Shaping the biogeography of the Mediterranean basin: one geologist's perspective

MARCO TAVIANI

*Istituto di Scienze Marine-Sezione Geologia Marina, CNR,
via Gobetti 101, I-40129 Bologna (Italy)
e-mail: marco.taviani@bo.ismar.cnr.it

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SUMMARY

The present Mediterranean biogeography is the transitory result of climatic and geological events suffered by this semi-enclosed basin throughout its history. The potential consequences over stenooecious marine ecosystems of the late Miocene “Messinian Salinity Crisis” are discussed. In particular, postulated frakhly-marine sanctuaries at the time of evaporite deposition and periodical intra-Messinian inundations are not considered sufficient in maintaining stenooecious ecosystems throughout the entire Messinian time. The biogeography of the Mediterranean deep-sea benthos is strongly affected by the geodynamic evolution of the basin and in particular by the post-Messinian establishment of a shallow sill (Gibraltar); since the Pleistocene at least, the sill acts as a filter biasing the flux of potential Atlantic deep-sea invaders. Finally, the Mediterranean basin boasts a remarkable history of deep-sea cold seep chemosynthetic ecosystems from the Oligocene up to Present. These peculiar biota, however, show a distinct evolution through time. The pre-Messinian ones are typically oceanic in affinity hosting, among other, large chemosynthetic bivalves (e.g. Calyptogena, Modiolus etc.) and tubeworms, while the post-Messinian and Modern ones are strongly impoverished. This trend is mainly controlled by the geological history of the Mediterranean region.

INTRODUCTION

In a recent paper I offered my personal perception of the history of the stenooecious marine benthic biota of the Mediterranean basin, Neogene to Present (Taviani, 2002). To my view, it was the interplay between global climatic signals and concomitant geodynamic evolution of the Tethys-Mesogean-Mediterranean basins (e.g., Biju-Duval et al., 1977; Krijgsman, 2002) that moulded the biogeography of the modern Mediterranean Sea. Arguments and data supporting this vision are reported in Taviani (2002) and are not repeated here.

However, one of the major issues for Mediterranean biogeographers was and is the significance of the late Miocene “Messinian Salinity Crisis” (MSC
hereafter) and its consequences over the biota. A widely shared view (with some opponents) endorses the concept that the MSC caused the extermination of the basin’s marine stenohaline organisms. The obvious corollary of such view is to consider the post-MSC marine inundation as the real starting point of the Mediterranean biogeographic history by re-importing into the basin a fresh wave of Atlantic organisms (e.g. Taviani, 2002, with references therein).

In this paper I will comment again some open problems related to the MSC. Furthermore, I will discuss the biogeographic evolution of deep-sea normal and chemosynthetic ecosystems. Most of my reasoning will be conducted by using benthic molluscs as a particularly suitable biogeographic tracer (Taviani, 2002).

BACK AGAIN TO THE MESSINIAN SALINITY CRISIS AND ITS ACTION ON BIOTA

The problem represented by the MSC is yet far from being adequately understood as proven by the steady publication of papers still dealing with this issue. The rather evocative but perhaps simplistic scenario (heralded by the slogan “the Mediterranean was a desert”) envisaged 30 and more years ago (Hsu et al., 1977) has been variously debated, refined, contrasted (e.g., Cita and McKenzie, 1986; Hsu, 1986; Busson, 1990; Benson and Rakic-El-Bied, 1991; Cita and Corselli, 1993; and many others).

Although in its intrinsic temporal brevity (<1my, Krijgsman et al., 1999) the MSC was an astonishingly complex event. The Messinian includes a (1) pre-evaporitic phase, punctuated by high frequency anoxic events leading to peculiar deposits (euxinic marls and Tripoli, i.e. diatomaceous muds), partly coeval or followed by (2) precipitation of mainly sulphatic layers (gypsum beds of the “Lower Evaporites”) beginning c. 5.96 Ma BP (Krijgsman et al., 1999); to follow is (3) the precipitation of the “Upper Evaporites” and the (4) late Messinian by the hypomeso-haline continental environments of Lago-Mare (Ruggieri, 1967; Rouchy et al., 2001; Roveri et al. 2003).

Biogeographically the big question is: were there open marine connections between the Atlantic and the Mediterranean during the Messinian? And, if so, when, where and how far inside the basin were they resented?

For instance, benthic fauna from intra-evaporitic marly beds of Sorbas basin (Southeastern Spain) has been taken as an indication that the MSC was not such from a biological perspective (Saint-Martin et al., 2000). In particular, Néraudeau et al. (2001) suggest that the stenohaline echinoid Brissopsis may have survived the crisis in a marine refuge like the Alboran Sea. Benthic foraminiferal evidence from these same beds also suggests their intra-Messinian survival (Goubert et al., 2001). This postulated “Alboran sanctuary” may have acted as such during part only of the entire Messinian crisis, as admitted by Ben Moussa et al. (1988).
Thus, some authors agree that the westernmost part of the Mediterranean basin was at least temporarily under marine conditions at times during the MSC. The same does not hold necessarily true for the rest of the basin (Taviani, 2002).

The potential existence of one or more “marine sanctuaries” within the Mediterranean proper, evoked by some biogeographers (e.g., Di Geronimo, 1990), is still largely based on circumstantial arguments, not on ground-truth evidence. Furthermore, it is not yet demonstrated that permanent marine interconnections between the Atlantic Ocean and the Mediterranean Sea existed throughout the Messinian to support the extreme view that the latter did not suffer (at times at least of the complex Messinian history) one or more lethal biological crises.

A connection between the Atlantic Ocean and Mediterranean basins as east as Sicily was postulated by Butler et al. (1996) based on the recovery of frankly marine plankton within Early Messinian diatomaceous marls. This suggestion, however, was not substantiated by later research on these same beds (Sprovieri et al., 1996).

A further argument on this line not to be neglected, calls for the evaluation of the basin-scale impact of the post-evaporitic event known as “Lago-Mare”, that imposed strong hypohaline conditions all over the Mediterranean, including its westernmost sectors as documented, among other, by the Messinian sequence of the Nijar basin, southeastern Spain (Fortuin and Krijgsman, 2003), ODP cores in both the Western and Eastern Mediterranean (Cita et al., 1990; Blanc-Valleron et al., 1998) and outcrop evidence in Cyprus (Krijgsman et al., 2002).

In summary, I am still convinced that overall the MSC imposed intolerable conditions, on a basin scale, capable to jeopardize the stenoecious benthic marine realm.

The re-flooding and, therefore, the re-colonization of the entire basin was a rapid event (Ryan, Hsü et al., 1973; McKenzie et al., 1999; Jacarino et al., 1999; Fortuin and Krijgsman, 2003) taking place at the beginning of the Pliocene, if not already during the latest Messinian (Steffahn and Michalzik, 2000). From a strict biogeographic perspective the implication is again that the real renewing of the Mediterranean benthos is accompanied by this inundation from the Atlantic Ocean.

THE DEEP-SEA BIOTA

In the past, the biogeography of the deep-sea Mediterranean benthos has been largely deduced from speculations upon the affinity of the present Mediterranean stocks more than on exhaustive paleontological data (e.g., Ekman, 1953; Pérès and Picard, 1960, 1964; Pérès 1967, 1989; Zibrowius, 1980; Raffi and Taviani, 1984; Fredj and Laubier, 1985; Por and Dimentman, 1985, 1989; Allouc, 1987;
Bouchet and Taviani, 1989, 1992a,b). A reverse to this approach took place in the last decade or so, especially because of the appearance of detailed taxonomic studies of Italian Plio-Pleistocene bathyal assemblages (Tabanelli, 1993; Di Geronimo et al., 1997; Di Geronimo and La Perna, 1996, 1997; Corselli, 2001). Some of these contributions were sensitive to the origination of the Mediterranean deep-sea faunas with respect to those of the adjacent Atlantic Ocean.

Based on the latest Pleistocene-Recent Mediterranean deep-sea mollusc fauna, Bouchet and Taviani (1992a) proposed the concept that a significant share of the recent Mediterranean deep-zoobenthos derived largely by the continuous meroplanktic larval influx from mother-populations in the Atlantic Ocean. This option is not accepted in his extreme terms by Di Geronimo and co-workers (e.g., Di Geronimo et al., 2001) who observe that this model does not account for the observed existence of a conspicuous stock of deep-sea organisms provided with either direct or lecithotrophic development, although this coexistence was already highlighted by Bouchet and Taviani (1992a). The Quaternary deep-sea benthos of the Mediterranean basin may, therefore, result from a stock of Atlantic organisms likely derived from pre-Pleistocene invasions when a deeper Gibraltar corridor connected the two basins plus a continuous larval influx from the Atlantic. Emig and Geistdoerfer (2004) predict that the Mediterranean will become an important center of evolution of deep-sea organisms, a view supported from data on deep-sea protobranchs (La Perna, 2004).

RISE AND DECLINE OF DEEP-SEA CHEMOSYNTHETIC COMMUNITIES IN THE MEDITERRANEAN BASIN

A decade ago it has been realized that the Mediterranean basin hosted ocean-like chemosynthetic communities with megafauna exploiting hydrogen sulphide and hydrocarbon enriched fluids (Taviani, 1994). These communities punctuated the history of the basin since the Oligocene at least up to Present (e.g., Conti and Fontana, 1998; Taviani, 2001). Late Miocene (Tortonian) cold-seep paleo-communities show strong taxonomic similarities with Modern hydrocarbon seep setting the northern Gulf of Mexico slope and West Africa. Noteworthy is the presence of chemosynthetic sulfide- (\textit{?Calyprogena, Solemya}, large lucinids, tubeworms, \textit{Beggiatoa}-like bacteria) and/or hydrocarbon-based (\textit{Bathymodiola, Thalassonera}) invertebrates (Taviani, 1994, 2001). Pliocene to recent deep-sea chemosynthetic macrofaunal communities are taxonomically impoverished and host \textit{Vesicomya, Solemya} and smaller lucinids (Taviani et al., 1997; Corselli and Basso, 1996; Taviani, 2001; Salas and Woodside, 2002). A trend is apparent showing a significant decline of such quasi-oceanic seep
communities with the beginning of the Pliocene, a possible consequence of diminishing propitious structural scenarios linked to the Apennine orogeny, coupled with the onset of a shallow sill at Gibraltar and the postulated Messinian biological extermination (Taviani, 2001, 2002). At present, deep-sea chemosynthetic communities including both microbial and macrofaunal organisms (small mytilids, lucinaceans, and vesicomyids) are located at various sites of the Eastern Mediterranean basin, including the Nile delta fan, Eratosthenes Seamount, Napoli Dome and other mud volcanoes and fault zones in the Marmara Sea (Fig. 1).

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