

Tethys returns to the Mediterranean: Success and limits of tropical re-colonization

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Abstract

Many thousands of tropical species have been settling in the Mediterranean during the last decades. This is the result of congruence between the present Climate Optimum, which is expressed in the warming of the sea and the opening of the contact with the Indo-pacific realm through the Suez Canal and a renewed entry through the Straits of Gibraltar. A historical review shows that tropical biota survived in the Mediterranean till the end of the Pliocene Climate Optimum and that presently we are witnessing a re-colonization of the Mediterranean by Tethyan descendants, rather than an invasion by harmful alien species as happens elsewhere. The limits of this resettling as witnessed today are discussed.

Keywords

Lessepsian migration, invasive species, climate change, Mediterranean biodiversity, Tethys

Introduction

Time is ripe for a historical appreciation of the impressive biogeographical events that brought into the Mediterranean thousands of tropical species during the last decades. As usual in such cases, several lines of thought and different fields of knowledge have to be called in. In order to better understand the broader significance of the dramatic changes in the biodiversity of the Mediterranean, I shall focus on those taxa, which have fossil documentation and temperature tolerance data to juxtapose with our recent and paleoclimatology knowledge.

The tropical Cretaceous-Neogene Tethys Ocean (Fig.1), is often known in its Mediterranean section, also as the Eocene "Nummulite Sea". It was characterized by an abundance of the large, small-coin sized benthic Nummulitidae, symbiont-bearing Foraminifera. They are best seen in the stones of the pyramids of Egypt. *Heterostegina*, the last surviving genus of this family, disappeared from the Mediterranean, some five million years ago. The recent discovery that *Heterostegina depressa* is again abundantly represented in the sandy sediments along the Israeli coast of the Mediterranean, together with other symbiont-bearing Foraminifera (Hyams et al. 2002) conferred the real historical dimension to the biodiversity shift happening presently in the Mediterranean.

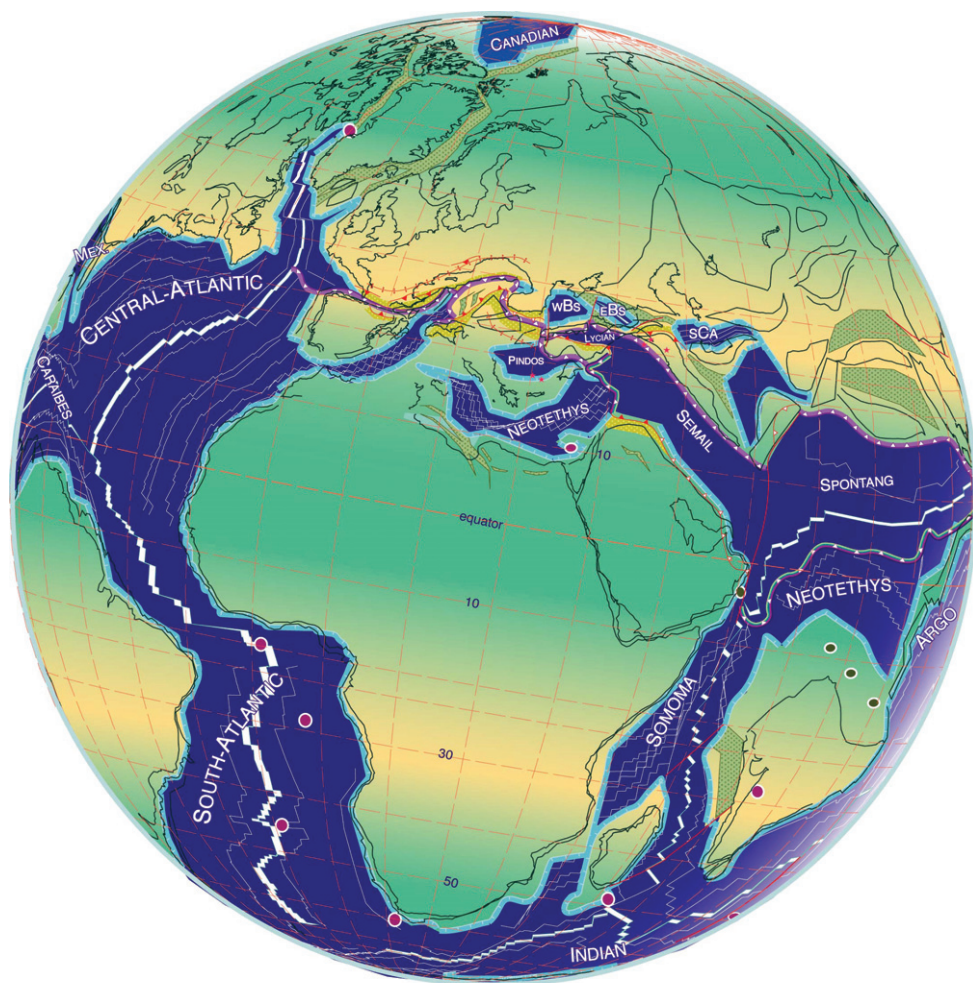


Figure 1. The Tethys in its Early Maastrichtian phase about 70 MA ago (from Stampfli and Borel 2004).

The Mediterranean is possibly and partly reverting to its original tropical warm-water biological condition, which was only relatively recently interrupted by the start of the glaciation cycles 2.58 million years ago. In a geological perspective, what is happening now, may be considered a return to normal conditions, possibly a normalization event.

Messinian survival

Although the circum-tropical Tethys Ocean ceased to exist when the Mediterranean basin finally lost its contact with the nascent Indian Ocean 13.6 million years ago in the area of the Mesopotamian trough (Harzhauser et al. 2007), its fauna continued to be tropical even when it started to be restricted at the base of the Messinian phase of the Miocene 7.1 million years ago. The climax of the Messinian salinity crisis with huge halite deposits lasted only between 5.6 and 5.5 million years ago and the definitive opening of the Mediterranean to the Atlantic and implicitly the start of the Pliocene is dated at 5.32 million years ago.

The original idea, which is still maintained by many, that during the Messinian high salinity crisis all the marine life of the Mediterranean was exterminated, is not correct. Marine life survived into the Pliocene in the near-shore environments, like those of southern Spain, from where *Porites* reefs are still reported, together with a variety of irregular tropical sea urchins (Esteban 1979/1980; Néraudeau et al. 2001). A variety of tropical fish were reported from the Messinian of Italy, among them the round herring *Spratelloides*, the razor fish *Centriscus* (Fig. 2) and the cornet fish *Fistularia* (Sorbini and Tirapelle Rancan 1980, Sorbini 1988).

The classical Tethyan relic, a Messinian survivor, is the dominant and characteristic Mediterranean seagrass *Posidonia oceanica*, whose congeners are known only from Australia, but it did not leave any fossil evidence prior to a putative one in the lower Pliocene (Aguirre et al. 2006)

The problem of the contact with the Red Sea

While the Mediterranean lost its contact with the Indian Ocean through the Mesopotamian through, the nascent Red Sea was its southern gulf. The northern Red Sea had also its period of halite deposition, but it occurred earlier than in the Mediterranean and the Messinian there was characterized by marine deposits (Griffin 2002). At some stage, the rifting process, which opened the Red Sea in the Eocene, turned eastward forming the deep Gulf of Aqaba. The Gulf of Suez remained shallow. A tectonic doming movement, sometime in the early Pliocene, lifted up the Isthmus of Suez, which ever since separates the Mediterranean from the Red Sea. Today the maximum elevation on the Isthmus is 23 m.

The exact date of the opening of the Red Sea to the Indian Ocean is unknown. Admittedly, it happened also at the start of the Pliocene, but if it was still in time for some



Figure 2. *Centriscus* sp. from the Neogene of Italy.

Indian Ocean species to make their way into the Mediterranean before the closure of the Isthmus of Suez is a question which will probably remain unresolved.

The mid-Pliocene optimum and the Gelasian crisis

The Mediterranean opened to the Atlantic Ocean but maintained its core tropical fauna, with many species, especially echinoderms and fishes, being documented survivors of the Messinian crisis. *Heterostegina*, though, did not survive into the Pliocene and the exact end of the last *Porites* reefs is uncertain.

The first two phases of the Pliocene, the Zanclean and the Piacenzian were warm. The so called Pliocene Optimum, between 3.60 and 2.58 million years ago was especially warm, Haywood et al. (2000) calculated a temperature 5 °C warmer and 400 to 1000 mm more precipitations at middle and high latitudes in Europe.

They consider that the Pliocene Optimum is a model for what is being called the present “Hyper Interglacial”. High sea levels of +20 m to +35 m are also mentioned. Indeed the fossil fish fauna from the classical Piacenzian Marecchia site in Italy contains a list of the very earliest Lessepsian migrants of today: *Spratelloides*, *Stephanolepis*, *Sargocentron*, *Hemiramphus*, and *Etrumeus* (Sorbini 1988, Sorbini and Tyler 2001, Landini and Sorbini 2005). They entered the Mediterranean already in the 1920’s and 1930’s ahead of most of the subsequent migrants (Por 1978), as if waiting for the first opportunity to return.

Concrete data about the paleo-temperature in the Mediterranean is supplied by the presence of the symbiont-bearing foraminiferan *Amphistegina* in the Tyrrhenian Sea, but the absence there of *Porites* reefs (Checconi et al. 2007). The foraminiferan is

limited by the winter isotherm 14 °C (Langer 2008), which is slightly higher than the 13.5 °C encountered there presently, but lower than the 15 °C which is the minimum for the hermatypic corals like *Porites* (Por 2008). *Amphistegina* resettled the Mediterranean recently (Hyams et al. 2002; Fig. 3), but although already widely spread, did not reach as yet the Tyrrhenian Sea.

The tropical sea urchin fauna, which survived the Messinian crisis, notably, different species of sand dollars (*Clypeaster*), cidaroids and *Diadema*, the needle-spined sea urchin, continued until the end of the Piacenzian. The Gastropoda of the Piacenzian Mediterranean were also typically tropical, with several species of auger shells (Terebridae), conus shells (Conidae), cowries (Cypreidae) and strombs (Strombidae). A sudden cooling started with the Arctic glaciation 2.58 million years ago. The third Pliocene phase, the Gelasian started the glacial cycles. It was the end of the tropical fauna of the Mediterranean.

Monegatti et al. (2002) use the complete disappearance of the augers as indicator for the start of the Gelasian. Cone shells and cowries were severely depleted and strombs disappeared altogether. Three species of cowry shells resettled the Mediterranean after 1980, coming from the Red Sea (Zenetos et al. 2004). The tropical sea urchin fauna suffered also a total depletion, but *Diadema*, re-colonized the Mediterranean after an interruption of more than two million years (Yokes and Galil 2006; Fig. 4).

The fishes from Marecchia also died out during the Gelasian, but used the Suez Canal to resettle the Mediterranean. Sorbini (1988) even considered that something similar to the Suez Canal connection of today might have made possible the influx of these Indo-pacific fish into the Pliocene Mediterranean.

The Pleistocene and the contact with the Tropical West Atlantic

During the low sea water temperatures of the Glacial periods, the Mediterranean was invaded by cold water biota from the northern Atlantic. Tropical biota live along the West African coast and the islands (Canaries, Madeira, Cap Verde), the so-called Senegalese fauna. They were, and still are to some extent separated from the Gibraltar portal, by the cold Canaries current. Furthermore, the west-east gradient of increasing temperatures within the Mediterranean, was steeper during the Glacial period than today. For instance, while in the Western Mediterranean, winter temperature fell as low as 7 °C, according to Thunell (1979), in the Levant basin the winter temperature was never lower than 16 °C. Today the gradient between west and east is only of 13 °C to 18 °C. The Levant basin functioned as a “cul de sac” of warm water, which was out of reach for the cold water species entering the Mediterranean.

During the last Interglacial, the Eemian Interglacial, dated between 125,000–110,000 years ago, with global temperatures 2 °C to 3 °C higher than today, there are fossil proofs that the West African tropical fauna succeeded to break the Canaries current barrier and the temperature barrier in the Mediterranean and reach the Levant. The whole episode lasted only for 14,000 years and was further subdivided into two warm pulses (van Kolf-

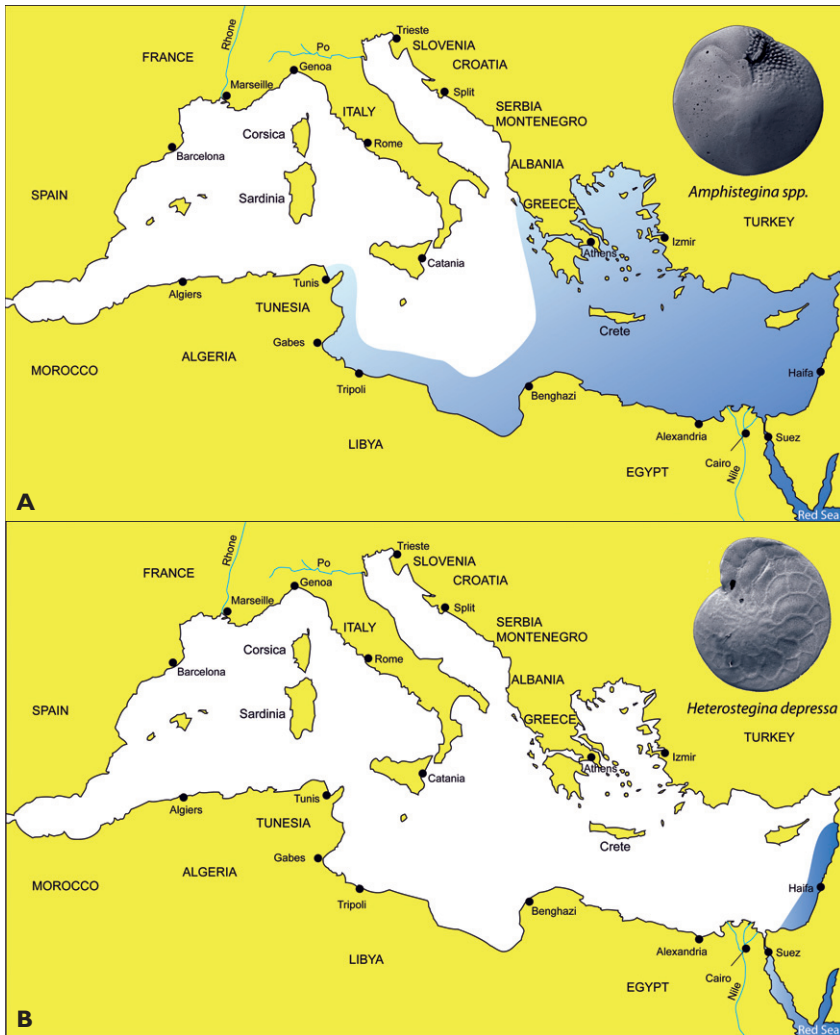


Figure 3. Distributional maps of the Lessepsian migrant Foraminifera (from Lange, 2008) **A** *Amphistegina* spp. **B** *Heterostegina depressa*.

schoten et al. 2003). It was characterized by a series of tropical Senegalese immigrant mollusk species such as *Strombus bubonius*, *Cardita senegalensis*, *Mytilus senegalensis*, and others.

It is interesting to comment that the Mediterranean, which lost its species of *Strombus* during the Gelasian crisis more than two million years ago, was episodically inhabited in the Eemian by the Senegalese *S. bubonius*, and recently received again two newcomer Indopacific Lessepsians, *S. mutabilis* and *S. persicus* (Zenetos et al. 2004).

Several species of fish with disjunct Levantine-Senegalese distribution, such as *Epinephelus haifensis* and *Sardinella madeirensis* are considered to be survivors of that Interglacial event, as well as a few invertebrates on record. It is evident that the high Interglacial sea level stands (sometimes +5 m are mentioned) were insufficient to sub-



Figure 4. The sea urchin *Diadema setosum* an Indo-pacific newcomer in the Mediterranean.

merge the Isthmus of Suez. Therefore, the input of the Senegalese biota through the Gibraltar portal has been the only possible tropical input during the Pleistocene.

Even today, the analysis of the “neo-Atlantic colonizers” among the fishes (Ben Rais Lasram et al. 2008) indicates that since 1980 none of the species originated from a latitude exceeding 42.350 N and the last five species that arrived came even from a latitude south of 24.230 N (Ben Rais Lasram and Mouillot 2009.)

Congruence and equifinality allow re-colonization and enrichment

The Levantine Basin of the Eastern Mediterranean, entered the Climate Optimum, which started in the 19th century in the state of the warm-temperate to sub-tropical cul-de-sac situation, in which it has been all along the Pleistocene, since it was cut off from the eastern seas. Taviani (2002) called the Eastern Mediterranean a “Godot Sea” as if waiting to be colonized.

In the recent decades, the global increase in temperature is very marked and also expressed in the sea surface temperature of the Mediterranean (Fig. 5). As the sea surface temperatures increased, the man-made contact through the Suez Canal, opened in 1869, started to give access to hundreds of Indo-pacific species to the Mediterranean. The canal could not have functioned that way, if it would have been built 100 or 200 years earlier, during the Little Ice Age.

The congruence of these two events, the warming of the sea and the influx of the Indo-Pacific biota, led to the present partial re-establishment of the Tethyan biota in the Mediterranean (Por 1990).

The extent of the anthropogenic factor in producing this global temperature increase is, as well known, a major issue of the public domain. However, as the results are concerned, both the natural and the human factors are equifinal, i.e. leading to similar results, although caused by different factors.

The principle of equifinality, fairly much used in geomorphology concerns also the much controversial subject of the nature of the Suez Canal connection. It is clearly anthropogenic, but it duplicates a natural seaway. Enlarged recently to 300 m in width, it is not much narrower than the Dardanelles in their narrowest part. The canal serves as a gateway for natural migration but facilitates also the expansion of ship-borne fouling biota. There are probably thousands of species that settled in the Mediterranean coming from the Red Sea and it is of no importance if they did it stepwise as “Lessepsian migrants” (Por 1978), or as one-jump noxious “Erythrean aliens” (Galil 2006). A warming Mediterranean is becoming more receptive also to species arriving accidentally with ship ballast and other artificial ways, adding to the number of successful establishment cases. The equifinal result is the same: it is a unique phenomenon of the establishment of a biogeographic province under our eyes. The last centuries of the Miocene Mediterranean with the Indian Ocean through the drying-out Mesopotamian trough must have been much more problematic and restrictive than the present so-called renewed “artificial” contact through the Suez Canal. Certainly, the 30 newly established tropical benthic foraminiferans (Hyams et al. 2002) will define a new Mediterranean geological phase for the future paleoecologists.

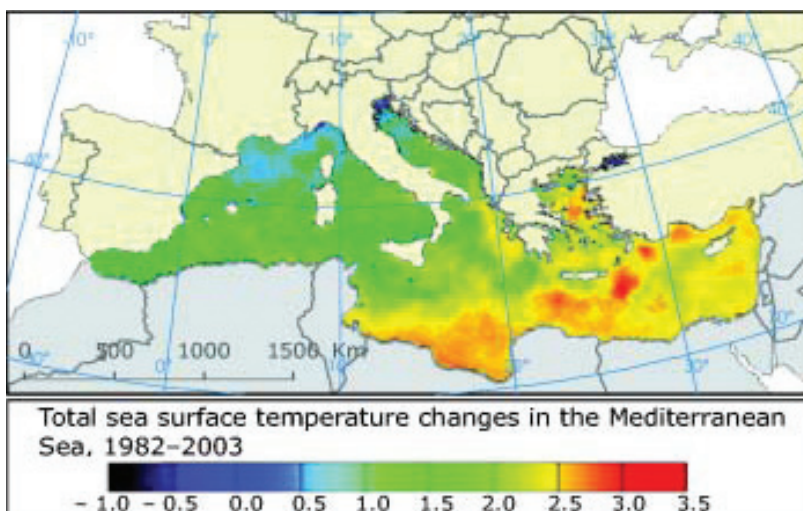


Figure 5. The rapidly expanding Lessepsian migrant cornet fish *Fistularia commersonii*.

Understandably, the issue of the alien invading species is a very worrisome one everywhere. Strangely so, not in the Mediterranean; unlike other marine water bodies, the Mediterranean, with the exception of the northern Adriatic, has been spared from the aggressive rogue invaders which wrought havoc elsewhere. This despite the famous case of *Caulerpa taxifolia* the horror-film “killer-alga”! The wide variety of probably thousands of species the newly settled Indopacific biota cannot be forced into the mold of aggressive invaders in order to conform to scientific fashion.

It seems that explosive blooms of an invader as common in invasive events, cannot easily occur in oligotrophic seas like the Mediterranean or the Red Sea (see discussion in Por and Dimentman 2006). The northern Adriatic, in this sense, with its several cases of established invaders, is a eutrophic exception. Likewise, there is no proof that any of the newcomers reached functions that deserve the title of “worst invasive species” (Zenetos et al. 2005). None of the new settlers has led to the much feared prejudice or even extinction of a local Mediterranean species despite the still prevalent suspicion (Galil 2009), although the influx of new species is going on for well over half a century. Quite on the contrary, the Mediterranean biodiversity is much enriched.

Also none of the newly arrived species has since disappeared. The new colonizers are gradually enlarging their area, most probably as a function of the gradual warming of the sea. The first species of fish and mollusks have already crossed the straits of Sicily and entered western Mediterranean. The pipe fish *Fistularia commersonii* (Fig. 6) an absentee since the Messinian (see above), is one of the latest Lessepsian migrants and has in two years since its first appearance in the sea reached the western Mediterranean and practically re-occupied its original area (Golani 2000, Ligas et al. 2007). It seems that the process of re-colonization is gaining speed and amplitude.

The Tethyan species and their descendants are returning to their old haunts in the Mediterranean. To call them aliens is an anthropomorphic view, considering our historical times as the normal ones. The present Climatic Optimum represents a return to the Pliocene Climatic Optimum and thus, can be seen as a repetition, a cyclic event and not as an artificial disruption. For the squirrelfish *Sargocentrum rubrum* (Fig. 7) for instance, which inhabited the Mediterranean already five million years ago, we the humans, would be the alien invaders.

The newly active Gibraltar Portal

While attention is concentrated almost entirely on the Indo-Pacific Lessepsian migrants, there is also an increasing settlement by tropical Atlantic newcomers entering the Mediterranean through the Straits of Gibraltar. Ben Rais Lasram and Mouillot (2009) consider that the currently warmer Mediterranean is acting increasingly as a “catchment basin” for southern species. Indeed of the 127 thermophilic species of fish which according to these authors supplemented the Mediterranean fauna, 65 fish are Lessepsians and 62 are Atlantic newcomers.

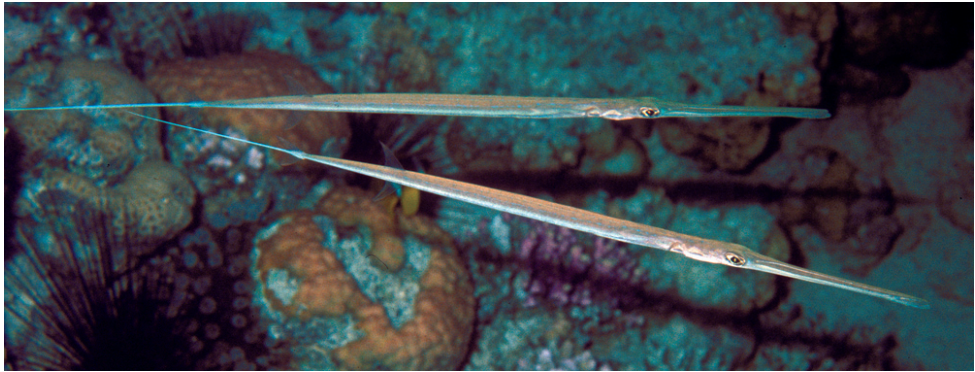


Figure 6. The quick migrant cornet fish *Fistularia commersonii*.

This two-pronged re-colonization of the Mediterranean is of course very evident in the mobile fish fauna and much less visible in the other biota. Yet there are cases already, for instance among the decapod crustaceans, such as of the stepwise advance of the boxer crab *Cryptosoma cristatum* (Galil et al. 2002)

Even with a warming western Mediterranean, the role of the Senegalese or the “Neo-Atlantic” colonizers will remain secondary to the Indopacific Lessepsian ones. First of all, the Senegalese province is not a typical tropical one, with coral species restricted to the two-dimensional reef-pavement stage, i.e. not building tri-dimensional reef structures. The reason for this is that the temperature of the coldest month can fall and has fallen in recent years below 18 °C, not allowing the buildup of reef structures. Besides, the interposed coasts of Mauritania and Morocco are influenced by the cold Canaries current and a strong upwelling and low winter temperatures. Only a radical change in the regime of the NAO (North Atlantic Oscillation) pattern will eventually allow easier access of tropical species to the Gibraltar portal.

The tropical enrichment of the Mediterranean

The influx of thousands of tropical species into the Mediterranean is without doubt the most remarkable biogeographic phenomenon of today. Even though its cause is closely related to the present climate change, there has not yet been any targeted national or international research effort to study this phenomenon. If something, even of a very much smaller scale, would be happening in the terrestrial domain, monitoring programs and computers would be churning, ecologists would be busy in the field and molecular biologists would analyze expatriate populations. We are mainly depending on decades on fishermen’s data, on divers’ observations and on information from shell collectors and beach combers. Even so, the number of reported newcomer species is around 1000, with a new report appearing at a weekly rate. The relatively few specialized studies of different taxa are of local faunas and not regional reviews. Considering that important and species-rich taxa like Porifera, Hydrozoa, Platyhelminthes, Nema-

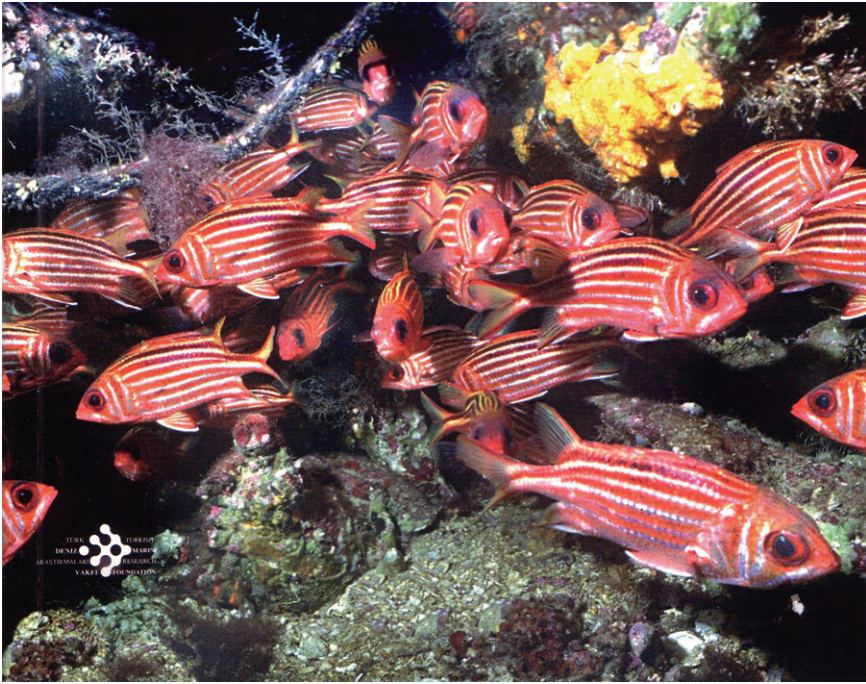


Figure 7. The red squirrelfish *Sargocentrum rubrum* successful migrant since the 1930's (photo M. Fine).

toda, Acari, Harpacticoida, Ostracoda, Amphipoda, to name only a few of them, have not been studied, one can say that we know only the tip of the iceberg.

When the Levantine basin reached the lowest winter isotherm of 18 °C, which among others allowed the re-establishment of the symbiont-bearing foraminiferan *Heterostegina depressa* (see above; Fig. 3), it became in many aspects a tropical sea. This is indicated by an accelerated entry of tropical species, such as the gorgonarian *Acabaria erythraea* (Fine et al. 2004), the sea urchin *Diadema setosum* (Yokes and Galil 2006; Fig. 4), the upside-down jellyfish *Cassiopea andromeda* (Özgür and Öztürk 2008; Fig. 8), and the sea slug *Hypselodoris infucata* (Fig. 9). However, coral reefs, the typical formations of a tropical sea did not appear yet, although the conditions for their development already exist.

The scleractinian *Oculina patagonica*, the ivory coral, a species of uncertain, but probably Atlantic origin, has taken advantage of the warming sea and has explosively expanded around the southern Mediterranean during the last years, building coral pavements (see latest updates in Sartoretto et al. 2008).

The limits of the Tethyan return

The Mediterranean was the evolutionary centre of the Cretaceous and early Tertiary Tethys fauna. During the Miocene this centre shifted to the Indo-Pacific as Mediterranean reefs became gradually depleted. The new Tethyan re-colonization of the Medi-



Figure 8 The Lessepsian migrant upside-down jellyfish *Cassiopea andromeda* in its natural benthic habitat (photo Matthias Schneider).



Figure 9. The newcomer Indo-Pacific sea slug *Hypselodoris infucata* (photo Sven Kahlenbrock, courtesy Nathalie Yonow).

terranean is for the time being a limited one, though not a completely new phenomenon as expected by Bianchi (2007). In fact, the temperatures in the Levant basin are already more hospitable for a tropical coral sea than those in the Gulf of Suez.

The contact with the Red Sea is still limited by the conditions existing in the Suez Canal. At least the Levant Basin could already harbor thriving communities of Indo-pacific hermatypic corals, such as *Stylophora pistillata* or *Siderastrea savigniana*. These species are resistant to temperatures as low as 13 °C in individual colonies and *Stylophora* forms reefs at minimum temperatures around 18 °C in the Gulf of Suez (Por 2008 and unpublished). The present constraints are that in the Suez Canal and mainly in the Bitter Lakes along the canal, winter temperatures are often below 15 °C, the substrate is soft and unsuitable for corals and turbidity is very high because of the passing ships. Corals have also short-lived larvae which cannot pass the more than 160 km long canal at once. They are also not able to live as ship-fouling or in ship ballast. Therefore, for corals, or for the Mediterranean to become a coral sea, the Suez Canal is still a barrier.

Together with the corals, a whole diversity of coral haunting fish, mollusks, echinoderms and other animals did not appear yet in the Mediterranean. For instance, the razor fish *Centriscus*, the Messinian survivor, extinct during the Gelasian (see above), which lives in a vertical position among coral branches and sea urchin spines, did not yet return to the Mediterranean. However, like *Fistularia*, the pipe fish, many species that have been retained by certain environmental constraints of the canal, will expand exponentially in the newly hospitable Mediterranean, once the barrier is broken.

It is probably only a matter of time till by natural or accidental means the first reef builders will emerge in the Levant Sea. Then, this sea, and together with it the whole Mediterranean will move another step closer to resemble the old coral sea of Tethys. This, of course, will only happen, if the current Climate Optimum will continue. If this trend of the tropical biodiversity enrichment of the Mediterranean is welcome and beneficial or not, belongs to the subjective domain and should not diminish by a iota the importance of and the scientific interest in this grandiose phenomenon.

References

- Aguirre J, Perez-Munoz AB, Sanchez-Almazo I (2006). Benthic foraminifera assemblages on the lower Pliocene deposits of the Almeria-Nijar Basin (SE Spain). *Revista espanola de micropaleontologia* 38(2–3): 411–428
- Ben Rais Lasram F, Tomasini JA, Guilhaumon F, Romdhane DD, Do Chi T, Mouillot D (2008) Historical colonization of the Mediterranean by Atlantic fishes: do biological traits matter? *Hydrobiologia* 607: 51–62.
- Ben Rais Lasram F, Mouillot D (2009) Increasing southern invasion enhances congruence between endemic and exotic Mediterranean fish fauna. *Biological Invasions* 11(3): 697–711.
- Bianchi CN (2007) Biodiversity issues for the forthcoming tropical Mediterranean Sea. *Hydrobiologia* 580: 7–21.

- Checconi A, Bassi D, Passeri L, Rettori R (2007) Coralline red algal assemblage from the Middle Pliocene shallow-water assemblage at Monte Cetona (Northern Apennines, Italy). *Facies* 53 (1): 57–66.
- Esteban M (1979/1980) Significance of the Upper Miocene coral reefs of the Western Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology* 29: 169–188.
- Fine M, Aluma Y, Meroz-Fine E, Abelson A, Loya Y (2004) *Acabaria erythraea* (Octocorallia: Gorgonacea) successful invader to the Mediterranean Sea? *Coral Reefs* 24 (1): 161–164.
- Galil BS (2006) The marine caravan: the Suez Canal and the Erythrean invasion. In Golasch S, Galil BS, Cohen AN (Eds) *Bridging divides: maritime canals as invasion corridors*. New York: Springer, 207–300.
- Galil BS (2009) Taking stock: inventory of alien species in the Mediterranean sea. *Biological Invasions* 11: 359–372.
- Galil BS, Frogia C, Noel P (2002) Crustacea Decapoda and Stomatopoda. In Briand F (ed.) *CIESM Atlas of Exotic Species in the Mediterranean* vol. 2.
- Golani D (2000) First record of the bluespotted cornetfish from the Mediterranean Sea. *Journal of Fish Biology* 56: 1545–1547.
- Golani D, Orsi Rellini L, Massuti F, Quignard JP (2002) Fishes. In: Briand F (Ed) *CIESM Atlas of Exotic Species in the Mediterranean*. Vol. 1. Fishes. CIESM Publishers, Monaco, 1–256.
- Griffin DL (2002) Aridity and humidity: two aspects of the late Miocene climate of North Africa and the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology* 182: 65–91.
- Haywood AM, Dellwood BW, Valdes PJ (2000) Regional warming: Pliocene (3 Ma) paleoclimate of Europe and the Mediterranean. *Geology* 28 (12): 1063–1066.
- Harzhauser M, Kroh A, Mandi O, Piller WE, Goehlich U, Reuter M, Berning B (2007) Biogeographic responses to geodynamics: a key study all around the Oligo-Miocene Tethyan seaway. *Zoologischer Anzeiger* 246: 241–256.
- Hyams O, Almogi-Labin A, Benjamini C (2002) Larger foraminifera of the SouthEastern Mediterranean shallow continental shelf off Israel. *Israel Journal of Earth Sciences* 51: 169–179.
- Kolfschoten Th van, Gibbard PL, Knudsen KL (2003) The Eemian Interglacial: a global perspective: introduction. *Global and Planetary Change* 35: 147–149.
- Landini W, Sorbini L (2005) Evolutionary dynamics in the fish faunas of the Mediterranean basin during the Plio-Pleistocene. *Quaternary International* 140–141: 64–89.
- Langer MR (2008) Foraminifera from the Mediterranean and the Red Sea. In Por FD (ed.) *Aqaba-Eilat, the improbable gulf: environment, biodiversity and preservation*. Jerusalem: Magnes Press, 397–415.
- Ligas A, Sartor P, Sbrana M, Sirna R, De Ranieri S (2007) New findings of *Fistularia commersonii* Rüppell, 1835 and *Spherooides pachygaster* (Müller & Troschel, 1848) in the northern Tyrrhenian Sea. *Atti Soc. Toscana Sci. Nat. Mem. Serie B*, 114: 131–133.
- Monegatti P, Canali G, Bertoldi R, Albinelli A (2002) The classical Piacenzian Monte Falcone-Rio Crevallese section (Northern Italy): palynological evidence and biomagnetostratigraphic constraints for climatic cyclicity and local mollusk extinctions. *Geobios* 35: 219–223.
- Néraudeau D, Goubert E, Lacour D, Rouchy JM (2001) Changing biodiversity of Mediterranean irregular echinoids from the Messinian to the Present Day. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175 (1–4): 43–60.

- Özgür E, Öztürk B (2008) A population of the alien jellyfish, *Cassiopea andromeda* (Forsskal, 1775) [Cnidara: Scyphozoa: Rhizostomea] in the Ölüdeniz Lagoon, Turkey. *Aquatic Invasions* 3 (4): 423–428.
- Por FD (1978) Lessepsian migration. The influx of the Red Sea biota into the Mediterranean by way of the Suez Canal. *Ecological Studies* 23. Berlin: Springer Verlag.
- Por FD (1990) Lessepsian migration. An appraisal and new data. In Godeaux J (ed.) *A propos des migrations lessepsiennes*. Bulletin de l'Institut Océanographique Monaco. Numéro spécial 7: 1–10.
- Por FD (2008) Life beyond 41 ppm. Metahaline environments and anchialine pools in the Gulf of Aqaba-Eilat. In Por FD (Ed) *Aqaba-Eilat, the improbable Gulf: environment, biodiversity and protection*. Jerusalem: Magnes Press, 125–152.
- Por FD, Dimentman Ch (2006) *Mare Nostrum*. Neogene and anthropic history of the Mediterranean with emphasis on the Levant. Sofia-Moscow: Pensoft. 349 pp.
- Sartoretto S, Harmelin J-G, Bachet F, Bejaoui N, Zibrovius H (2008) The alien coral *Oculina patagonica* De Angelis 1908 (Cnidaria; Scleractinia) in Algeria and Tunisia. *Aquatic Invasions* 3 (2): 173–180
- Sorbini L (1988) Biogeography and climatology of Pliocene and Messinian fossil fish from Eastern Central Italy. *Bollettino del Museo di Storia Naturale di Venezia* 14: 1–85.
- Sorbini L., Tirapelle-Rancan S., 1980. Messinian fossil fish of the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology* 29:143–154
- Sorbini L, Tyler JC (2001) Review of the fossil filefish of the family Monacanthidae (Tetraodontiformes) from the Pliocene of Italy. VI European Workshop on Vertebrate Paleontology, Florence and Montevarchi, September 19–21 2001. Abstract volume. p 56.
- Stampfli GM, Borel GD (2004) The TRANSMED transects in space and time: Constraints on the paleotectonic evolution of the Mediterranean Domain. In: Cavazza W, Roure F, Spakman W, Stampfli GM, Ziegler P (Eds) *The TRANSMED Atlas: the Mediterranean Region from Crust to Mantle*. Springer Publishers, 53–80.
- Taviani M. (2002) The Mediterranean benthos from late Miocene up to present: ten million years of dramatic climatic and geologic vicissitudes. *Biologia marina mediterranea* 9: 445–463.
- Thunell RC (1979) Climatic evolution of the Mediterranean Sea during the last 5.0 million years. *Sedimentary Geology* 23: 67–79
- Yokes B, Galil BS (2006) The first record of the needle-spined urchin *Diadema setosum* (Leske, 1778) (Echinodermata: Echinoidea: Diademataidae) from the Mediterranean. *Aquatic Invasions* 1 (3): 188–190.
- Zenetos A, Gofas S, Russo G, Templado J (2004) Mollusks. In Briand F (ed.) *CIESM Atlas of exotic species in the Mediterranean vol. 3 Monaco* (updated website, May 2008)
- Zenetos A, Cinar ME, Pancucci-Papaodopoulou MA, Harmelin JG, Furnari G, Andaloro F, Bellou N, Streftaris N, Zibrovius H (2005) Annotated list of marine alien species in the Mediterranean with record of the worst invasive species. *Mediterranean Marine Science* 6/2: 63–118.