significant biogeographic change currently underway in the world.

Lessepsian migration apart, humans introduce exotic species into the Mediterranean Sea intentionally or accidentally, via ship fouling, ballast waters, aquaculture, trade of living bait, wrapping fresh sea-food with living algae, aquariology, and even scientific research (Bianchi and Morri, 2000). Anthropogenic introduction of species started early in Mediterranean history (Giaccone, 2002), but greatly increased since the World War II (Boudouresque and Ribeira, 1994) and continues to increase at a fast pace in this era of trade globalization (Zenetos et al., 2005, 2008). Due to the intensity of human activities in the Mediterranean, the number of alien species in that sea is greater than in any other seas of Europe (Streftaris et al., 2005) and may reach 1,000, that is 5 % of the total biodiversity of the basin (Coll et al., 2010).

The impact of alien species on Mediterranean Sea biodiversity is highly debated. Some authors (Zenetos et al., 2005; Streftaris and Zenetos, 2006; Galil, 2007a, 2009) see the risk for competition with native species, which might be driven to extinction. Por (2009) minimizes such a risk, observing that no extinction has been recorded so far. Thinking that in a few decades some species could have already become extinct from a basin as wide as the Mediterranean is unrealistic: nevertheless, there are clues that some aliens are responsible for the local reduction of the populations of some autochthonous species (Galil 2007a, b). Lack of evidence of species extinction coupled with establishment of alien species is apparently leading to an increased richness of the Mediterranean (Por, 2009). Richness is increasing at whole basin scale (λ diversity), but what do we know really about local scales (α diversity)? Cases of local replacement have been reported (Galil, 2007a). In addition, the spatial overlap between alien and indigenous species causes biotic homogenization (Ben Rais Lasram and Mouillot, 2009), and hence a depression in β diversity. Thus, the relationship between the entering of alien species and threats to biodiversity is not straightforward. There are aliens that exhibit invasive behaviour and the capacity to modify the receiving ecosystems. Two alien species of the green algal genus *Caulerpa* (*C. racemosa* and *C. taxifolia*) have been particularly studied in this respects (Montefalcone et al., 2007, 2010b; and references therein). The recent expansion of the comb-jelly *Mnemiopsis leidyi* raises great concern because it is known to affect fish stocks (Boero et al., 2009). Some aliens pose problems to human health, as they include poisonous or venomous fishes (Galil, 2007b), toxic microalgae (Cattaneo Vietti et al., 2010) and stinging cnidarians (Boudouresque and Verlaque, 2005; Morri, 2008). Thus, alien species may be a threat not only to biodiversity *per se*, but also to human welfare (Raitsos et al., 2010).

The Footprint of Humans

Besides species introductions, humans are greatly altering marine biodiversity in many ways, ranging from pollution and habitat modification to the overexploitation of biological resources. These impacts are particularly intense in the Mediterranean, a semi-enclosed basin experiencing heavy demographic, urban and industrial pressures (Bianchi and Morri, 2000).

Overexploitation of biological resources of the Mediterranean dates back to Roman times, and has historically been the most important factor causing or contributing to the reduction of marine biodiversity (Lotze et al., 2006; Coll et al., 2010). Today, the high demand for marine resources continues and has resulted in generalized overfishing (Papaconstantinou and Farrugio, 2000). Stock depletion has been the main concern to date; however, the indirect effects of overfishing are even more important, causing alteration of marine ecosystem functioning (Coll et al., 2009). Pelagic food webs are shifting from fish to jellyfish (Purcell et al., 2007), whereas trawling by-catch reduces the biodiversity of demersal ecosystems, killing high numbers of macro-epibenthic organisms (Colloca et al., 2003) and producing community shifts (De Juan et al., 2007). Coastal fisheries include highly destructive practices such as date-mussel harvesting (Rovere et al., 2009, and references therein), but even the 'innocent' angling, which is normally considered of minor impact and is often allowed within MPAs, may lead to ecosystem alteration through trophic cascades (Parravicini et al., 2010a).

Today, the impact of pollution is being mitigated thanks to the generalized adoption of treatment plants and more restrictive rules about water quality. What is always increasing at ever greater rapidity is habitat modification caused by coastal development, sediment loading, and other anthropogenic disturbances (Coll et al., 2010). Along the highly populated and industrialized coast of Liguria, an administrative region of Italy, up to 30 % of the *Posidonia oceanica* meadows were lost since the 1960s (Bianchi and Peirano, 1995), while what remains is degraded (Montefalcone et al., 2010a). Habitat loss and degradation is a kind of impact that has not been as much a focus of marine science and conservation as in terrestrial environments. This is mostly due to the limited knowledge and perception of the marine environment by administrators and laymen alike (Bianchi, 2008). Many of the principal marine habitats of the Mediterranean are presently endangered but concern focuses almost exclusively on *Posidonia oceanica* meadows (Boudouresque et al., 2006); only recently has attention begun to be paid to coralligenous reefs (Ballesteros, 2006) and submarine caves (Cicogna et al., 2003). All of the remaining extraordinary habitat richness of the Mediterranean is virtually ignored.

Typically, habitat destruction implies a transition from a more complex to a less complex physical structure, e.g. macroalgal canopies are replaced by turf-forming seaweeds (Thibaut et al., 2005; Mangialajo et al., 2008): turfs, in turn, facilitate the invasion by *Caulerpa racemosa* and retain sediment, further reducing biotic complexity (Airoldi et al., 2008).

Because of these habitat alterations, attention has been given to the macroalgal communities in the European Water Framework Directive (WFD) 60/2000 and the relevance of macroalgal related indices in the assessment of water quality has been established in many areas (Asnaghi et al., 2009; and references therein).

Generally, the marine environment is getting flatter (loss of three-dimensional structure) and less diverse, and habitat modification combines with species introduction to cause biotic homogenization (Bianchi and Morri, 2000). Human pressure on native species may have left unused resources, thus facilitating the establishment of new invaders (Raitsos et al., 2010). Biological invasions are considered as a component of global change in stressed marine ecosystems (Occhipinti-Ambrogi and Savini, 2003).

Some Like it Hot (But Some Do Not)

In the Mediterranean, as elsewhere, sea water temperature is rising (Bianchi and Morri, 2004). After the LIA, in the late 19th through the early 20th century, a natural warming occurred in the entire northern hemisphere. Since at least 1750, the Mediterranean climate has been dominated by multidecadal variability with a period of about 70 years (Felis and Rimbu, 2010), roughly corresponding to the cyclicity of the Atlantic Multidecadal Oscillation (AMO). Biological response to climatic cycles have been little studied in the past, the best known being the 'Russell Cycle', so-called after Sir Frederick Russell who first described changes in the English Channel ecosystem during the 20th century (Southward et al., 2005). Similar changes in the Mediterranean Sea are less documented (Bianchi, 1997). The North Atlantic Oscillation (NAO) is a climatic phenomenon known to influence the Mediterranean Sea (Morri and Bianchi, 2001). The prevalence of positive NAO phases in the last decades corresponded to warmer years in the Mediterranean region. However, since the late 20th century, anthropogenic forcing is the main factor responsible for the current global warming (Lejeusne et al., 2010).

Satellite observations have shown that surface water temperatures of the Mediterranean Sea have increased to around 0.8-1 °C in the period 1985 to 2006 (Nykjaer, 2009), which is distinctly higher than the warming trend of 0.7-0.8 °C observed between 1885 and 1967 (Lejeusne et al., 2010). In the last 3-4 decades, therefore, the rise in temperature has accelerated from less than 0.01 $°C \cdot a^{-1}$ to about 0.04 $°C \cdot a^{-1}$. Both the 15 °C and the 14 °C divides have apparently moved northward in recent times (Figure 19). At the same time, many native thermophilic species appeared or became common in northern sectors, where they were formerly absent or rare (Bianchi and Morri, 1994; Vacchi et al., 1999; Guidetti et al., 2002; Grubelić et al., 2004; Sara et al., 2005; Parravicini et al., 2008; Lipej et al., 2009; Puce et al., 2009). Initial northward and westward expansion of the range of two Levantine-Senegalese species, *Sparisoma cretense* and *Ocypode cursor*, has also been detected (Bianchi and Morri, 1994; Guidetti and Boero, 2002; Abecasis et al., 2006; Relini, 2009).

A warming Mediterranean is becoming more receptive also to the alien species (Ben Rais Lasram et al., 2008b; Raitsos et al., 2010): Atlantic newcomers and Lessepsian immigrants are evidently tropical species, but also the species intentionally or accidentally introduced by humans are of tropical origin (Galil, 2008), with few exceptions (Boudouresque and Verlaque, 2002; Faccia et al., 2009). Several tropical invaders have already reached the northernmost sectors of the Mediterranean Sea (e.g., Francour and Mouine, 2008; Dulčić et al., 2008; Daniel et al., 2009). The northward range extension of either native thermophilic or alien species has been favoured not only by the direct influence of increased temperature, but also by modifications in the emphasis of water flow and in the pattern of water circulation forced by climate change (Astraldi et al., 1995; Bianchi, 2007).

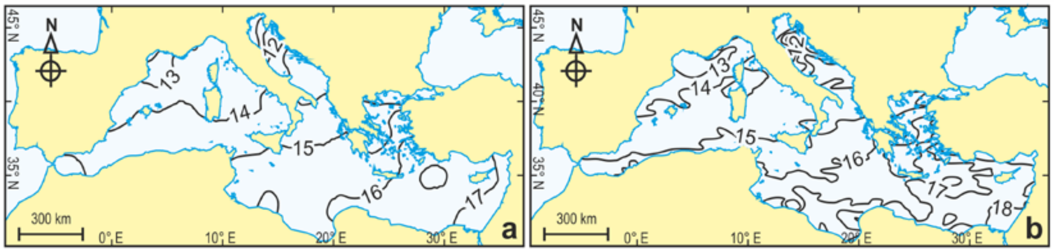

Figure 19. Surface isotherms of February of the Mediterranean Sea: a) climatological means from the historical data set 1906-1985; b) means for 1985-2006.
Redrawn and modified from Bianchi (2007) and Coll et al. (2010).

The appearance and spread of tropical organisms together with sea water warming are leading to what has been called the 'tropicalization' of the Mediterranean Sea (Bianchi and Morri, 2003). If the Mediterranean Sea is getting 'tropical', what will happen to those species of boreo-Atlantic origin that entered the Mediterranean during glacial periods and established themselves in the northern and therefore colder areas of the basin? The geographic configuration of the Mediterranean is such that they cannot migrate further northward: are they at risk of extinction? Rarefaction or even disappearance of cold-water species from their refuges in the Gulf of Lions - Ligurian Sea and the northern Adriatic has been recorded (Bombace, 2001; Grbec et al., 2002; Chevaldonné and Lejeusne, 2003; Boero and Bonsdorff, 2007; Ben Rais Lasram et al., 2010). Concurrent expansion of the range of warm-water species and contraction of that of cold-water species are disrupting the present biogeographic patterns within the basin, and again imply biotic homogenization.

Sea water warming not only favours aliens, but also stresses the native dwellers, adding extra pressure on the ecosystem (Raitsos et al., 2010). Another consequence of higher temperature has been the mass mortality of long-lived invertebrates such as sponges, corals and seafans, the majority of which are endemics. Early mortality episodes have been recorded in the 1970s and 1980s, while the first well-documented Mediterranean multispecies die-offs were those of 1999 and 2003, in coincidence with summer heat waves (Garrabou et al., 2009). These mass mortalities occurred along several hundred kilometres of coastline between the Tyrrhenian Sea and the Catalan Sea and were linked to the hydrological changes resulting from climate anomalies. This area is dominated by a large and well-defined anticlockwise circulation fed by two distinct currents (Astraldi et al., 1995): the Western Mediterranean Current (WMC) and the Tyrrhenian Current (TC). The first, with a yearly average flux of about $1.3 \cdot 10^6\ m^3 \cdot sec^{-1}$, is rather stable and flows along the western coasts of Corsica whereas the second, having a flow of half that intensity, crosses the Corsica Channel and is more variable, with larger fluxes being observed in colder winters (negative values of NAO index). In winter, in synergy with strong northern winds (Tramontane), TC is able to displace the WMC gyre south-westwards. In recent decades, the TC flux has been relatively intense also in summer, when winds are feeble and blow from the south. The TC alone has not been able to displace the WMC gyre, so that the water transported by the TC accumulated along the coast:

this implied the raising of the sea-level (as observed from satellites) and the gravitative deepening of the thermocline. Coming from the south, the TC water is warmer, and therefore less dense, than the the northwest Mediterranean water. The resulting water temperature at the level of the thermocline was 1.4 °C warmer, lethal to many circalittoral sessile invertebrates adapted to live in cooler water (Cerrano et al., 2000). In addition, a prolonged time of unmixed water resulted in reduced food availability for filter feeders (Coma et al., 2009). The same hydrological processes might have induced the development of mucilage (Figure 20), which further stressed the marine ecosystems (Martín and Miquel, 2010, and references therein).

The summer seawater temperatures of 1999 and 2003 have been the warmest ever measured in the Mediterranean Sea (Garrabou et al., 2009). Since 2003, however, localised mortality episodes have been observed almost every year in different parts of the northwestern Mediterranean (Lejeusne et al., 2010). Apparently, it was not the heat stress that directly killed the invertebrates: rather, it triggered diseases when their thermal tolerance thresholds were exceeded (Martin et al., 2002). Among the pathogens associated with gorgonian necrosis, Bally and Garrabou (2007) isolated *Vibrio coralliilyticus* and proved experimentally that it was the major factor responsible for the mortality. *V. coralliilyticus* is a thermo-dependent pathogen of tropical corals, previously known only from the Red Sea and Indian Ocean: its discovery in the Mediterranean may imply that it is another example of recent introduction and dissemination of an alien species or, alternatively, that it is a natural resident in Mediterranean waters previously unnoticed. Were the first hypothesis true, it would further highlight the synergistic action of different stressors (raised temperature and introduction of aliens) on Mediterranean Sea biodiversity.

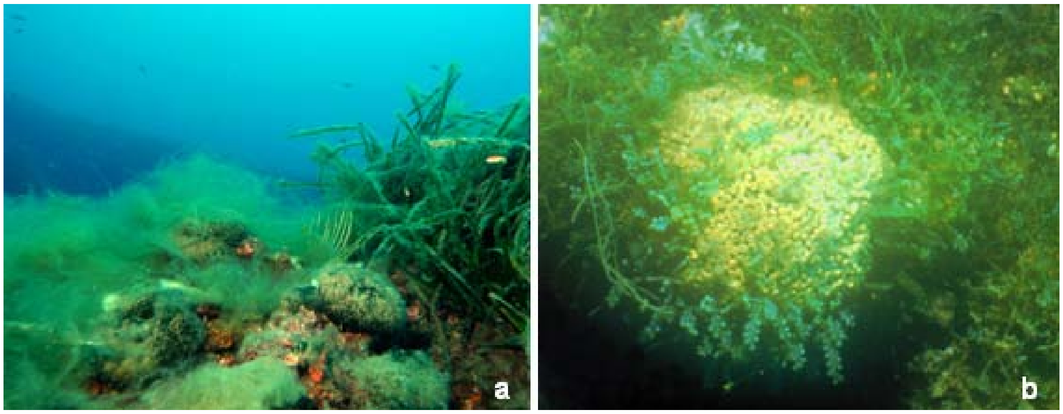

Figure 20. Examples of alteration of Mediterranean Sea ecosystems: a) deposition of mucilage on coastal habitats; b) the invasive alien alga *Caulerpa racemosa* overgrowths a colony of the endemic coral *Cladocora caespitosa*.

Confronting the Acid Bath

Due to continuous gas exchange between air and seawater, an increasing atmospheric CO_2 concentration enters the oceans, the principal sink for anthropogenic CO_2. As CO_2 dissolves in water, it reacts to form carbonic acid (H_2CO_3), which in turn dissociates into bicarbonate (HCO_3^-) and carbonate anions ($CO_3^=$), and hydrogen cations (H^+). Because of this chemical reaction, sea water pH will decrease (Zeebe and Wolf-Gladrow, 2001). Sea water acidification reduces calcium carbonate ($CaCO_3$) saturation state, which is likely to have a large impact on marine life and biogeochemical processes (Guinotte and Fabry, 2008). Many marine organisms, such as corals, coralline algae, coccolithophores, foraminifera, molluscs, crustaceans, echinoderms and others, have carbonatic skeletons, whose deposition will be impaired in waters with low pH. Their response to ocean acidification is highly variable (Fabry, 2008), partly depending on the different mineralogical nature of their carbonate skeletons. Of the major biologically secreted forms of $CaCO_3$, high-magnesian calcite and aragonite are more soluble than calcite (Zeebe and Wolf-Gladrow, 2001). Among calcifiers, those taxa that have carbonatic skeletons also during the larval or early life stages, such as molluscs and echinoderms, could be more severely affected.

The effects of ocean acidification on marine organisms have been described mostly by mesocosm experiments (Shirayama and Thornton, 2005), while little evidence has been produced at community or ecosystem levels (Wootton et al., 2008). In the Mediterranean Sea, Hall-Spencer et al. (2008) analyzed the ecosystem-scale consequences of lowered pH on coastal habitats in the field. In stations where CO_2 outgasses from the seafloor naturally lowering ambient pH down to 7.4, they observed a 30 % reduction in species numbers compared with the normal pH stations. Coralline algae and other calcifiers (notably sea-urchins and gastropods) were significantly scarcer or totally absent and less developed or weakened in acidified stations. Although scleractinian corals have been shown to survive and recover from decalcification (Fine and Tchernov, 2007), *Balanophyllia europaea* and *Cladocora caespitosa* were common in normal pH stations but absent at low pH. *C. caespitosa*, endemic to the Mediterranean, is a colonial zooxanthellate coral showing constructional ability (Morri et al., 2000a) and its bioherms constitute a priority habitat according to EU (Bianchi, 2009a). Aquarium experiments indicate that increasing CO_2 concentration does not reduce the calcification rate of *C. caespitosa* (Rodolfo-Metalpa et al., 2010a), thus apparently contradicting field data.

Many Mediterranean submarine seascapes of high ecological and economical values are shaped by constructional organisms that play the role of ecosystem engineers laying down calcium carbonate (Bianchi, 2002b). These include many reef-forming species such as vermetid gastropods (Antonioli et al., 1999), serpulid polychaetes (Bianchi and Morri, 1996), deep-water corals (Mastrototaro et al., 2010), and, most importantly, coralline algae. Coralline algae are the primary builders of coralligenous reefs (Ballesteros, 2006) and form the basal concretions of many other sublittoral habitats (Laborel, 1987), but acidification will probably impair their role (Martin and Gattuso, 2009). Should Mediterranean waters become acidified, all these important habitats will probably be severely compromised.

Reduced opportunities of growth for sessile calcifiers might favour their soft-bodied competitors; in addition, increased CO_2 concentration might advantage non-calcareous photosynthetic organisms. Hall-Spencer et al. (2008) observed that the sea anemone *Anemonia viridis*, which hosts endosymbiotic dinoflagellates, replaced zooxanthellate scleractinian corals in stations with lowered pH. Similarly, fleshy and filamentous algae were seen to out-compete coralline algae: the former included invasive alien species. For scleractinian corals and coralline algae, sea water acidification implies a dual, antagonistic action, hampering calcification while enhancing photosynthesis. A dual action of sea water acidification might also be envisaged in the case of *Posidonia oceanica*: under increased CO_2

concentration, both density and production of this seagrass were enhanced (Hall-Spencer et al., 2008); however, the loss of its characteristic calcareous epiphytes (Martin et al., 2008) makes it more susceptible to grazing, with potential alteration of energy fluxes in coastal ecosystems.

Motile organisms with carbonate skeletons, such as molluscs, echinoderms and some crustaceans, play major ecosystem roles as keystone predators or grazers, in bioturbation and remineralization, and as food sources for higher trophic levels. They are negatively affected by sea water acidification (Cigliano et al., 2009). Hall-Spencer et al. (2008) reported a dramatic decrease in echinoderm abundance in stations with lowered pH. Reduced grazing by sea urchins may have cascading effects on coastal ecosystems, eventually causing phase shifts (Figure 21).

Sea water acidification would also affect pelagic communities: calcifying phytoplankton (coccolithophores) plays a major role in the primary productivity of the oligotrophic Mediterranean Sea (Coll et al., 2010). It has also been suggested that acidification may favour jellyfish increase (Richardson and Gibbons, 2008).

Finally, we do not have sufficient information to understand the effects of acidification on the production and accumulation of Mediterranean shelf carbonate sediments (Milliman and Droxler, 1996): these harbour priority habitats where calcifying organisms, such as bryozoans, are important constituents (Bianchi, 2009b). Field experiments demonstrated that bryozoan ability to calcify is compromised by the combined action of higher temperatures and lowered pH (Rodolfo-Metalpa et al., 2010b).

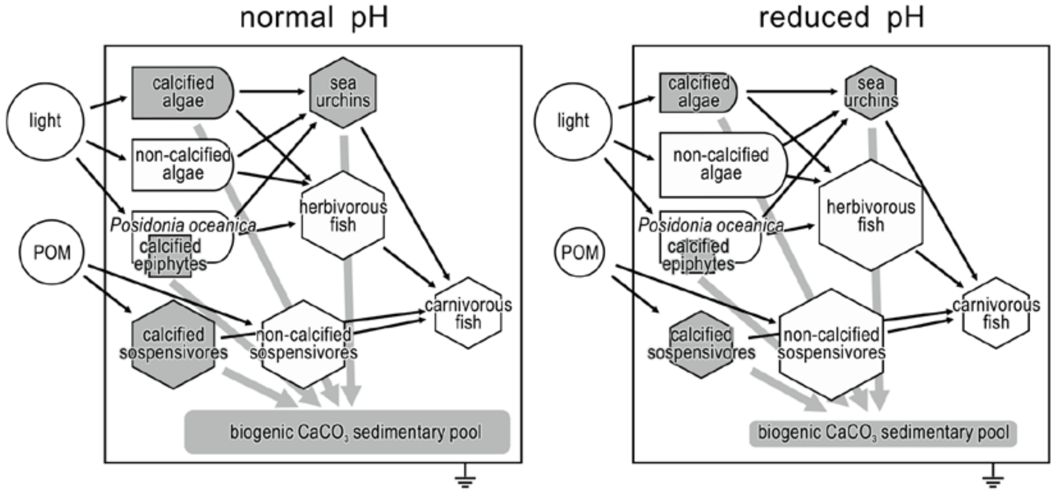

Figure 21. Scheme of the putative ecosystem effects of water acidification on Mediterranean shelf biota and biogenic carbonate flux.

CONCLUSION

Mediterranean biodiversity has experienced many impressive modifications in the past, because of the geological evolution of the basin and climatic changes. Major crises, like the Messinian or the Gelasian ones, caused extirpation of a huge number of species, while the ice age cycles were mirrored in the alternation of different biotas. In comparison, what we observe today might really seem insignificant. Some naturalists and paleoecologists have observed that similar situations must have happened several times during the Quaternary, possibly at each interglacial, and tend therefore to ridicule the Cassandra claims of those ecologists who predict a dark future for the Mediterranean ecosystems. A rather radical point of view, for instance, has been taken by Por (2009), who maintained that the present tropicalization is doing nothing but taking the Mediterranean back to the Tethys: the Tethyan species and their descendants are returning to their old haunts in the Mediterranean. In his opinion, to call them aliens is an anthropomorphic view, considering our historical times as the normal ones. He says that the present climatic phase represents a cyclic event and not an artificial disruption: for the squirrelfish *Sargocentrum rubrum*, which inhabited the Mediterranean already five million years ago, the humans and not itself would be the alien invaders.

We do believe, on the contrary, that what is happening in the Mediterranean Sea is a completely new phenomenon: the descendants of the biota of the former Tethys, i.e. the Indopacific species coming in through the Suez Canal, are getting flanked by novel species of Atlantic origin (including neoendemics) and by new dwellers intentionally or accidentally introduced by humans. They all participate in shaping an unprecedented biota, and there is no going back for species and ecosystems (Barnard and Midgley, 2009). History never repeats itself, and the huge evolutionary change represented by the settlement of early human civilizations on the Mediterranean shore was significant. Humans, a driver of change that was not present five millions years ago, are modifying the global climate and individual ecosystems at increasingly fast rate (Jackson, 2008). There have been 39 glacial–interglacial shifts over the past two million years, and most warming events happened over timeframes of perhaps 5,000 years, rather than the past century of accelerated change. The present situation has been compared to a wrecking ball breaking down in hours a building that took years to construct (Barnard and Midgley, 2009). Taking into account the human factor, to speak about natural cycles and returns does not seem rational.

The Mediterranean region has been inhabited for millennia and marine ecosystems have been altered in many ways. Human involvement in marine ecosystem functioning, therefore, is proportionally stronger in the Mediterranean than in any other sea of the world (Costello et al., 2006). The Mediterranean is highly populated (more than 130 million inhabitants, distributed in 20 modern states) and the greatest tourist destination in the world (approximately 200 million tourists per year): both these human pressures are expected to rise substantially in the future (Turley, 1999). The most densely populated country in the world, the Principality of Monaco, lies on the Mediterranean shore. The continuous increase in coastal settlers is today of great importance in terms of economic income to the Mediterranean region, but it is also causing intense environmental degradation through excess coastal development, pollution and consumption of natural resources, adding pressure to the marine environment (Coll et al., 2010). The term Anthropocene was coined by Crutzen and Stoermer (2000) to define a geological epoch started with the Industrial Revolution (late 18th century) or even earlier, with the rise of agriculture and farming in the Neolithic. Contrary to previous epochs, the Anthropocene is characterized by human influence on ecosystems overwhelming that of climate, as happened in the rest of the Quaternary, or even tectonics, as happened in the Tertiary (Steffen et al., 2007). The Anthropocene concept seems particularly appropriate for the Mediterranean, where most of the ups and downs in the biota are closely linked with human population pressures, which have changed many times through the long common history of ecological systems and human societies. The dynamics of human populations will be a major factor in the future of the Mediterranean. In this context, the future of biological diversity will depend on how human societies will learn to live together with their natural heritage in the forthcoming decades (Blondel and Médail, 2009). If humans are affecting marine ecosystems more now than ever in the past, the reverse is also true: the change in marine ecosystem functioning may have tremendous significance for society, as people are increasingly living on the coast. The projected changes of human population in coastal areas are 200 million in 2025, with 170 million living in urban areas. The economy of those millions will depend more and more on marine resources. Imagine, for instance, the problems of coastal erosion or water quality worsening: they would have impacted little more than some fishermen's villages at the time of the MWP but are causing great concern in this 21st century to both urban settlements and tourism development.

Mediterranean biodiversity will inevitably need to get reshaped to survive the Anthropocene together with the humans, intact marine ecosystems belonging to a lost era (Stachowitsch, 2003). Future ecosystems must become closely managed 'new commons', where natural and socio-economic components are integrated (Bradbury and Seymour, 2009). Human pressures are part, and surely not the least, of the set of multiple affectors (either disturbances or stressors) that alter the structure of marine ecosystems (Montefalcone et al., 2010c). Although much is known about the consequences of individual affectors, much less is available on how cumulative impacts interact (Coll et al., 2010). Interactions are not simply additive in space and time, and the same affectors may interact idiosyncratically to produce different effects in different sites because their intensity, frequency, variance and the state of the receiving ecosystem are context-dependent variables. Thus, when many affectors act in synergy, they may eventually have unexpected and irreversible consequences. An extraordinary example is the interaction between climate warming and Lessepsian immigration: the Suez Canal could not have played the role it plays today, if it had been cut one or two centuries earlier, during the LIA (Por, 2009). The single factor approach that has characterized most environmental research to date must be considered as insufficient and inadequate (Abbiati et al., 1987).

A complex scenario is therefore emerging, whose future is both undetermined and unpredictable. Changes that occurred in the past, before Anthropocene, cannot help us in understanding the future of Mediterranean biodiversity. Habitats that in the past acted as refuges for endangered species are unlikely to play the same role in the future (Coll et al., 2010). Submarine caves are showing susceptibility to climate change (Chevaldonné and Lejeusne, 2003; Parravicini et al., 2010b), while the intertidal, like all the other very shallow habitats, is the most impacted by coastal urbanization (Montefalcone et al., 2010a). Potential refuges at depth are also questionable, due to deep water warming (Lejeusne et al., 2010) and fisheries extending down to the bathyal zone (Papaconstantinou and Farrugio, 2000).

While there is no doubt that the biodiversity patterns are changing, it is impossible at present to foresee how the future Mediterranean Sea ecosystems will appear. Mediterranean communities are losing their peculiar character (Bellan-Santini and Bellan, 2000) to become similar to their tropical analogues, especially in the southern portions of the basin (Fishelson, 2000; Zaouali, 2008). Tropical marine ecosystems are characterized by coral reefs, and eight of the coral species living in the Mediterranean Sea are potentially reef-forming (Morri et al., 2000b). While ocean acidification is presumed to negatively affect their growth, climate warming might be presumed to act positively. *Cladocora caespitosa*, the most important among the shallow-water zooxanthellate species living in the Mediterranean, was more abundant and built more conspicuous formations during periods of the Quaternary when Mediterranean climate was subtropical (Peirano et al., 2004): however, warming episodes in recent summers coincided with mass-mortality events of this coral (Rodolfo-Metalpa et al., 2000, 2006), colonies with partial mortality being overgrown by the alien alga *Caulerpa racemosa* (Figure 20). No coral species are listed among the many Red Sea invaders, although species of *Pocillopora* would in theory be good candidates, due to their dispersal ability and their capacity to adapt to a wide variety of environmental fluctuations (Liñán-Cabello et al., 2010); another candidate could be *Stylophora pistillata*, which in the Gulf of Suez forms reefs at minimum temperatures around 18 °C (Por, 2009). For the Mediterranean to become a coral sea, the Suez Canal is still a barrier. To date, the only alien coral established in the Mediterranean is *Oculina patagonica*, perhaps passively transported by ships from the SW Atlantic: it is showing some constructional capacity along the southern shores of the basin (Sartoretto et al., 2008, and references therein) but also underwent mortality in the presence of elevated sea temperatures (Rodolfo-Metalpa et al., 2006). Thus, while Mediterranean ecosystems are being tropicalized at a fast rate, it seems unlikely that the Mediterranean Sea of the future will exhibit significant coral constructions. The overwhelming number of Lessepsian immigrants will make the composition of the biota recall more and more that of the Red Sea. However the future Mediterranean communities will probably look like those characterising today southern Macaronesia and the Cape Verde region, with scanty coral and abundant algae (Bianchi et al., 1998, 2000; Morri et al., 2000c), rather than those of the Red Sea. The dominant algae will probably be not the many endemics of today but rather aliens species such as *Stypopodium schimperi* (Cocito et al., 2000), *Caulerpa taxifolia* and *C. racemosa* (Montefalcone et al., 2010b), and diverse filamentous species (Airoldi et al., 2008). These newly configured ecosystems will be increasingly exposed to pollution, overfishing, rising temperatures, and acidification. Looking at the past to imagine their trajectory will be of little help. Rather, we see three tools that, combined, can help understanding and managing change: MPAs, field models, and long term monitoring.

MPAs are currently seen as sites where biodiversity is protected against anthropogenic impacts: in a sea overwhelmed by humans, this is just a form of ‘genteel managed decline’ rather than conservation (Bradbury and Seymour, 2009). On the contrary, MPAs must be seen as selected sites where human impact is kept to a minimum and natural change can freely play its role, not as sites where nature is ‘conserved’ as it stands (Bianchi and Morri, 2000). What is important is the establishment of networking initiatives, as neither species nor ecosystems recognize the boundaries of the individual MPAs, nor climate or even large scale human impacts do so (Montefalcone et al., 2009). Communities do not stand as single units but are interconnected within metacommunities, implying the interplay between large-scale connectivity and local dynamics in driving change at multiple spatial scales. MPAs would be those parts of the new commons to be used as laboratories where criteria and methods for the integrated management of the sea could be developed (Bianchi, 2008).

Field models may enable developing predictions. Laboratory experiments can deliver information about specific mechanisms but will hardly help our understanding of what may happen in complex systems. The latter goal can be achieved by studying shallow-water hydrothermal vents. While deep-sea hydrothermal vents give rise to a distinct ecosystem fuelled by chemiolithosynthesis, those on the continental shelf induce change in ecosystems otherwise ‘normal’. They emit warm water, carbon dioxide, toxic chemicals, nutrients and reduced compounds that altogether mimic climate and human impacts. Volcanic systems giving rise to submarine hydrothermalism have been present, probably continuously, since the Mediterranean was first formed and several such hydrothermal vents occur in the present-day Mediterranean Sea (Dando et al., 1999). They may provide unique opportunities for field observations about biodiversity alteration and ecosystem response. In the past, they would have provided refugia for species adapted to such conditions and, conversely, have contributed to the extinction of species, a good example being the destruction of the last stromatolites existing in the Mediterranean by the eruption of the Santorini volcano (Eriksen et al., 1989). Many thermophilic/hyperthermophilic taxa isolated from shallow Mediterranean vents have also been found at deep-sea hydrothermal vents. Of course, vent systems may not be taken as perfect predictors, owing to the spatial proximity of ecosystems unaffected by their emissions; however, they exert their influence on sufficiently large spatial and temporal scales to integrate most significant community processes (Cocito et al., 2000).

Finally, long-term monitoring is the only means to follow ecosystem evolution in a changing environment and to track future trends. It is essential to start monitoring biodiversity at a whole Mediterranean scale, with projects that have to use a similar approach and to implement easily comparable methods. Monitoring should encompass periods that correspond at least to the expected lifetime of the dominant organisms and the time scale of the most important factors acting upon them. Funding and other constraints force ecologists into 2-3-year projects at maximum; few natural patterns are of such short duration, major changes in biota occurring in cycles of several years (Bianchi and Morri, 2004). With a small-scale and short-term approach to ecological monitoring and research, attempts to distinguish irreversible trends from recurrent ‘natural’ cycles will results in frustration.

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