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Mediterranean calanoid copepods biogeography: new species identification and first records of hyperbenthic forms

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SUMMARY

The spatio-temporal distribution patterns of the Mediterranean planktonic and hyperbenthic calanoid copepods were analysed. The atlantic origin of the major part of planktonic calanoid copepods was defined, distinguishing between Mediterranean own species and the Alboran Sea, and Levantine Basin populations migrated, respectively, from Atlantic and Indo-Pacific Oceans. In the Mediterranean the presence, as other oceans of the world, of a hyperbenthic specific calanoid copepods community was showed. In this "ecological group" were identified populations of atlantic and indo-pacific origin, of recent and ancient migration in the Mediterranean.

INTRODUCTION

Copepoda, a subclass of the phylum Crustacea, consists of ten orders: Platycopioidea, Calanoida, Misophrioida, Mormonilloidea, Cyclopoida, Gellyelloidea, Harpacticoida, Poecilostomatoida, Siphonostomatoida and Monstrilloidea.

Copepods are aquatic, mainly marine, organisms that have spread by adaptive radiation into all habitats, including the ocean depths, brackish coastal lagoons, submarine caves, and fresh waters of high mountain rivers and lakes.

Humes (1994) estimated that by the end of 1993 about 11,500 species of Copepoda had been identified. Excluding Diaptomidae, around 1800 species of Copepoda Calanoida have been censused in the marine ecosystem (Huys and Boxshall, 1991; Humes, 1994).

In their inventory of Mediterranean planktonic Copepoda, Razouls and Durand (1991) listed 301 species of Calanoida, to which must be added 11 new species identified between 1991 and 2000 for a total of 312 species. There are records of 173 species of Copepoda Calanoida in Italian seas (Argano et al., 1995), i.e. 55.8% of the total identified in the Mediterranean. Since there

should not be substantial differences in the species composition of Copepoda among the various regions of the Mediterranean, much work of identification remains to be done to define the biodiversity of the Italian seas.

Of the 312 species of Copepoda Calanoida in the Mediterranean, around half were identified in the XIX century (beginning from 1837) and the rest in the last century (Fig. 1). After the fundamental works of Giesbrecht (1892), Farran (1908), Sars (1921), Rose (1933), Sewell (1947) and other authors, the knowledge of planktonic Copepoda Calanoida reached such a high level that the discovery of a new species or first records of known species for the Mediterranean could be considered rare events. The only exceptions are the very small forms belonging to the genus *Calocalanus* which, because of their size, evaded sampling and were identified by Shmeleva only in the period 1960-1980.

Renewed interest in the identification of new species and in first records of Copepoda Calanoida in the Mediterranean has come from the recent discovery of a new “ecological group”. It has been defined by different authors as hyperbenthic, benthoplanktonic and demersal because of the particular habitat in which the species live, i.e. the sediment-water interface. Most authors use the term “hyperbenthic”, even though it is somewhat inappropriate.

The spatial distribution of this group of species of Copepoda Calanoida is very broad and varied, extending from submarine caves to brackish lagoons and from shallow coastal waters to depths of over 1200 m. The distribution of the

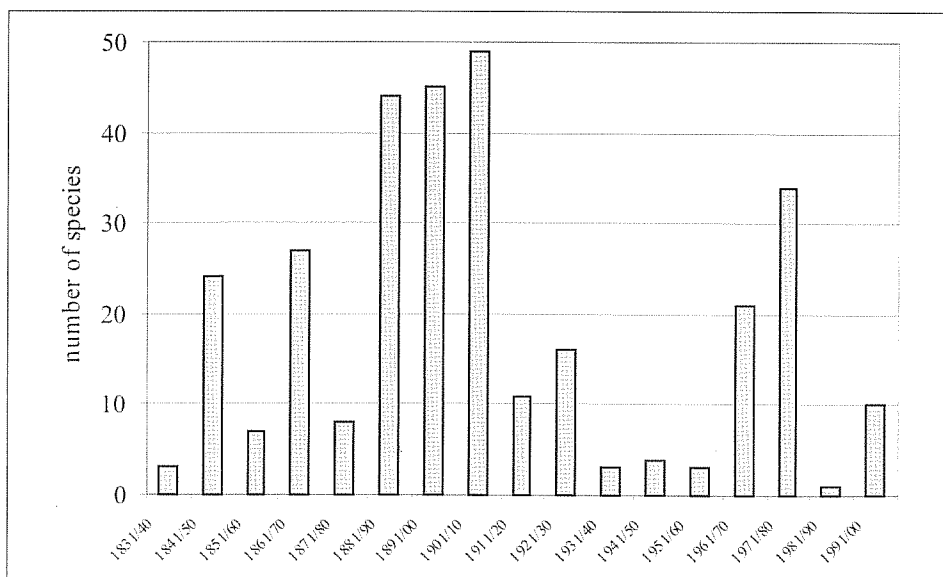


Fig. 1 - Cumulative numbers of Mediterranean calanoid copepod species described up to 2000.

hyperbenthic species is limited to muddy substrates rich in organic detritus consisting mainly of remains of *Posidonia oceanica* (Campolmi et al., 2002; Jaume et al., 2000).

The presence of this hyperbenthic and/or benthoplanktonic component in the Mediterranean demonstrates the existence of a specific community of Copepoda Calanoida living near the bottom, similar to the one described in all oceans of the world. In the past, species of this particular community had not been recorded in the Mediterranean because of the difficulty of sampling in their habitat and the low abundance of individuals. Most marine species of Copepoda Calanoida are planktonic, while only a few are hyperbenthic.

RELATION BETWEEN ATLANTIC CALANOID COPEPOD POPULATIONS AND MEDITERRANEAN ONES

Because of the geological events that determined the present state of the Mediterranean basin (Hsü et al., 1978), most species of planktonic Copepoda Calanoida are of Atlantic origin, although they possess characteristics that distinguish them from the populations of the Atlantic Ocean. Owing to the physical differences between the Atlantic and Mediterranean basins, the Strait of Gibraltar does not constitute a route of entry of the Atlantic planktonic copepod populations into the Mediterranean and, vice versa, of the Mediterranean ones toward the Atlantic.

Planktonic copepod species of the superficial Atlantic waters that enter the Mediterranean remain confined to the Alboran Sea and are not able to spread into the whole basin. Consequently, the Alboran Sea is characterized by a higher Margalef index of species diversity than the neighbouring Atlantic area (Greeze et al., 1985) and probably the whole Mediterranean. For this reason, the Mediterranean species of planktonic Copepoda Calanoida can be considered relict populations of Atlantic origin. An example of separation between the Atlantic and Mediterranean populations is provided by the species of planktonic Copepoda Calanoida, *Pseudocalanus elongatus*; it is confined to the upper and middle Adriatic Sea (Hure et al., 1980) and presents clear biometric differences from the Alboran Sea population, of evident Atlantic origin (Vives et al., 1981). The Atlantic species group found in the Alboran Sea (Greeze et al., 1985; Scotto di Carlo, 1985) but not yet recorded in other areas of the Mediterranean could include species as *Metridia lucens*, *Pleuromamma borealis*, *Heterostylites longicornis*, *Calanoides carinatus*, *Eucalanus hyalinus*, *Calocalanus gracilis*, *C. indicus*, *Acrocalanus gibber*, *Euchirella intermedia*, and *Centropages chierchiai*.

Therefore, it can be concluded that: a) the current Mediterranean populations of planktonic Copepoda Calanoida do not have relationships with the Atlantic

ones; b) the Mediterranean species are evolving independently of the Atlantic ones; and c) the Mediterranean is the site of formation of new species.

RELATION BETWEEN RED SEA CALANOID COPEPOD POPULATIONS AND MEDITERRANEAN ONES

By restoring the communication between the Mediterranean and the Indo-Pacific Ocean after millions of years, the Suez Canal has probably allowed the passage of pelagic fauna between the two basins (Por, 1978). However, the shallow water of the Suez Canal and the strong differences in salinity between the two basins have permitted the diffusion of only a few planktonic forms. Therefore, very few species can be defined as "Lessepsian immigrants". Species of Copepoda Calanoida, broadly distributed in the Red Sea and Suez Canal (Gurney, 1927), that have been recorded in the "Lessepsian province" include: *Calanopia elliptica*, *C. media*, *Acartia centrura* (Berdugo, 1968; 1974); *Labidocera madurae*, *Acartia detruncata*, *A. fossae* (Lakkis, 1981), *Paraeuchaeta concinna* (Casanova, 1973) and *Arietellus pavoninus* (Moraitou-Apostolopoulou, 1985).

PLANKTONIC CALANOID COPEPOD SPATIO-TEMPORAL DISTRIBUTION IN THE MEDITERRANEAN SEA

In the Mediterranean, as in all oceans and seas of the world, the copepods are the dominant component of zooplankton for most of the year. The population structure of the planktonic copepods is generally uniform throughout the Mediterranean, except for the areas of the Alboran Sea, northern Adriatic and eastern end of the Levantine basin (Scotto di Carlo, 1985; Estrada et al., 1985; Scotto di Carlo et al., 1991). The spatial distribution of the plankton in the Mediterranean is generally divided into neritic and pelagic communities, there being no significant differences between the various regions. Regarding the temporal distribution, the species composition of the neritic copepods is characterized by the dominance of a small group of key species like *A. clausi*, *P. parvus*, *C. typicus* and *T. stylifera* (Mazzocchi and Ribera d'Alcalà, 1995); they succeed each other throughout the year and by their abundance determine the structure of the whole zooplankton community (Scotto di Carlo et al., 1985). Interestingly, a similar species composition characterizes the copepod population of many temperate marine environments (Raymont, 1983). In spring-summer, the dominant species are mainly *A. clausi*, *P. parvus* and, to a lesser degree, *C. typicus*; between the end of summer and autumn, they are succeeded in the dominance relationships by *T. stylifera*. The winter period is characterized by low abundance and greater homogeneity of the percentage ratios of the species, without any species of *Clausocalanus*, *Oithona* and

Ctenocalanus becoming particularly dominant (Scotto di Carlo et al., 1985). During the seasonal succession of neritic copepod species, the lack of overlap of their abundance peaks (the result of a long process of co-evolution) minimizes the negative effects of the interspecific competition.

The pelagic ecosystem of the Mediterranean, with more stable physico-chemical parameters than the neritic system, is characterized by a copepod population with higher species diversity and smaller seasonal fluctuations in species composition. The planktonic copepod community of the Mediterranean pelagic ecosystem is generally much poorer in species than that of the Atlantic Ocean (Vives et al., 1975). It is characterized by mixing with neritic species, which extend into the superficial pelagic waters in the period of maximum abundance (Scotto di Carlo et al., 1984), and by a small group of species belonging, mainly, to the genera *Calanus*, *Nannocalanus*, *Candacia*, *Euchaeta*, *Eucalanus*, *Oithona*, *Clausocalanus*. The mesopelagic community, extending 100 to 600 m in depth, consists of typical species of this habitat, characterized by large circadian vertical migrations. The most frequent copepod species of the mesopelagic zone are: *Pleuromamma gracilis*, *P. abdominalis*, *Paraeucaeta acuta*, *P. hebes*, *Haloptilus longicornis*, *Neocalanus gracilis*, *Lucicutia flavicornis*, *Heterorhabdus papilliger*, *Euchirella messinensis*, *Eucalanus elongatus*.

The deep copepod community, beyond 600 m, consists of several mesopelagic species able to perform large vertical migrations. Therefore, the deep system of the Mediterranean is clearly different from the oceanic one because of the absence of a true bathypelagic community. All this is determined by the threshold of the Strait of Gibraltar, only around 320 m deep, and by the consequent model of thermospheric circulation of the water masses. Thus the deep waters of the Mediterranean present a stable temperature of 12-13°C, which is incompatible with the thermal demands of typical oceanic bathyal species.

MEDITERRANEAN HYPERBENTHIC CALANOID COPEPOD SPECIES COMPOSITION

This particular ecological group of Copepoda Calanoida is very interesting on account of various ecological, biogeographic and taxonomic aspects.

Despite the small number of species and the low abundance, this ecological group plays a very important role since it increases the functional diversity of the marine ecosystem. With their circadian vertical migrations in shallow coastal water systems (Campolmi et al., 2002), the hyperbenthic copepods represent an interesting link in the transfer of energy between the planktonic and benthic systems.

With respect to most planktonic Copepoda Calanoida, the species *P. xiphophorus* and *P. umbraticus* have a low mean production of eggs per female when raised in the laboratory (Zagami, unpublished data), which could explain the low abundance of hyperbenthic Copepoda Calanoida recorded in the neritic ecosystem (Campolmi et al., 2002).

From the biogeographic point of view, the hyperbenthic Copepoda Calanoida recorded in the Mediterranean, both as new species and as first reports of species known in other areas, will provide an important contribution to our knowledge of the origin of the Mediterranean fauna and of the relationships of the Mediterranean basin with the Atlantic and Indo-Pacific oceans during geological evolution.

From the taxonomic point of view, the hyperbenthic Copepoda include the most ancestral families of Copepoda Calanoida, such as Pseudocyclopidae and Ridgewayidae, or little known ones like Stephidae and Arietellidae.

The observation of new species and their developmental stages (obtained in the laboratory) will provide an important contribution to our knowledge of the evolution of copepods.

Knowledge about the Mediterranean species of hyperbenthic Copepoda Calanoida is very limited, referring mainly to the genera *Stephos*, *Paramisophria*, *Metacalanus*, *Ridgewayia*, and *Pseudocyclops* (Tab. I).

The genus *Stephos* T. Scott, 1892 comprises 26 species, all of small size. Most of them live in shallow coastal waters in close contact with the bottom. However, several species were recently discovered in coastal submarine caves of islands in the Western Atlantic (Boxshall et al., 1990) and Mediterranean (Riera et al., 1991; Carola and Razouls, 1996). From the biogeographic point of view, the species of *Stephos* are widely distributed in all oceans of the world, including tropical, temperate and polar waters. Five *Stephos* species have been identified in the Mediterranean: *S. gyrans* Giesbrecht, 1892; *S. margalefi* Riera et al., 1991;

Tab. I - Hyperbenthic calanoid copepod species described in the Mediterranean Sea.

FAMILY	GENERA	SPECIES
Arietellidae	<i>Metacalanus</i> <i>Paramisophria</i>	<i>acutioperculum</i>
		<i>bathyalis</i>
		<i>intermedia</i>
		<i>mediterranea</i>
		<i>lilibeitana</i>
		<i>ammophila?</i> <i>cluthae</i>
Pseudocyclopidae	<i>Pseudocyclops</i>	<i>xiphophorus</i> <i>umbraticus</i> <i>obtusatus</i>
Ridgewayidae	<i>Ridgewayia</i>	<i>minorcaensis</i>
Stephidae	<i>Stephos</i>	<i>margalefi</i> <i>cryptospinosus</i> <i>marsalensis</i>

S. balearensis Carola and Razouls, 1996; *S. cryptospinosus* Zagami et al., 2000; *S. marsalensis* Costanzo et al., 2000.

The genus *Paramisophria* T. Scott, 1897 includes 14 species, widely distributed from tropical to subtemperate and temperate waters of the Atlantic, Pacific and Indian oceans. A primary hyperbenthic habitat has been attributed to the species of *Paramisophria*, although they have spread to shallow coastal waters in recent times, both in submarine caves and on the bottom of pelagic waters to around 1200 m (Jaume et al., 2000). Six species have been recorded in the Mediterranean: *P. cluthae* T. Scott, 1897; *P. ammophila* Fosshaghen, 1968; *P. mediterranea*, *P. bathyalis*, *P. intermedia* Jaume et al., 2000; *P. lilibetana* Campolmi et al., unpublished. The record of *P. ammophila* in the Mediterranean (Carola et al., 1995) should be considered with caution, since the species was identified only in female specimens while the most important diagnostic characters for species identification in this genus are based on male morphology.

The genus *Metacalanus* Cleve, 1901 consists of 4 species, characterized by a broad geographic distribution extending from tropical to subtemperate and temperate waters of the Atlantic, Pacific and Indian oceans. In the Mediterranean, this genus is represented by only one species, *M. acutioperculum* Ohtsuka, 1984, recorded for the first time in coastal waters of the southern Tyrrhenian Sea, near the Marsala Lagoon (Campolmi et al., 1999). The discovery of this species in the Mediterranean was the first record after that of Ohtsuka (1984) in Japanese waters. Despite the great geographic distance between the two habitats, there are no significant differences between the two populations. The specimens found in the Mediterranean can be considered a relict population of Indo-Pacific origin.

The genus *Pseudocyclops* includes 33 species, mainly distributed in tropical and subtemperate waters of the Atlantic, Pacific and Indian oceans, except for *P. obtusatus* present also in the northeastern Atlantic. This genus is represented by two species in the Mediterranean, *P. obtusatus* Brady and Robertson, 1873 and *P. umbraticus* Giesbrecht, 1893. Recently, *P. xiphophorus* Wells, 1967 was recorded for the first time in the Mediterranean, in the brackish lake of Faro, Messina, Italy (Zagami et al., unpublished). This species has previously been found only in the Indian Ocean, in coastal waters of Inhaca Island, Mozambique (Wells, 1967). The Mediterranean specimens of *P. xiphophorus* can be considered a relict population of Indo-Pacific origin.

The genus *Ridgewayia* Thompson and Scott, 1903 comprises 13 species, mainly distributed in warm waters of the Suez Canal, Indian Ocean, Bermuda, Bahamas, Florida, Panama, Australia and Japan. In the Mediterranean, *Ridgewayia* is represented by a single species, *R. minorcaensis*. It was found for the first time by Razouls and Carola (1996) in a cave in the island of Minorca and described as a subspecies, *R. marki minorcaensis*, although it has recently been raised to the species rank, *R. minorcaensis*, by Ohtsuka. This species has also been recorded in the

central Mediterranean in the shallow coastal waters in front of the Marsala Lagoon (Campolmi et al., 1999). The close morphological affinities of *R. minorcaensis* with *R. marki*, recorded only in Bermuda (Esterly, 1911; Yeatman, 1969), suggest that the Mediterranean specimens are of Atlantic origin.

Other species of Copepoda Calanoida, presumably with hyperbenthic habits and belonging to the genera *Tharybis*, *Phaenna*, *Aetideus*, *Scolecithricella*, must still be studied in the Mediterranean in order to identify their primary habitat, and their biogeographic relations with populations of the Atlantic and Indo-Pacific Oceans.

DISCUSSION

Since they are not distributed in the entire Mediterranean, the Atlantic species of planktonic Copepoda Calanoida present in the Alboran Sea and the Indo-Pacific species of the Lessepsian province cannot be considered Mediterranean populations. However, it is difficult to distinguish between the species that are true immigrants, i.e. which adjust to the Mediterranean environment and can realize their entire life cycle there, from the species that occasionally pass through the Strait of Gibraltar and the Suez Canal but are not able to survive in the new environment and spread to the rest of the Mediterranean. While most of the relict Mediterranean populations of planktonic Copepoda Calanoida are of Atlantic origin, the populations of hyperbenthic Copepoda Calanoida are of both Atlantic and Indo-Pacific origin because of their type of habitat which allowed them to survive the salinity crisis in the Messinian. From this point of view, the group of species of hyperbenthic Copepoda Calanoida is very complex. It consists of genera of probable recent migration into the Mediterranean, e.g. *Stephos*, *Paramisophria* and *Metacalanus* which do not fit the Tethyan distribution model since they contain species distributed in temperate and polar marine areas, and genera like *Pseudocyclops* and *Ridgewayia* that exhibit a complete Tethyan pattern (Razouls and Carola, 1996; Ohtsuka et al., 1999). Many demersal Calanoida and Platycopioidea of shallow coastal waters present a Tethyan distribution model (Ohtsuka et al., 1998). Stock (1993) suggested that these species have existed since the time of the Tethys Sea. The characteristic factors considered to define true Tethyan taxa are: the status of relict species and a limited warm-waters distributional pattern for the genus (Jaume et al., 2000).

The separation and isolation of the Copepoda Calanoida species, due to continental drift and consequent oceanographic barriers that interrupted gene flow from ancient populations, could have favoured allopatric speciation. The species that followed separate evolutionary lines, together with others that maintained the ancestral lineages and acquired the status of relict populations, constitute the current planktonic and hyperbenthic community of Copepoda Calanoida of the Mediterranean. Future researches on calanoid copepods

hyperbenthic component are interesting in the hope of shedding new light on Mediterranean calanoid copepods origin, and their relations with Atlantic and Indo-Pacific populations during geological evolution of the Mediterranean Sea.

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