**BIODIVERSITY IN ENCLOSED SEAS** 

# **Biodiversity issues for the forthcoming tropical Mediterranean Sea**

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Abstract Present-day Mediterranean marine biodiversity is undergoing rapid alteration. Because of the increased occurrence of warmwater biota, it has been said that the Mediterranean is under a process of 'tropicalization'. This paper analyses the main patterns of the Mediterranean Sea tropicalization and considers briefly its extent and consequences. As happened during previous interglacial phases of the Quaternary, Atlantic water, entering via the Straits of Gibraltar, carries into the Mediterranean species that are prevalently of (sub)tropical affinity. On the other side of the basin, Red Sea species penetrate through the Suez Canal, a phenomenon called lessepsian migration from the name of F. de Lesseps, the French engineer who promoted the cutting of the Canal. Also the many exotic species introduced by humans voluntarily or involuntarily are nearly always typical of warm waters. Climate change combines with Atlantic influx, lessepsian migration and the introduction of exotic species by humans to the establishment of tropical marine

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biota in the Mediterranean Sea. Present-day warming ultimately favours the spread of warmwater species through direct and indirect effects, and especially by changing water circulation. It is impossible at present to foresee to what extent the exuberance of warm-water species will affect the trophic web and the functioning of marine ecosystems in the Mediterranean Sea of tomorrow. While Mediterranean Sea communities are modifying their pattern of species composition, they do not seem to be acquiring a more marked tropical physiognomy: Mediterranean coastal marine ecosystems are still dominated by frondose algae (even if the species that are gaining ascendancy are of tropical origin) and not by corals as is normal in tropical seas.

**Keywords** Marine biodiversity · Marine biogeography · Climate change · Species distribution · Range extension · Mediterranean Sea

# Introduction

The status of Mediterranean Sea biodiversity has been reviewed by Bianchi & Morri (2000) on the basis of information collected mostly in the mid 1990s (Bianchi, 1996). Their review was organised around six main points: (1) how many species are there in the Mediterranean Sea; (2) origins and causes of Mediterranean biodiversity; (3)

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biodiversity and climate change; (4) the footprint of man; (5) protecting marine biodiversity; (6) the role of scientific research. Nearly ten years later all of these points need updating, as renewed research on Mediterranean Sea biodiversity has provided a wealth of new information on all of them. For instance, the number of macroscopic marine species inhabiting the Mediterranean, then reckoned as 8,565, is today estimated at about 12,000 (Boudouresque, 2004) and further increments may be expected by the study of 'inconspicuous' taxa or undersampled habitats such as submarine caves or the depths (Bianchi & Morri, 2002). The origins of the Mediterranean Sea biodiversity have been reanalysed by Taviani (2002), Boudouresque (2004), and Emig & Geistdoerfer (2004). A deficiency lamented by Bianchi & Morri (2000) was the derisory extent of marine protected areas (MPAs) in the Mediterranean Sea. Fortunately things have started to change, as numerous MPAs have been established in the last few years (Carrada et al., 2003); among them is the first international off-shore MPA in the world: the so-called 'whale sanctuary' of the Ligurian Sea (Diviacco, 2002).

In this paper, I will try to update knowledge about another point touched by Bianchi & Morri (2000): the rate of change that Mediterranean Sea biodiversity is presently facing under the action of climate and humans. While climate variation is apparently modifying the distribution patterns of Mediterranean Sea biodiversity (Bianchi & Morri, 1993, 1994; Francour et al., 1994; Bianchi, 1997; Morri & Bianchi, 2001; Bianchi & Morri, 2004a, 2004b), humans are altering the composition of Mediterranean marine biota by the introduction of exotic species (Zibrowius, 1991; Boudouresque & Ribeira, 1994; Occhipinti-Ambrogi, 2001; Occhipinti-Ambrogi & Savini, 2003; Streftaris et al., 2005). Since introduced species are nearly always typical of warm waters, anthropogenic and climatic actions combine to allow for an increased abundance and distribution of (sub)tropical species in the warm-temperate Mediterranean Sea. It is therefore often said that the Mediterranean Sea is heading towards a generalised phenomenon of 'tropicalization' (Bianchi & Morri, 2003). For example, out of 90 exotic fish species that entered the Mediterranean Sea in recent years, only three

are boreal, all the others are tropical (Golani et al., 2002). I am inclined, however, to include in the phenomenon of Mediterranean tropicalization also the northward spread of Mediterranean indigenous species with (sub)tropical affinities that were confined in the southern parts of the basin until recently (Bianchi & Morri, 1993, 1994, 2004b). I believe, in fact, that the patterns of distribution change will be similar for all warmwater species, whether recently introduced in or native to the Mediterranean, and will be governed by the same climatic, hydrological and ecological factors.

This paper aims to analyse the main patterns of the Mediterranean Sea tropicalization and to consider briefly its extent and consequences. I will concentrate on the coastal benthos, for which I have more information, but the same phenomenon is observed in the pelagic realm (see Gómez & Claustre, 2003, for an example). Information on Mediterranean deep-water biota is still too scarce (Bellan-Santini et al., 1992; Emig & Geistdoerfer, 2004) for proper consideration.

# The driving factors

The occurrence and spread of warm-water species in the Mediterranean Sea results from the action of four distinct causes, namely: Atlantic influx, lessepsian migration, introductions by humans, and present-day sea warming. The first is a natural cause, while the second and the third are clearly anthropogenic; the fourth may be considered natural only in part, as we are well aware that humans play a major role in planetary warming. These four causes act on very different time scales, but all have apparently accelerated in the last two decades or so.

The time scale of Atlantic influx is of the order of  $10^4$  years, i.e., since the beginning of the last interglacial. As happened during the Quaternary, Atlantic water, entering through the Straits of Gibraltar, carries into the Mediterranean species of prevalently (sub)tropical affinity (Bianchi et al., 2002). Many of these species originally established themselves exclusively in areas close to Straits of Gibraltar but, especially in recent years, some have penetrated farther east, reaching for instance the coasts of Sicily, i.e., the region that is traditionally taken as the boundary between western and eastern Mediterranean basins (but see below). A recent and well documented example is the crab *Percnon gibbesi* (H. Milne Edwards), of western tropical Atlantic origin (Relini et al., 2000; Pipitone et al., 2001; Mori & Vacchi, 2002). In addition to Sicily, this species is now found at the Pontine Islands, in the central Tyrrhenian Sea (Russo & Villani, 2004), in southern Sardinia (P. Panzalis, personal communication) and at Capo Rizzuto, on the Ionian coast of Calabria (I. Faccia, personal communication).

The phrase lessepsian migration was coined from the name of Ferdinand de Lesseps, the French engineer and diplomat who promoted the cutting of the Suez Canal, and was adopted to indicate the penetration of Red Sea species into the Mediterranean (Por, 1978). The time scale of lessepsian migration is of the order of 10<sup>2</sup> years, as it started soon after the opening of the Canal in 1869. However, it remained inconspicuous until the 1970s, when the penetration of lessepsian migrants increased because of the progressive reduction of salinity of the Bitter Lakes and the diminished outflow of the Nile at the northern end of the Canal, caused by the building of the Aswan dam. The spreading into the eastern Mediterranean of stenohaline Red Sea species was therefore facilitated (Galil, 1993). For a long period, the vast majority of these lessepsian migrants remained confined to the Levant Sea, where they now shape the coastal communities (Fishelson, 2000). However, many of them have now penetrated into the western Mediterranean (Galil et al., 2002; Golani et al., 2002; Ribera Siguan, 2002; Zenetos et al., 2003).

Lessepsian migration apart, the introductions of exotic species by humans have acted on a time scale of  $10^3$  years (Giaccone, 2002): well before the Christian era, Greek sailors travelled perhaps as far as Iceland, the Phoenicians circumnavigated Africa, and Punic merchants possibly reached Macaronesia, Brazil and the Maldives (Bianchi & Morri, 2000). We cannot say how many species the wooden ships of ancient times would carry with them. However, it seems indisputable that the amplitude of this phenomenon greatly increased since the World War II (Boudouresque & Ribeira, 1994). Species are being intentionally or accidentally introduced via ship fouling, ballast waters, aquaculture, trade in live bait, wrapping of fresh seafood with living algae, aquariology, and even scientific research (Bianchi & Morri, 2000).

Finally, sea warming has a time scale of  $10^1$  years: despite large cyclic fluctuations, a positive trend in Mediterranean temperatures is clearly seen after the mid 1980s: its effects include the northward extension of the range of warm-water species within the Mediterranean Sea (Bianchi & Morri, 1994; Astraldi et al., 1995; Bianchi, 1997, Vacchi et al., 2001).

#### A scope for biogeography

Biogeography is the study of the spatial and spatio-temporal patterns of biodiversity (Zunino & Zullini, 1995). Although long neglected in the recent past (Bianchi & Morri, 2000), Mediterranean marine biogeography is at present enjoying a certain revival (Koukouras et al., 2001; Arvanitidis et al., 2002; Bianchi & Morri, 2002; Baccetti, 2003; Harmelin, 2004; Logan et al., 2004). Tropicalization is said to be changing the pattern of Mediterranean Sea biodiversity, and changes in species distribution should be particularly obvious in those transitional areas that are close to biogeographic boundaries, i. e., at the limits of regions inhabited by a different biota (Bianchi & Morri, 2004b).

The Mediterranean Sea as a whole constitutes a distinctive province of the Atlantic-Mediterranean warm-temperate region. However, the Mediterranean is far from being homogenous biogeographically: its tormented geological history and the present-day variety of climatic and hydrologic situations that are found in the different areas of the basin have traditionally led to the recognition of ten distinct biogeographic sectors (Bianchi & Morri, 2000: 370, Fig. 2). Thanks to new knowledge (including the considerations below), I am now inclined to recognise at least two additional sectors (Bianchi, 2004), to distinguish the southern Tyrrhenian Sea from the Balearic-Sardinia area and the Ionian Sea from the Aegean Sea (Fig. 1). A thirteenth sector may well be recognised in the Straits of Messina: although small, this area harbours a wealth of biogeographic peculiarities, including Pliocene Atlantic remnants and local endemisms (Fredj & Giaccone, 1995).

While the core-zones of these biogeographic sectors are easily identifiable, tracing their boundaries on a map is difficult. A major boundary, often mentioned in Mediterranean literature, is that between the western and eastern basins of the Mediterranean Sea. In their highly influential 'Nouveau manuel', Pérès & Picard (1964) placed this boundary somewhere in the mid Ionian Sea, thus including the whole Sicily, Calabria and the Gulf of Taranto in the western Mediterranean (Fig. 1, line i). Sarà (1968) expressed doubts about the placement of the Ionian coast of Calabria and the Gulf of Taranto in the western Mediterranean but nevertheless adopted the same scheme, which was later popularised in university text books (Cognetti & Sarà, 1974; Cognetti et al., 1999). The existence of a mid-Ionian boundary found confirmation in a recent

study of the biogeography of Mediterranean Proseriata (a group of tiny interstitial flatworms supposedly provided with low dispersal capacity): species assemblages from the eastern Ionian Sea turned out more similar to those of other eastern Mediterranean localities, whereas assemblages from the western Ionian Sea grouped together with those from western Mediterranean localities (Curini-Galletti & Casu, 2003). A different picture was suggested by Giaccone & Sortino (1974) who, working on the algal flora, established the boundary between the western and the eastern Mediterranean in the middle of the Straits of Sicily, so that the island of Pantelleria should belong to the western Mediterranean, while the Pelagie islands and Malta should belong to the eastern Mediterranean (Fig. 1, line ii). Bianchi & Morri (2000) picked up the idea of excluding the Ionian coast of Calabria and the Gulf of Taranto from the western Mediterranean but still included in it the whole of Sicily, putting the Pelagie Islands in the eastern Mediterranean and leaving Malta on the border (Fig. 1, line iii). Despite minor differences, these last views agree in



Fig. 1 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 Lions and Ligurian Sea; (6) northern Adriatic Sea; (7) central Adriatic Sea; (8) southern Adriatic Sea; (9) Ionian Sea; (10) northern Aegean Sea; (11) southern Aegean Sea; (12) Levant Sea; (13) Straits of Messina. Position of the boundary between the western and eastern Mediterranean according to different authors (see text): i Pérès & Picard (1964); ii Giaccone & Sortino (1974); iii Bianchi & Morri (2000);

iv Costagliola et al. (2004). Mediterranean countries (clockwise): E Spain; F France; I Italy; SLO Slovenia; HR Croatia; BIH Bosnia-Herzegovina; SGC Serbia-Montenegro; AL Albania; GR Greece; TR Turkey; CY Cyprus; SYR Syria; RL Lebanon; IL Israel; ET Egypt; LAR Libya; M Malta; TN Tunisia; DZ Algeria; MA Morocco. Some additional localities mentioned in the text are also indicated: *a* Ligurian Sea; *b* Gibraltar Straits; *c* Sicily; *d* Tyrrhenian Sea; *e* Pontine Islands; *f* Calabria; *g* Suez Canal; *h* Gulf of Taranto; *i* Pantelleria Island; *j* Pelagie Islands; *k* Peloponnese; *l* Port-Cros Island

considering the area around the Straits of Sicily as the boundary zone between the western and eastern Mediterranean. This seems reasonable also in the light of geology and patterns of water circulation (Bianchi et al. 2002; Pinardi & Masetti, 2000). A radical departure from this established scheme was offered by population genetic studies on fish and invertebrates (Costagliola et al., 2004 and references therein), which revealed a strong genetic break between the Peloponnese and the Aegean and not at the Strait of Sicily (Fig. 1, line iv). However, in a recent population genetic study on the endemic seagrass Posidonia oceanica (L.) Delile, samples from the Gulf of Taranto showed greater genetic similarity to those from the Aegean Sea than to those from the Tyrrhenian Sea, thus supporting the traditional view that the Straits of Sicily represents the major biogeographic barrier separating western and eastern Mediterranean biota (Micheli et al., 2005).

#### Physical versus physiological barriers

The contrasting views about the position of the western/eastern Mediterranean boundary are of particular interest in considering the relatively recent colonisation of the Mediterranean from the Atlantic, after near extinction of the Mediterranean biota in the Messinian period, approximately 5.6 million years ago (Bianchi & Morri, 2000). It has been said that the Straits of Sicily acted as a filter to the recolonisation of the eastern Mediterranean, so that species richness should be lower there than in the western basin. This seems to be true for the Levant Sea: Taviani (2002) called it a 'Godot' basin, i. e., a basin waiting for Atlantic colonisers that were not arriving (colonisers are coming from the Red Sea, now!), but does not hold for the Aegean Sea, where recent research showed that its species richness is comparable to that of the western Mediterranean (Zenetos, 1997; Morri et al., 1999; Logan et al., 2002).

Mapping the surface isotherms of the Mediterranean Sea, averaged over a century of records and therefore representing the climatology of the basin (Brasseur et al., 1996), shows that the isotherm of 15°C for February (the coldest month in the year) crosses the Straits of Sicily, splits the Ionian Sea into a north-western and a southeastern part, and finally separates the Peloponnese from the Aegean Sea (Fig. 2). In other words, the February 15°C surface isotherm follows quite closely all the biogeographic boundaries between the western and eastern Mediterranean proposed in turn! If temperature matters, that may be why the Aegean Sea biota is more similar to that of the western Mediterra-



Fig. 2 Surface isotherms of February (traced every  $0.25^{\circ}$ C) of the Mediterranean Sea (climatological means from the historical data set 1906–1995). The 14°C and the

15°C 'divides' (see text) are highlighted by a thicker tract. Modified after MEDATLAS (Brasseur et al., 1996)

nean (both basins laying mostly to the north of the February 15°C surface isotherm) than to that of the Levant Sea (which remains to the south of that isotherm).

I am therefore tempted to suspect that the biotic differences between western and eastern Mediterranean are due more to differences in temperature regime, i.e., a physiological barrier, than to the physical barrier of the Straits of Sicily. This may have profound implications: sea warming will easily move isotherms but cannot change the morphology of straits. What evidence can species distribution provide with this respect?

If recent introductions (the already mentioned Atlantic and lessepsian migrants) are excluded, there are not many examples of well-known species occurring exclusively in only one of the two basins (Bianchi et al., 2002). One such example is found in the genus Charonia, one of the biggest Mediterranean gastropods, which is represented by C. lampas lampas (L.) in the western basin and by C. tritonis variegata (Lamarck) in the eastern basin; the two species meet in the Straits of Sicily (Russo et al., 1990). However, both species exist in the Atlantic Ocean, where the former exhibits a typical warm-temperate distribution (English Channel to West Africa) while the latter thrives in tropical and subtropical waters of both sides of the Atlantic. The February 15°C surface isotherm might well act as a divide between the ranges of two closely related species with distinct temperature requirements. Also the February 14°C surface isotherm may have a major biogeographic interest, as I will show later.

*Charonia tritonis variegata* is not the only species thriving in (sub)tropical Atlantic water and in the eastern Mediterranean but not in the area in between: other well-known examples are the ghost crab *Ocypode cursor* (L.) and the club-tipped anemone *Telmatactis cricoides* (Duchassaing). These species penetrated the Mediterranean during a warm interglacial period in the Quaternary and disappeared from the western basin when the climate got cooler. They have now a population 'trapped' in the warmer eastern basin, but sea-warming might join the Atlantic and Mediterranean populations again in the near future (Wirtz & Debelius, 2003).

# **Changing species ranges**

A species once restricted to the eastern Mediterranean but now crossing the 15 °C divide is the parrotfish *Sparisoma cretense*: apart from two sightings in the Tyrrhenian Sea in summer 1991 (Bianchi & Morri, 1994), this species has become established since summer 2000 in the southern Adriatic (Guidetti & Boero, 2001, 2002).

The most striking example of a species that has recently expanded its range within the Mediterranean is the scleractinian coral Astroides calvcularis (Pallas). This was the preferred example of a south-western Mediterranean species that 'does not go east' (Pérès & Picard, 1964; Zibrowius, 1980, 1983, 1995): its range before 1989 was confined to the south-western Mediterranean between the 15°C and 14°C divides (Fig. 3). It was explained that this species cannot go east because the life-span of its pelagic larva is too short to overtake the wide expanse of the Ionian Sea by means of the eastward flowing currents (Fig. 4). On the other hand, it could not cross this sea step by step along the coast: the northern coast would be too cool for this warm-water species, the southern coast is sandy and does not offer this rocky-bottom species place to settle (Pérès & Picard, 1964). Apparently, A. calycularis was not aware of these thoughtful explanations and went east anyway: it has recently been discovered along the coast of Croatia, in the Adriatic Sea (Kružić et al., 2002; Grubelić et al., 2004). It jumped at once over both the western/ eastern Mediterranean boundary and the 14°C divide.

It might not be coincidental that the conspicuous range expansion of *A. calycularis* took place in the same years of the so-called Eastern Mediterranean Transient (EMT), a dramatic change in thermohaline circulation that involved the inversion of surface currents in the Ionian Sea (Briand, 2000). This may have provided *A. calycularis* with the carrier that brought it from the Straits of Sicily to the Adriatic (if so, the normal cyclonic circulation along the Ionian coast of Calabria and not the lower temperature was the obstacle to the eastward spreading of *A. calycularis*). It would be worth looking for this species along the Ionian coast of Calabria, but no



**Fig. 3** Variations of the range of the scleractinian coral *Astroides calycularis* within the Mediterranean Sea. Open circles = confirmed distribution before 1980 (based on information in Zibrowius, 1980). Solid circles = later records within the known range (various sources). Open triangles = historical occurrences (1899 and 1904) not confirmed in recent decades (Grubelić et al., 2004). Solid

information is available at present. Changing surface circulation pattern in the Ionian Sea may also be invoked for the above-mentioned sudden appearance of the parrotfish *Sparisoma cretense* in the southern Adriatic. Galil & Kevrekidis (2002) attributed to the EMT the penetration of Indo-West Pacific crustacean species into the southeastern Aegean.

triangles = recent records outside the known range: Cape Palos, Spain (Zibrowius, 1983); Giglio Island, Italy (Bianchi & Morri, 1994); islands and coast of Croatia (Kružić et al., 2002; Grubelić et al., 2004). + = Pleistocene fossil records (Zibrowius, 1995). The 14°C and 15°C 'divides' are also illustrated (see Fig. 2)

It is probable that the EMT has also influenced the western Mediterranean (Briand, 2000) but it cannot be said, at present, if the changes in species distribution observed in the latter basin hold any relationship with the transient. What can be said is that around 1990 many southern species moved northwards. The best studied case is that of the ornate wrasse *Thalassoma pavo* (L.), a



**Fig. 4** A schematic summary of the major current and gyre systems of the Mediterranean Sea and their seasonal variability. Thick line = winter circulation; thin 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: Iera-Petra gyre; M: western Cretan gyre; N: Pelops gyre; O: Ionian cyclonic current; P: southern Adriatic gyre; O: eastern Adriatic coastal current; R: western Adriatic coastal current; s: western Ionian gyre. Modified after Pinardi & Masetti (2000) species once confined to the southern portions of the Mediterranean Sea, which has penetrated into the Ligurian Sea, where it is now able to reproduce, thus becoming 'naturalised' (Vacchi et al., 1999, 2001; Sara & Ugolini, 2001; Guidetti et al., 2002; Sara et al., 2005).

If southern, warm-water species move northwards, what happens to the cold-water species long established in the northern sectors of the Mediterranean Sea? Are they at risk of extinction? Studying the marine decapod crustaceans of the Port-Cros National Park (France, Ligurian Sea), where a direct human action may be excluded, Noël (2003) related the increased rarity of the European lobster Homarus gammarus (L.), a northern species, to the increased abundance of the Mediterranean locust lobster Scyllarides latus (Latreille), a southern species. A well demonstrated case is that of two cavedwelling mysids, the warm-water species Hemimysis margalefi Alcaraz, Riera and Gili and the coldwater species H. speluncola Ledoyer: in the submarine caves of the northern Mediterranean. the former is replacing the latter, which is therefore going extinct (Chevaldonné & Lejeusne, 2003).

## **Changing ecosystems**

The two cave mysids above provide an example of change in biodiversity pattern that is likely to have great influence on ecosystem functioning. Mysids stay in caves during the day but move outside at night to feed. In so doing, they import organic matter from outside into the oligotrophic cave ecosystem, providing cave consumers with their faecal pellets or even falling prey to resident carnivores (Bianchi et al., 2003). As *H. speluncola* typically forms huge swarms and *H. margalefi* small groups, this must make a big difference to the energy budget of cave ecosystems (Bianchi et al., 1998).

Submarine caves are nothing but a very small portion of the Mediterranean Sea. Is there any indication that tropicalization is inducing major changes in marine ecosystems?

The most distinctive feature of tropical marine ecosystems are coral reefs. True reefs do not exist

in the Mediterranean, but several Mediterranean organisms build significant bioconstructions. These organisms include primarily coralline algae, but also some invertebrates, such as scleractinian corals, vermetid molluscs, serpulid polychaetes and cheilostomate bryozoans (Bianchi, 1997; Bianchi & Morri, 2004b). The bioconstructions of the Mediterranean are monospecific or, at most, oligospecific, as far as the species responsible for their building are concerned (Bianchi, 2002).

Harriot (1999) considered 14°C as a threshold value for bioconstructional corals. In the Mediterranean Sea, the 14°C divide seems to represent the northern limit for the bioconstructional activity of the vermetid Dendropoma petraeum (Monterosato) (Antonioli et al., 1999) and of the scleractinian Madracis pharensis (Heller) (Morri et al., 2000a). During Quaternary phases warmer than at present, the bioconstructional activity of coralline algae in the Mediterranean Sea was more intense (Boudouresque et al., 1980; Sartoretto et al., 1996). Taken as a whole, these facts suggest that the present-day Mediterranean Sea represents a sort of hinge zone in space and time between a marine biota dominated by bioconstructors and one (nearly) deprived of them. The carbonate production by Mediterranean bioconstructors, taking into account both corals and other organisms, may be estimated around 10<sup>3</sup> gCaCO<sub>3</sub> m<sup>-2</sup>y<sup>-1</sup>, so being included in the range recorded for the tropics (Bianchi, 2002).

Eight coral species, out of the 37 presently occurring in the Mediterranean, are potential bioconstructors (Morri et al., 2000a). Five of them always lack zooxanthellae as they live in deep waters, which are not reached by the light necessary to microalgal endosymbionts. Dendrophyllia ramea (L.) and D. cornigera (Lamarck) are known as 'yellow corals' and live in the circalittoral zone, especially in the south-western areas of the Mediterranean, therefore showing a distribution typical of warm-water species. Madrepora oculata L., Desmophyllum cristagalli Milne Edwards and Haime and Lophelia pertusa (L.) are grouped under the name of 'white corals', live in the bathyal zone and have a strong affinity for cold waters. The three infralittoral species,

obligatorily or facultatively zooxanthellate, are Madracis pharensis, Oculina patagonica De Angelis and Cladocora caespitosa (L.). M. pharensis occurs, without zooxanthellae, in submerged caves all over the Mediterranean, showing no significant bioconstruction capacity; however, in the south-eastern Mediterranean, beyond the 14°C divide, it may be found outside caves and with zooxanthellae, and in these situations it may play a significant bioconstructional role (Morri et al., 2000a). O. patagonica, probably originating from the south-western Atlantic, has been involuntarily introduced by humans to the Mediterranean: it is normally zooxanthellate and is able to build large colonies; although found also in the cold Ligurian Sea, it is especially abundant in western and eastern Mediterranean coasts to the south of the 14°C divide (Fine et al., 2001).

Cladocora caespitosa, the only species studied in some detail, is obligatorily zooxanthellate and may build banks more than one meter thick and several tens of meters wide (Morri et al., 1994, 2000b; Peirano et al., 1998, 2002; Kružić & Pozar-Domac, 2003). This species belongs to the family Faviidae, one of the most important in coral reef formation, and its calcification rates compare with those of tropical constructional corals (Rodolfo-Metalpa et al., 1999; Peirano et al., 2001). Growth of Cladocora caespitosa seems to be correlated with climate fluctuations (Morri et al., 2001; Rodolfo-Metalpa et al., 2002a, 2002b). Retrospective analysis, by X-radiography, on colonies older than 60 years, demonstrated that the highest growth rates coincided with the 'warm' period of the 1940s and the lowest with the 'cold' period of the 1970s (Peirano et al., 1999). This agrees with the palaeoecological information, indicating that C. caespitosa was more abundant-and its formations more conspicuous-during the warm periods of the Quaternary, and especially during the Tyrrhenian stage, when Mediterranean climate was subtropical (Peirano et al., 2004). It could therefore be supposed that, if the present sea-water warming continues, Cladocora caespitosa will play the role of constructional coral in a more and more 'tropical' Mediterranean Sea. In reality, in coincidence with positive anomalies of sea surface temperature recorded in these last few summers, this species underwent mass-mortality 15

events, recalling those observed in the tropics (Rodolfo-Metalpa et al., 2000). Cases of massmortality correlated with high temperatures were recorded also in other organisms, such as sponges and gorgonians (Cerrano et al., 2000; Perez et al., 2000; Romano et al., 2000, Laubier, 2001; Garrabou et al., 2001, 2002; Sara et al., 2003).

### Hypotheses, predictions and uncertainties

The tropicalization of the Mediterranean cannot be considered as a sort of improbable return of this sea to its ancient past of equatorial Mesozoic ocean, the Tethys. It is a completely new phenomenon that may rather be seen as the resultant of changes, not necessarily correlating among each other, induced by climate and human action.

Climate change combines with Atlantic influx, lessepsian migration and the introduction of exotic species by humans to favour the occurrence and establishment of warm-water species, whether exotic or native, in the Mediterranean Sea. While the latter three factors provide the 'raw material' (i. e., the warm-water species), the former is the 'mechanism' that ultimately favours the spread of these species through direct and indirect effects (Southward et al., 1995; Bianchi, 1997; Hiscock et al., 2004). Direct effects depends on temperature affecting survival rate, reproductive success and behaviour of organisms; indirect effects include those mediated by biotic interactions (e.g., conferral of competitive advantage to one of a pair of overlapping species, increased incidence of a parasite, or modified abundance of a predator) or by marine currents (climatic change may alter the emphasis of water flow and the pattern of water circulation, with great repercussions on the dispersal ability of marine organisms).

All these effects have been recognised in the Mediterranean biota (Morri & Bianchi, 2001; Chevaldonné & Lejeusne, 2003; Bianchi & Morri, 2004a). Perhaps, the change operated through marine currents has provided the most spectacular examples (Astraldi et al., 1995). In this paper, I am hypothesising that the surface current inversion in the Ionian Sea during the EMT is likely to have allowed species to cross the alleged boundary between western and eastern Mediterranean at the Straits of Sicily. If the hypothesis of a link between the EMT and the range extension of certain species would prove true, this might provide us with clues to previous occurrences of similar climatic events in the past. Records of Astroides calycularis in the Adriatic Sea at the turn of the XIX and XX centuries were later reputed erroneous by Zibrowius & Grieshaber (1977) but are now revalidated by Grubelić et al. (2004). Again at the turn of the XIX and XX centuries, Thalassoma pavo occurred in the Ligurian Sea (Vacchi et al., 1999). Was it a pure coincidence? Or should we read in that a proof that a climatic event similar to the recent EMT had happened a century earlier?

The two examples provided by the coral Astroides calycularis and the crab Percnon gibbesi show that warm-water species, whether they are native like the former, or exotic like the latter, have apparently followed the same route to cross the Straits of Sicily from west to east. On the other side, many lessepsian species have crossed the Straits of Sicily from east to west (see Pipitone et al., 2004, for a recent example). Thus, the traditional idea of a major biogeographic boundary between western and eastern Mediterranean should be abandoned in favour of a series of boundaries (or gradients, perhaps) in a southnorth direction. Even the alleged difference in trophic status between eastern and western Mediterranean (the former being usually considered more oligotrophic than the latter) has to be questioned, as recent investigation in the southwestern Mediterranean revealed a trophic regime similar to that of the eastern Mediterranean (D'Ortenzio, 2004). I am not therefore surprised that two recent thorough studies on within-Mediterranean distributions of sponges (Pansini & Longo, 2003) and pycnogonids (Chimenz-Gusso & Lattanzi, 2003) found higher faunal affinities between eastern and south-western Mediterranean localities than between north-western and south-western localities. I predict that while the southern portions of the Mediterranean will be more and more occupied by tropical exotic species, the northern portions will be invaded by warm-water native species that were once called 'southern'. Native cold-water species, typically confined to the northern portions of the basin, will probably rarefy and eventually be lost from the Mediterranean if sea-warming continues.

While there is no doubt that the biodiversity patterns are changing, it is impossible at present to foresee to what extent the exuberance of warm-water species in the Mediterranean Sea of tomorrow will affect the trophic web and, more in general, the functioning of marine ecosystems. The links between biodiversity and ecosystem functioning are elusive and perhaps insubstantial (Duarte, 2000; Price, 2001; Boero et al., 2004).

Tropical species are becoming more numerous in the Mediterranean Sea (Galil et al., 2002; Golani et al., 2002; Ribera Siguan, 2002; Zenetos et al., 2003), but the marine ecosystems do not seem yet to be acquiring a more marked tropical physiognomy. While the coastal seascape of tropical marine ecosystems is normally characterised by corals, the coastal seascape of the Mediterranean Sea is still dominated by frondose algae. Among these, however, the species that are gaining supremacy are introduced and exhibit a tropical affinity, such as Stypopodium schimperi (Buchinger ex Kützing) Verlaque and Boudouresque (Sartoni & De Biasi, 1999; Cocito et al., 2000) and the two species of Caulerpa, C. taxifolia (Vahl) C. Agardh (Meinesz et al., 2001) and C. racemosa (Forsskål) J. Agardh (Verlaque et al., 2000). Corals or other constructional organisms are not getting more abundant: on the contrary, the native constructional coral Cladocora caespitosa and other large invertebrates that 'shape' the submarine seascape of coastal Mediterranean ecosystems are perhaps going to face more frequent mass mortality events. The Mediterranean Sea biocoenoses might loose in the near future what have been called their 'peculiarities' (Bellan-Santini & Bellan, 2000) and acquire a different and unprecedented configuration and structure.

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