

The biogeography of Mediterranean cephalopods*

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*To the memory of Dr. Kir Nesis, who suddenly passed away in a cold winter day.
He was a great cephalopod systematist and biogeographer, and a kind Man.

Key words: Cephalopoda, Mediterranean Sea, distribution, alien species, evolution.

SUMMARY

This paper presents an updated picture of the Mediterranean teuthobiogeography. Sixty-five cephalopod species have been recorded in the Mediterranean, i.e., about 9% of the world teuthofauna, belonging to the following orders: Spirulida (1 species), Sepiida (4), Sepiolida (15), Teuthida (30), and Octopoda (15). Only 53 of them are represented by well established populations in this basin; all the others either have been very rarely collected or are recent occurrences, including cephalopods recently entered from the Atlantic Ocean and from the Red Sea through the Suez Canal. The width of the cephalopod horizontal distribution is discussed in relation to their modes of life and reproduction. In particular the *in situ* speciation of a flock of endemic or quasi-endemic sepioline species is attributed to certain body features (small size, "lock-and-key" copulatory organs), reproductive strategies, short life span, and habitat. A concise history of the knowledge of the Mediterranean teuthofauna is also illustrated. A list of the Mediterranean cephalopods is reported in Appendix I.

INTRODUCTION

Mangold and Boletzky (1988) published an essay on "Mediterranean Cephalopod Fauna", which represents the first modern piece of literature dedicated to the biogeography of the Mediterranean cephalopods. In that paper the Mediterranean was dealt with in geological and paleogeographic contexts.

In more recent years, new data have been accumulated on the distribution and, more important, on the taxonomy, ecology and reproductive biology of cephalopods living in the Mediterranean and the eastern Atlantic Ocean, producing a positive impact on the field of cephalopod biogeography (Boletzky, 1999).

The purpose of this paper is to present an updated picture of the Mediterranean teuthobiogeography with respect to the paper by Mangold and Boletzky (1988) as well as to more recent faunistic lists, such as the “Checklist delle specie della fauna italiana” (Bello, 1995).

OVERVIEW

The biogeographical history of the Mediterranean basin has been recently reviewed by Taviani (2002, with references therein). Concerning the history of marine ecosystems, it is widely accepted that a fairly sharp landmark is represented by the Messinian salinity crisis marking the end of the Miocene epoch, c. 5.5 Ma. Although controversial views exist regarding a complete desertification of the basin (e.g., Stanley, 1990), it has been suggested that hydrological conditions during the Messinian caused the basinal extinction of stenoeccious biota (Taviani, 2002), including cephalopods (Mangold and Boletzky, 1988). Hence the starting point for the biological history of the Mediterranean teuthofauna may be the post-Messinian (early Pliocene) re-connection with the Atlantic Ocean that allowed the re-colonization of the Mediterranean by Atlantic fauna (Taviani, 2002). This process has never stopped since then, although important faunal re-arrangements have punctuated the basin in response of climatic-driven perturbations (see below). At present the bulk of the Mediterranean teuthofauna is made of cephalopods coming from the Atlantic Ocean.

In addition to those species, a most interesting contribution to the Mediterranean teuthofauna was added by *in situ* speciation of several new species.

Lastly, recent and very recent additional sources of extraneous fauna became available with the opening of the Suez Canal connecting the Mediterranean to the Red Sea 140 years ago; the transportation into the Mediterranean by ships and other carriers; the warming up of the Mediterranean waters, through the greenhouse effect, which in turn favoured the entrance – from any “access gate” – and, most important, allowed the survival of tropical and sub-tropical fauna.

To sum up, 65 cephalopod species have been recorded in the Mediterranean, i.e., about 9% of the world teuthofauna, belonging to the following orders: Spirulida (1 species), Sepiida (4), Sepiolida (15), Teuthida (30), and Octopoda (15). Only 53 of them are represented by well established populations in this basin; all the others either have been very rarely collected or are recent occurrences. In the next paragraphs I shall mainly refer to the 53 well established species; the remaining 12 cephalopods will be dealt with in some detail in the two sections dedicated to them.

Because of the medium-latitude position of the Mediterranean Sea and the present existence of the relatively shallow and narrow sill of Gibraltar, the

biogeographic history of this basin strongly reflects the Plio-Pleistocene global climatic events responsible of episodes of species extinctions, migrations and adaptations. In particular, the present composition of the Mediterranean fauna was heavily shaped by the sequence of Pleistocene glaciations and interglaciations that brought into the Mediterranean cold and warm elements respectively (Taviani, 2002, 2003). This fact, notwithstanding the lack of good fossils of modern coleoids, is also illustrated by the living teuthofauna that includes species of Mauretanian (i.e., warm) and Lusitanian (i.e., cold) affinities (Ekman, 1953). A peculiar vertical distribution occurs in pairs of related species of opposite affinities; in general the cold-water species inhabit deeper layers than warm-water species, e.g., the pairs *Rossia macrosoma* – *Neorossia caroli*, *Loligo vulgaris* – *Loligo forbesii*, *Octopus defilippi* – *Octopus salutii*, *Eledone moschata* – *Eledone cirrhosa* (in all these pairs the first item is Mauretanian, the second one is Lusitanian). Such a phenomenon takes place despite the fact that the temperature of the Mediterranean deep waters, viz., below the deep thermocline, is fairly high and constant, about 13–14 °C. Indeed, several species do not follow this pattern, e.g., the warm water *Pteroctopus tetracirrhus*, a deep species of Mauretanian affinity, and the three species of *Sepia*.

DISTRIBUTION, MODE OF LIFE AND EGG SIZE

According to the extent of their horizontal distribution, the Mediterranean cephalopods may be subdivided into six categories of increasingly narrower distribution:

- Panoceanic: holopelagic and mostly circumtropical species (24 species, e.g., *Ommastrephes bartramii*, *Ancistrocheirus lesueurii*, *Ocythoe tuberculata*);
- Atlantic: mainly oceanic, mainly Middle- and North-Atlantic (8 species, e.g., *Heteroteuthis dispar*, *Ancistroteuthis lichtensteinii*, *Histioteuthis reversa*);
- Amphiatlantic: benthic and nekto-benthic, littoral and slope (4 species, e.g., *Stoloteuthis leucoptera*, *Octopus vulgaris*, *Pteroctopus tetracirrhus*);
- Eastern Atlantic: benthic and nekto-benthic, mainly littoral (18 species, e.g., the three species of *Sepia*, *Sepietta oweniana*, *Opisthoteuthis calypso*, *Eledone cirrhosa*);
- Quasi-endemic (viz., occurring in the near Atlantic, but most probably speciated in the Mediterranean): benthic and nekto-benthic, littoral (4 species, e.g., *Sepiola intermedia*, *Eledone moschata*) (the term “quasi-endemic” merely serves to distinguish some species from others with a more restricted range; according to the classification by Myers and De Grave [2000], all taxa are endemic and display gradients of endemism);
- Endemic: benthic and nekto-benthic, mainly littoral (3 species, e.g., *Sepiola affinis*, *Sepiola steenstrupiana*).

A category of its own is represented by the anthropically dispersed cephalopods (see further below), containing three lessepsian migrants and one passively transported species.

All the widely distributed cephalopods, i.e., those fitting the first three categories, are mostly oceanic (Teuthida, Heteroteuthinae, holopelagic Octopoda); if benthic or nekto-benthic, they reproduce through small eggs (Octopodinae, *partim*). On the contrary, the mode of life of all narrowly distributed cephalopods, i.e., those fitting the last three categories, is benthic or nekto-benthic and reproduction is marked by large eggs (Sepiidae, Sepiolinae and Rossiinae, Octopodinae *partim*, Eledoninae, Bathypolypodinae). The effects of relative egg size on the hatchling and early juvenile mode of life has been described by Boletzky (1974, 1977): newborns hatching from large eggs generally are benthic. In the Octopodidae, in particular, when the egg diameter is less than 8-10% of adult mantle length (ML) the hatchlings have comparatively short arms and are planktonic; on the contrary when the egg diameter is more than 10-12% of ML hatchling's arms are comparatively long and the newborns settle on the bottom.

It appears clear that the horizontal distribution of cephalopods depends to a great extent on the mode of life of adult as well as early juvenile stages (Boletzky, 1987), viz., their dispersal capability. Oceanic cephalopods have a wider distribution (cosmopolitan or holoatlantic) than benthic and nekto-benthic ones (amphiatlantic to endemic). As for bottom cephalopods, their distribution depends on the mode of life of early juveniles, which in turn depends on the relative egg size.

On this account the overall distribution of the speciose family Sepiidae is noteworthy. The restriction to the Old World of these littoral and upper slope benthic animals is seemingly due to the absence of planktonic early juvenile stages – all cuttlefish species are large-egged – in addition to historical reasons (Neige, 2003).

Incidentally, the relative egg size is of great relevance for the fecundity and reproductive strategy of cephalopods (Boletzky, 1999), especially in the case of small species (cf. Boletzky's [2003] discussion on the different adaptive solutions evolved in coleoids within the scope of small adult size; see also Gabel-Deickert [1995]).

ENDEMIC AND QUASI-ENDEMIC CEPHALOPODS

The group of endemic and quasi-endemic Mediterranean comprises seven cephalopods or 10.4% of the teuthofauna of this sea.

Mangold and Boletzky (1988) already discussed the distribution of the quasi-endemic octopodids *Eledone moschata* and *Octopus salutii* (however they did not refer to them as “quasi-endemic”). In particular *E. moschata* is deemed a twin species of the Mediterranean-eastern Atlantic *Eledone cirrhosa*.

They emphasized that “It is interesting that the only cephalopod species exclusively known from the Mediterranean are among the Sepiolinae (*Sepiola affinis*, *S. ligulata*, *S. robusta*, *Sepietta obscura*)” (Mangold and Boletzky, 1988) (*S. obscura* was subsequently found in the Atlantic Ocean [Pereira, 1996]). To those sepiolid species *Sepiola intermedia*, *Sepiola rondeletii*, *Sepiola steenstrupiana* and *Sepietta neglecta* have to be added, despite their occurrences recorded outside the Mediterranean, close to Gibraltar however (Guerra, 1992), or even in the Red Sea (Adam, 1973).

Indeed, it is very interesting to find a comparatively large number of Mediterranean endemics and quasi-endemics among the Sepiolinae (three genera), i.e., six out of eleven species. All the 11 Mediterranean sepioline species share the following features:

- very little somatic differences within each of the genera *Sepiola* and *Sepietta* (the genus *Rondeletiola* is monotypic);
- fairly diverse copulatory organs, *hectocotylus* in males and, less conspicuously, *bursa copulatrix* in females (somatic differences between species are quite subtle; for species identification it is necessary to examine the copulatory organs; cf. Bello, 1995);
- small body size;
- number of eggs and, hence, fecundity reduced with respect to other Mediterranean cephalopods (Gabel-Deickert, 1996);
- nekto-benthic mode of life (Bello and Biagi, 1995);
- reproduction by large eggs that give birth to benthic early juveniles (Boletzky, 1974 and 1977);
- mostly living in shallow waters;
- short life cycle (less than a year) (Boletzky, 1975).

Some of the above characteristics greatly favour speciation. For instance the comparatively low number of eggs causes a reduced gametic genetic pool and, hence, a reduced genetic variability; the mode of life of both early juveniles and adults affects the overall dispersal capability of sepiolines and, hence, restricts the geographical width of their populations; littoral habitats are rather unstable and are in general more selective; thanks to their short life cycle, sepiolines have a generation renewal rate at least twice that of other Mediterranean cephalopods.

According to the theory of punctuated equilibria (Eldredge and Gould, 1972), the process of speciation may occur more efficiently in small, marginal populations, rather than in large populations where it might be easily suppressed. This can be easily supposed to be the case of the forerunners of present day Sepiolinae in the post-Messinian scenario, when the Mediterranean basin was subdivided in partly disjointed seas.

Furthermore, sepiolines living in littoral environments appear to fit fairly well the statement of Hutchinson (1959) in his "Homage to Santa Rosalia": "... small size, by permitting animals to become specialized to the conditions offered by small diversified elements of the environmental mosaic, clearly makes possible a degree of diversity quite unknown among groups of larger organisms."

Lastly, the notable lock-and-key type of copulatory organs of Sepiolinae represents a very effective interspecific mating barrier, which is necessary whenever there is a great array of allied sympatric species (Hutchinson, 1959). On the other hand, the diversity of *hectocotylis* is based just on small extent variations of a few suckers (enlargement) and sucker stalks (lengthening and/or widening) (Bello, 1995a), which supposedly have been produced by few genetic mutations starting off a proto-hectocotylus (see also Bello, 1996).

To sum up, it can be hypothesized that the Mediterranean Sepiolinae are a flock of species that has undergone *in situ* phylogenesis after the vicariant event(s) of (recurring) connection to the Atlantic and isolation of the Mediterranean (Myers and De Grave, 2000).

Beside the branching speciation of the Sepiolinae, additional episodes of cryptic speciation seem to have occurred in the Mediterranean, most probably under the pressure of the many climatic changes (cf. Oliverio [2000] on the phenomenon of micro-evolution in marine gastropods driven by climatic variations). For instance, Roeleveld (1995 and personal communication) found that the Atlanto-Mediterranean ommastrephid squid *Todarodes sagittatus* is indeed a complex of three species; the Mediterranean species of the "*Todarodes sagittatus*" complex may have evolved following the separation of the Mediterranean population(s) from those outside this sea. Most probably the phenomenon of cryptic speciation or micro-evolution involves further Mediterranean cephalopods.

RARE SPECIES FROM THE ATLANTIC

In the Mediterranean some Atlantic cephalopods have been recorded over the last two decades, all of them in the western basin.

Such are the cases of *Teuthowenia megalops*, one juvenile off the Catalan coast (Sánchez, 1985); *Cycloteuthis sirventi*, four specimens in the western and southern Mediterranean (Guerra, 1992); *Megalocranchia* sp., in the eastern Ligurian Sea (Bello and Biagi, 1999); *Cranchia scabra*, one specimen off the Spanish coast (Quetglas et al., 1999); and one *Architeuthis* sp. stranded on the coast of the Alboran Sea (González et al., 2000). These are all oceanic squids belonging to the Teuthida suborder Oegopsida.

Somewhat less rare cephalopods are the micronektonic *Spirula spirula* and the nekto-benthic sepiolid *Stoloteuthis leucoptera*. The former species has been

recorded in the southern Mediterranean since the XIX century (Bello, 1992) thanks to stranded dead specimens (not only the plain shell, but also the shell with fleshy remains). The latter species has been recorded several times along the Italian Ligurian and Tyrrhenian coasts, and once along the Catalan coast (e.g., Orsi Relini and Massi, 1991; Volpi et al., 1995; Sánchez et al., 1998).

In all reported cases, it is not known whether these cephalopods have established stable populations in the Mediterranean. Most probably they did not, perhaps with the exception of *S. leucoptera*. In particular, as for *S. spirula* it was hypothesized that although it enters frequently the Mediterranean, it does not survive because of the unsuitable environmental conditions (Bello, 1992). The same is true for the giant squid, *Architeuthis* sp., which was found in the westernmost Mediterranean (González et al., 2000); it is well known that the squids of this genus can survive only at low temperature (Brix, 1983), so the warm Mediterranean waters are unsuitable for their life. The events of cephalopods entering the Mediterranean and not surviving or not reproducing are similar to those of shelled molluscs that after their entrance in the Mediterranean at larval stages form “pseudo-populations” in the most western part of the sea, since they either do not survive till adulthood or are not capable of reproducing (Bouchet and Taviani, 1992). The main difference is that the shelled molluscs (gastropods and bivalves) may passively enter the Mediterranean as larvae, i.e., at the only highly mobile stage of their biological cycle, whereas cephalopods may pass the Straits of Gibraltar both passively during their early juvenile phases and actively through swimming at older stages.

In this regard it must be recalled that in the last decade or so the migration and post-migration survival of allochthonous organisms from the Atlantic (as well as from the Red Sea; see further below) to the Mediterranean was greatly increased due to the warming of the Mediterranean waters. This phenomenon, named “tropicalization” of the Mediterranean, concerns all taxonomic groups, both vegetal and animal, and is somewhat re-shaping the whole biodiversity of the basin (Bianchi and Morri, 2003).

ANTHROPOCHORIC DISPERSAL

The Lessepsian migrations are ascribed to the anthropochoric dispersal since they are events mediated by the man-made opening of the Suez Canal.

No immigrant from the Red Sea was reported by Mangold and Boletzky (1988). In the last decade several occurrences of Lessepsian immigrants have been recorded, all of them in the Levant Sea, i.e., the Mediterranean basin east of Suez.

Salman et al. (1999) reported the capture of 13 specimens of the *Octopus aegina* complex (*O. kagoshimensis*?) in April 1992 along the southern coast of Turkey; see Toll and Voss (1998) and Salman et al. (1999) about the taxonomic

status of this *Octopus* species complex. Salman and Katagan (2002) referred the occurrence of a few specimens of *Sepioteuthis lessoniana* in the Aegean Sea. Mienis (2003) gives details of the recent stranding ashore of many cuttlefish (cuttlebones with and without flesh) *Sepia pharaonis* along the Israeli coast; cuttlebones of the latter species were found in the past in the Bitter Lakes, along the Suez Canal (Barash and Danin, 1972). Lastly Orsi Relini et al. (2004), based on recent underwater photographs of a mature female and on the review of old literature, report and discuss the occurrence in the Mediterranean of *Tremoctopus gracilis* (Eydoux and Souleyet, 1852), an Indopacific cephalopod.

It appears that the immigration into the Mediterranean of many Red Sea marine organisms was enhanced by the lowering of salinity in the Bitter Lakes, which earlier represented a barrier against the passage of stenohaline animals, including cephalopods.

To explain the occurrence of *Tremoctopus gracilis* along the Istrian coast (northern Adriatic Sea) in 1936, reported by Kramer (1937), Orsi Relini et al. (2004) suggest transport by ships. Incidentally, it has been repeatedly shown that many small organisms cross the oceans passively when carried by ships in ballast waters (e.g., Hutchings et al., 1987).

FISHERIES AND TEUTHOBIODIVERSITY

In the last two or three decades, the Mediterranean fisheries have greatly affected very many populations of marine organisms (bony fishes, chondrichthyans, crustaceans, molluscs), including cephalopods. This problem deserves a profound discussion, which goes beyond the purpose of the present paper.

In this paper I report only a few examples about the southern Adriatic cephalopod populations of the cuttlefishes *Sepia elegans* and *Sepia orbignyana*, and the octopus *Eledone cirrhosa*. All of them are exploited by the south-western Adriatic multi-species trawl fishery.

The *Sepia* species are a by-catch of this fishery. Its values of CPUE (Captures per Unit Effort) have been dramatically reduced in the last two decades and are now the lowest in the Italian waters (compare for instance data in Bello [1984] and Belcari [1999]). Unfortunately no analytical data have been published on the present status of these populations; nevertheless the fact that only very few specimens, if any at all, are presently caught in a one-day fishing, shows that their populations have dramatically decreased. Such a phenomenon is most probably due to overfishing.

Eledone cirrhosa was the most important target species in terms of weight of Mola di Bari trawl fishery, and one of the most important of the whole southern Adriatic trawl fishery. In the middle 90s the CPUEs dropped drastically and are only in recent years slowly recovering (author's personal observations). No analytical account of such events is published in the scientific literature (see

negative evidence in Belcari, 1999); because of the economic importance of those events, some news were reported in the local newspapers (Bello, 1995c; Lorusso, 1995). Whichever the causes of the decrease of *E. cirrhosa* CPUEs, they are connected to an incorrect management of the trawl fishery.

The above species are benthic; the cuttlefishes lay large eggs that produce benthic hatchlings, whereas the octopus reproduce by relatively large eggs and early juveniles that live shortly in the plankton before settling down (Sweeney et al., 1992). Thus the decline of their southern Adriatic populations is to be related to their limited capabilities of recovering because of their bio-ecological constraints.

A word of concern about the negative effects of anthropogenic factors – including unrestrained fishing activities, but not only those – has to be said here.

DISTRIBUTION OF CEPHALOPODS WITHIN THE MEDITERRANEAN

It has been generally accepted that the Mediterranean cephalopod biodiversity, in terms of species richness, displays an East-West distributional gradient, and that the eastern basin is inhabited by fewer species than the western basin (Mangold and Boletzky, 1988). Indeed the many recent demersal surveys carried out in the eastern Mediterranean, namely in the Adriatic, Ionian, and Aegean Seas, have shown the occurrence of many cephalopod species previously unnoted there. Therefore the theory “west-more-species-than-east” is in need of some adjustment according to the presently available information on cephalopod distribution (Tab. I).

Tab. I - Number of cephalopod species in different regions of the Mediterranean; comparison between present results and Mangold and Boletzky (1988). The limit between the Western and Eastern Mediterranean is represented by the Sicilian sill.

	Western Mediterranean	Adriatic Sea	Eastern Mediterranean
Mangold and Boletzky (1988)	59	38	47
Present results	61	45	55

A more marked gradient in species richness occurs in the South-North direction. In the southern stretch of water along the African and Middle East coasts, including the southernmost parts of the Tyrrhenian and Ionian Seas, several species have been recorded that were never or very rarely collected further North (e.g., *Pterygioteuthis giardi*, *Pyroteuthis margaritifera*, *Ancistrocheirus lesueurii*).

The Adriatic teuthofauna is comparatively poor. Among the species absent from the Adriatic Sea there is the deep benthic octopus *Bathypolypus sponsalis*, although the environmental conditions of the southern part are seemingly appropriate for this cephalopod. No hypothesis has been put forth for such an absence.

A CONCISE HISTORY OF THE KNOWLEDGE OF THE MEDITERRANEAN TEUTHOFAUNA

The dividing line between the ancient and modern Mediterranean teuthology may be placed between the two cephalopod monographs of the “Fauna und Flora des Golfes von Neapel”, both originating at the Stazione Zoologica di Napoli. The first one is by Giuseppe Jatta (1896), an Apulian scientist, and the second one by Adolf Naef (1923), a Swiss scientist whom we may appropriately consider the father of modern teuthology. Indeed Naef, who was a keen systematist and embryologist, by describing or re-describing the Mediterranean cephalopod taxa, including the description of several new species of Sepiolidae (Naef, 1912a, 1912b, 1916), disentangled most pending systematic problems, thus providing the basis for the further growth of teuthology.

Little work was accomplished in the Mediterranean area in the decades following Naef's work. In the late '50s research on cephalopods resumed in Banyuls-sur-Mer, where Wirz (1958) produced a list of cephalopods for the “Faune des Pyrénées Orientales”, but in fact covering the whole Mediterranean. This list was followed by Torchio's (1968) list. By the end of the '70s, very few people were working on the Mediterranean cephalopods, apart from the small group of workers at the Laboratoire Arago in Banyuls-sur-Mer (including Katharina Mangold-Wirz and Sigurd von Boletzky) that played an important role in the advancement of the Mediterranean teuthology in the late '70s; moreover that group has represented since then the reference point for further research in this field.

Within the “Società Italiana di Malacologia”, whose members produced a catalogue of the Mediterranean molluscs (Sabelli et al., 1990-1992), a list of the Mediterranean living cephalopods was prepared by Bello (1986), who tried to solve all pending nomenclatural problems. Shortly after the FAO catalogue of the Mediterranean species of fishery interest was published; the chapter “Céphalopodes” was organized by Mangold and Boletzky (1987). The same authors at about the same time published the first true piece of biogeographical literature concerning the Mediterranean teuthofauna (Mangold and Boletzky, 1988), as mentioned above.

In the last two decades the study of cephalopods in the Mediterranean increased thanks to several factors. The most important is a series of surveys, mostly on the demersal fauna (e.g. “Valutazione delle risorse demersali” carried out in all the Italian seas since 1985; Relini, 1998), which later on involved also the Aegean and Levant Seas, and several studies on cephalopods as prey (e.g., Bello 1997) that allowed the finding of “rare” cephalopod remains in the stomach contents of several predators. In this context the manual for cephalopod beak identification, edited by Malcolm Clarke (1986), was of paramount importance. Additional works to be mentioned are the “Fauna Iberica” volume dedicated to the Iberian cephalopods, i.e. eastern

north Atlantic and western Mediterranean cephalopods (Guerra, 1992), and the paper by Bello (1996), concerning the biodiversity of benthic Mediterranean cephalopods, as well as several regional lists (e.g. Bello, 1990; Katagan et al., 1993; Jereb and Ragonese, 1994). The Mediterranean “fresco” may be completed with the checklist of Cephalopoda (Bello, 1995) in the “Checklist delle specie della fauna italiana” – which is the official reference list for all the Italian fauna edited by Minelli et al. (1995) – and its update (Bello, 2004), and lastly the collective volume “I Molluschi Cefalopodi dei mari italiani” edited by Jereb and Orsi Relini (in prep.).

On a world-wide basis the biogeography works by Nesis (e.g., 1997), including his book “Cephalopods of the World” (Nesis, 1987) deserve to be mentioned, as well as the collective volume “Systematics and biogeography of Cephalopods” edited by Voss et al. (1998). The review of oceanic squids by Clarke (1966), although not a strictly biogeographic paper, deals too with the geographical distribution of teuthids. Lastly, a significant recent piece of theoretical cephalopod biogeography literature was produced by Boletzky (1999), in which the author carries out an analysis of the literature and discusses several aspects of the bio-ecology of these animals that are to be taken into account in order to understand their geographic distribution.

CONCLUSIONS

Despite the fact that the Mediterranean teuthofauna is one of the better known in the world, many events that occurred in the last decade have shown that our information contains some obscure areas.

The most obvious drawbacks are due to gaps in our information pertaining to elusive species such as the several cephalopods collected only once or a very few times: are they part of stable Mediterranean populations or just stray specimens or new colonizers? In this regard, one has to recall that in the recent past several “rare” and “very rare” species were found to be just elusive species, as shown by studies of teuthivorous predators (Bello, 1997, 2000). For instance, in the stomach contents of large pelagic predators, beaks have been found that do not belong to any cephalopod known to live in the Mediterranean (unpublished author’s observations). Moreover the presently occurring lessepsian immigrations represent an additional dynamic element of uncertainty.

Boletzky (1999) summarized that the distribution of cephalopods depends on many factors including their evolutionary history, the geological history, and the environmental conditions. Several biological, ecological as well as systematic aspects are to be taken into account if we want to get to the full understanding of the processes underlying geographical distribution. He also pointed out the necessity of multidisciplinary collaboration involving geologists, paleontologists, and biologists. On this account the XXXIV meeting of the Società Italiana di

Biogeografia dedicated to the Marine Biogeography of the Mediterranean – Ischia, 2003 – as well as the meeting on Coleoid Cephalopods – Berlin, 2003 – represent definite steps in the direction suggested by Boletzky.

The need of new original approaches to the study of biogeography may be illustrated for example by a recent study on the living Sepiidae by Neige (2003). In this paper the hypothesis of two centers of origin for this taxon – one in the Indo-Pacific and the other in the eastern Atlantic – is put forth, whereas, according to an earlier paper by Khromov (1998), all members of the Sepiidae originated in the area between the Indian and Pacific Oceans. An additional tool that has not been extensively used in the study of cephalopod distribution is the cladistic biogeography (Myers and De Grave, 2000); incidentally Veller et al. (2003) discuss the suitability of combining the cladistic with the phylogenetic biogeography as a hypothetico-deductive approach to generate reliable results.

As regards the Mediterranean cephalopod biogeography, several aspects need to be addressed, such as the definition of the occurrence and distribution of cryptic sibling species by means of morphological and genetic analyses of potential species, and the definition of populations and the genetic exchange among them. Certain biological and ecological features should also be dealt with, concerning the population homeostasis (fecundity, early juvenile and overall mortalities, etc.), as well as the capacity to expand the population (ecology of early stages, ecophysiological requirements, etc.) (see also Boletzky, 1999).

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Note added in proofs: When this paper was already in press Dr. Chingis Nigmatullin (AtlantNTRO, Kaliningrad) – whom I warmly thank – made me aware of an important Mediterranean biogeography paper by the late Dr. Nesis. This remarkable paper deserved to be quoted and discussed herein. Its reference is: Nesis K.N. 1982 - Zoogeographic position of the Mediterranean Sea. In: Kussakin O.G. (ed.). *Marine Biogeography: Subject, methods, principles of regionalization*. Moscow: Nauka Press. p. 270-299 (In Russian).

Appendix: List of the Mediterranean cephalopods.

Compiled after several sources, including Mangold and Bolerzky (1987), Nesis (1987), Bello (1995), and Voss et al. (1998).

Occurrence in different Mediterranean regions: WM = West Mediterranean; EM = East Mediterranean; AS = Adriatic Sea.

		WM	EM	AS
SPIRULIDA				
Spirulidae				
<i>Spirula spirula</i> (Linnaeus, 1758)	P	+	-	-
SEPIIDA				
Sepiidae				
<i>Sepia elegans</i> Blainville, 1827	EA	+	+	+
<i>Sepia officinalis</i> Linnaeus, 1758	EA	+	+	+
<i>Sepia orbignyana</i> Férussac, 1826	EA	+	+	+
<i>Sepia pharaonis</i> Ehrenberg, 1831	L	-	+	-
SEPIOLIDA				
Sepiolidae				
<i>Sepiolo affinis</i> Naef, 1912	E	+	+	+
<i>Sepiolo aurantiaca</i> Jatta, 1896	EA	+	-	-
<i>Sepiolo intermedia</i> Naef, 1912	QE	+	+	+
<i>Sepiolo ligulata</i> Naef, 1912	QE	+	+	+
<i>Sepiolo robusta</i> Naef, 1912	E	+	+	+
<i>Sepiolo rondeletii</i> Leach, 1817	EA	+	+	+
<i>Sepiolo steenstrupiana</i> Levy, 1912	E	+	+	+
<i>Sepietta neglecta</i> Naef, 1916	EA	+	+	+
<i>Sepietta obscura</i> Naef, 1916	QE	+	+	+
<i>Sepietta oweniana</i> (d'Orbigny, 1841)	EA	+	+	+
<i>Rondeletiola minor</i> (Naef, 1912)	EA	+	+	+
<i>Heteroteuthis dispar</i> (Rüppell, 1844)	A	+	+	+
<i>Stoloteuthis leucoptera</i> (Verrill, 1878)	AA	+	-	-
<i>Rossia macrosoma</i> (Delle Chiaje, 1830)	EA	+	+	+
<i>Neorossia caroli</i> (Joubin, 1902)	EA	+	+	+
TEUTHIDA				
Loliginidae				
<i>Loligo forbesii</i> Steenstrup, 1856	EA	+	+	+
<i>Loligo vulgaris</i> Lamarck, 1798	EA	+	+	+
<i>Alloteuthis media</i> (Linnaeus, 1758)	EA	+	+	+
<i>Alloteuthis subulata</i> (Lamarck, 1798)	EA	+	+	+
<i>Sepioteuthis lessoniana</i> Férussac, 1830	L	-	+	-
Chtenopterygidae				
<i>Chtenopteryx sicula</i> (Vérany, 1851)	P	+	+	-
Thysanoteuthidae				
<i>Thysanoteuthis rhombus</i> Troschel, 1857	P	+	+	+

		WM	EM	AS
Architeuthidae				
<i>Architeuthis</i> sp.	A?	+	-	-
Brachiteuthidae				
<i>Brachiteuthis riisei</i> (Steenstrup, 1882)	P	+	+	+
Pyroteuthidae				
<i>Pyroteuthis margaritifera</i> (Rüppell, 1844)	P	+	+	-
<i>Pterygioteuthis giardi</i> Fischer, 1895	P	+	+	-
Enoploteuthidae				
<i>Abralia veranyi</i> (Rüppell, 1844)	AA	+	+	+
<i>Abraliopsis morisii</i> (Vérany, 1839) (= <i>A. pfefferi</i> Joubin, 1896)	A	+	+	-
Onychoteuthidae				
<i>Onychoteuthis banksii</i> (Leach, 1817)	P	+	+	+
<i>Ancistroteuthis lichensteinii</i> (Férussac, 1835)	A	+	+	+
Ommastrephidae				
<i>Ommastrephes bartramii</i> (Lesueur, 1821)	P	+	+	+
<i>Illex coindetii</i> (Vérany, 1839)	AA	+	+	+
<i>Todaropsis eblanae</i> (Ball, 1841)	P	+	+	+
<i>Todarodes sagittatus</i> (Lamarck, 1798)	EA	+	+	+
Bathyteuthidae				
<i>Bathyteuthis abyssicola</i> Hoyle, 1885	P	-	+	-
Histioteuthidae				
<i>Histioteuthis bonnellii</i> (Férussac, 1835)	P	+	+	+
<i>Histioteuthis reversa</i> (Verrill, 1880)	A	+	+	+
Ancistrocheiridae				
<i>Ancistrocheirus lesueurii</i> (d'Orbigny, 1842)	P	+	+	+
Octopoteuthidae				
<i>Octopoteuthis sicula</i> Rüppell, 1844	P	+	+	-
Cycloteuthidae				
<i>Cycloteuthis sirventi</i> Joubin, 1919	A	+	+	-
Chiroteuthidae				
<i>Chiroteuthis veranii</i> (Férussac, 1835)	P	+	+	+

		WM	EM	AS
Cranchiidae				
<i>Cranchia scabra</i> Leach, 1817	P	+	-	-
<i>Galiteuthis armata</i> Joubin, 1898	P	+	+	-
<i>Megalocranchia</i> sp.	A?	+	-	-
<i>Teuthowenia megalops</i> (Prosch, 1847)	A	+	-	-
OCTOPODA				
Opisthoteuthidae				
<i>Opisthoteuthis calypso</i> Villanueva, Collins, Sánchez and Voss, 2002	EA	+	-	-
Octopodidae				
<i>Octopus</i> cf. <i>aegina</i> Gray, 1849 / <i>kagoshimensis</i> Ortmann, 1888	L	-	+	-
<i>Octopus defilippi</i> Vérany, 1851	P	+	+	+
<i>Octopus macropus</i> Risso, 1826	P	+	+	+
<i>Octopus salutii</i> Vérany, 1839	QE	+	+	+
<i>Octopus vulgaris</i> Cuvier, 1797	P	+	+	+
<i>Scaevargus uniccirrhus</i> (Delle Chiaje, 1841)	P	+	+	+
<i>Pteroctopus tetracirrhus</i> (Delle Chiaje, 1830)	AA	+	+	+
<i>Eledone cirrhosa</i> (Lamarck, 1798)	EA	+	+	+
<i>Eledone moschata</i> (Lamarck, 1798)	QE	+	+	+
<i>Bathypolypus sponsalis</i> (P. Fischer and H. Fischer, 1892)	EA	+	+	-
Argonautidae				
<i>Argonauta argo</i> Linnaeus, 1758	P	+	+	+
Ocythoidae				
<i>Ocythoe tuberculata</i> Rafinesque, 1814	P	+	+	+
Tremoctopodidae				
<i>Tremoctopus violaceus</i> Delle Chiaje, 1830	P	+	+	+
<i>Tremoctopus gracilis</i> (Eydoux and Souleyet, 1852)	T (L)	+	-	+

P=Panoceanic; A=Atlantic; AA=Amphiatlantic; EA=Eastern Atlantic; QE = Quasi-endemic; E = Endemic; L=Lessepsian migrant; T=Passively transported.