The Zooplankton

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Abstract

The Mediterranean Sea bears one of the longest traditions in the study of zooplankton. Pioneer work focused more on taxonomy to suit the high diversity of zooplankton that inhabits the Mediterranean, and indeed very few ecosystems have such a deep and broad knowledge on zooplankton like the one gathered in the Mediterranean. Further research into ecological aspects encompassed more descriptive studies on distribution and seasonality patterns, to lead in current times to more functional and modelling approaches. In this chapter we present an overview of the seasonality and distribution patterns of zooplankton in the Mediterranean, with special emphasis on the driving mechanisms behind. We will focus essentially on the western basin, and provide an overview on the outcome of the studies conducted by the different schools of marine biologists and oceanographers established in the geographical areas surrounding the Catalan/Balearic Sea, the Ligurian Sea and the Thyrrenian Sea. The latitudinal gradient, the marked seasonality, and the particular productivity patterns in the Mediterranean provide a frame for a zooplankton community in which the succession of species and assemblages occurs with not drastic changes in the whole standing stocks. As in other seas, examples of diel, ontogenetic and seasonal vertical migration can be found in the Mediterranean; however, the presence of a deep chlorophyll maximum during the stratified period drives a distinct vertical distribution of epipelagic zooplankton. Mesoscale singularities such as density fronts and eddies, the presence of submarine canyons which modify the general circulation, and other local phenomena like riverine runoff are responsible for the enhancement of production and favours the aggregation of zooplankton, either by local increase phenomena or by passive accumulation. Finally, current challenges in zooplankton research in the Mediterranean, such as the long-term changes in relation to large-scale atmospheric forcing, the occurrence of gelatinous zooplankton proliferations and the changes in species distribution and presence of non-indigenous ones will be also discussed.

Keywords

Mediterranean Sea • Zooplankton • Diversity of zooplankton • Distribution and seasonality patterns • Western basin • Catalan/Balearic Sea • Ligurian Sea • Thyrrenian Sea • Zooplankton community • Diel • Ontogenetic and seasonal vertical migration • Deep chlorophyll maximum • Epipelagic zooplankton • Long-term changes • Large-scale atmospheric forcing • Gelatinous zooplankton • Non-indigenous species

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Introduction

The general composition and diversity of the Mediterranean zooplankton is the consequence of a set of recent geological events occurred since the Messinian Salinity Crisis 5 M years ago, which resulted in extreme climatic changes caused by the combination of glaciations and interglacial periods. For that reason, it is difficult to know the original composition of the planktonic fauna in the Mediterranean. The present zooplankton in the Mediterranean is a mixture of faunas with diverse origin, which have experienced severe selective environmental pressures and followed different evolution processes (Pérès 1985; Fredj et al. 1992). Overall, the Mediterranean zooplankton can be considered as a true Atlantic fauna, composed mainly of subtropical species together with a component of clearly tropical origin and another one of northern species (combination of a minority of boreal origin and a mayor set of species from temperate and cold areas); in addition, an influence from oriental origin, especially in the Eastern Mediterranean, cannot be dismissed (Furnestin 1968, 1979; Bianchi and Morri 2000; Gómez 2006). Moreover, the recent discovery in deep habitats, such as the submarine canyons, of endemic species considered as Thetian relicts (Gili et al. 2000), reinforces the hypothesis that the deep Mediterranean basins are semi isolated habitats that contribute to the speciation processes (Fredj et al. 1992).

The study of zooplankton in the Mediterranean has a long tradition of more than two centuries. Pioneering work was carried out at the marine stations in Villefranche-sur-Mer (France) and Naples (Italy), which rendered excellent publications still in use, such as the *Manuel de Planctologie Méditerranéne* by Trégouboff and Rose (1957) and the collection of the *Fauna und Flora des Golfes von Neapel*, and from the Spanish side it deserves special consideration the *Introducción al estudio del plancton marino* by Massutí and Margalef (1950). The information gathered from the numerous studies carried out during the last 100 years originates mainly from the coastal and neritic environments, sampled along the different seasons of the year, but oceanic research on vessels has also been carried out with obvious temporal and geographical constraints; in addition, several long-term series of plankton collection are also available in the western Mediterranean, the Adriatic Sea and the Aegean Sea. Even if some specific taxonomic groups have received particular attention (e.g. copepods), the Mediterranean is perhaps one of the marine regions where a broad knowledge of practically all groups is available. Through time, different schools have developed and gathered the major part of specialists in the surrounding land (the south of France: Banyuls-sur-Mer, Marseille, and Villefranche-sur-Mer; Italy: Genova, Naples, and Trieste; Spain: Barcelona, Malaga and Mallorca), which have contributed to improve our understanding of the systematics, and the population and community ecology of the zooplankton in the western Mediterranean (e.g. synthesis works of Vives 1966; Furnestin 1968; Estrada et al. 1985; Gaudy 1985; Champalbert 1996). Recent monographic studies on the fauna and taxonomy of the Mediterranean zooplankton (Bouillon et al. 2004; Vives and Shmeleva 2006, 2010) and other more ecological reviews (Siokou-Frangou et al. 2010; Durrieu de Madron et al. 2011) are good examples of the contemporary dynamism of zooplanktonic and oceanographic research in the Mediterranean.

This chapter does not intend to be a complete analysis of the zooplankton ecology in the Mediterranean Sea. Focused mainly on the western Mediterranean, we will make an effort to summarize, in a descriptive and comprehensive manner, the major patterns of zooplankton distribution and seasonality in the area in relation to the environmental mechanisms behind, and will also appraise the variations that zooplankton might be experiencing under the current global threat of climate change.

The Physical Framework for Zooplankton

The Mediterranean Sea is located in the temperate zone of the Northern Hemisphere in a relatively narrow band of latitudes (30º to 45º N) (Fig. 11.1). This implies a certain latitudinal gradient but, essentially, a marked seasonal cycle. In the western basin, the surface temperature ranges from 12 to 13 °C in winter to 26 °C in summer, while in the eastern basin the surface temperature is approximately 16–17 °C in winter and 27 °C in summer. The deep Mediterranean waters (from 250 m to maximum depth) are very homogeneous and well oxygenated, with a temperature of about 12.8 °C and a salinity of about 38.2 (Durrieu de Madron et al. 2011).

The Mediterranean is a deep basin with typically narrow continental shelves, which account for less than 20 % of the total sea surface. Within the NW Mediterranean, however, some relatively wide continental shelves are found near the main river mouths (Gulf of Lions and Ebro shelf). Over most of the Mediterranean Sea annual evaporation exceeds rainfall and river runoff, so on average it behaves as a concentration basin (Lacombe et al. 1981; Hopkins 1985). As a result of the net nutrient export, the Mediterranean is globally considered as oligotrophic. As a whole, the biological production decreases from north to south and west to east and is inversely related to the increase in temperature and salinity (Béthoux et al. 1992; Siokou-Frangou et al. 2010). However, the complex coastline and bathymetry of the Mediterranean basin, added to a strong seasonality, circulation patterns and river runoff lead to a high environmental

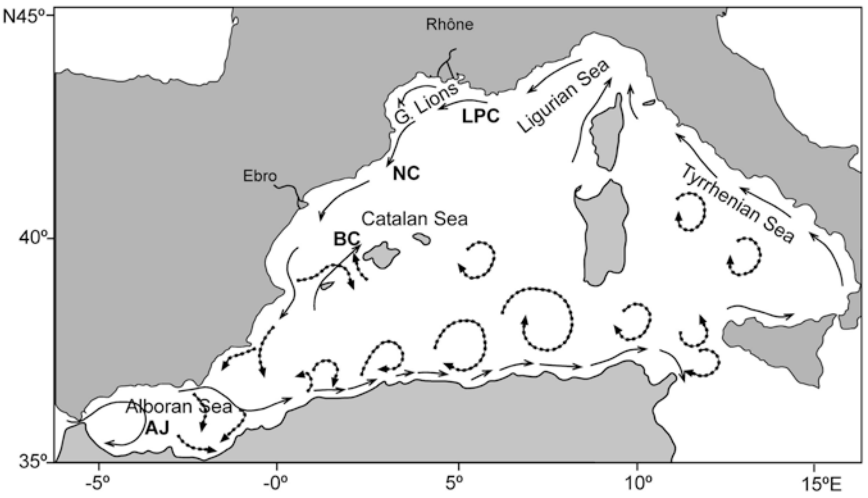

Fig. 11.1 Surface circulation of the western Mediterranean Sea (Redrawn from Millot and Taupier-Letage 2005). Acronyms: *LPC* Liguro-Provençal Current, *NC* Northern Current, *BC* Balearic Current, *AJ* Atlantic Jet

diversity at both regional and local scales, which may enhance production. The existence of these mechanisms would explain the moderate levels of primary production recorded, especially in the western basin, which sustain large fisheries and marine mammals communities (Estrada 1996; Coll et al. 2010).

The variety of habitats in the Mediterranean, together with a succession of colonization events, has shaped a remarkable diversity of species (Bianchi and Morri 2000). The latitudinal and longitudinal temperature gradients determine the distribution of the species. Thus, the species of subtropical origin are mainly found in the eastern basin and southern Mediterranean, where water temperature is higher than average. Cold-temperate species inhabit the northern areas (Gulf of Lions, Ligurian Sea, northern Adriatic) where water temperature is colder. Although the Mediterranean only represents 0.82 % in surface and 0.32 % in volume of the world's oceans, the Mediterranean Sea holds 4–18 % of all known marine species and has a high level of endemism (Bianchi and Morri 2000; Coll et al. 2010).

The general circulation of the Mediterranean is thermohaline and current patterns are cyclonic, adapted to the shape of the continental slopes (Millot 1999, 2005) (Fig. 11.1). The input flow of Atlantic Waters from the ocean follows the northern African coast. This current, and its geostrophic adjustment, are responsible for the existence of a strong thermohaline front (Tintoré et al. 1988; Prieur and Sournia 1994). However, part of this becomes unstable and forms a series of anticyclonic eddies (Millot 1985, 2005), which can be either trapped by the topography of the Alboran Sea or freely move around the Algerian basin and reach the Balearic Islands. The Balearic Islands can be considered the transitional region between the two main western Mediterranean subbasins: the Liguro-Provençal and the Algerian. Part of the Atlantic water flows across the Balearic channels forming the Balearic Current that follows the northern side of the Balearic Islands to the west coast of Corsica (Hopkins 1985; García et al. 1994). A surface front, which is not deeper than 200 m, associated with the Balearic Current, separates recent Atlantic water brought by the current from the resident waters of the centre of the northern basin (Salat 1995). The Balearic Current displays high variability, mainly driven by the fluctuations on the input from the Algerian basin through the Balearic channels (e.g. López-Jurado et al. 1995; Pinot et al. 2002; Millot 2005).

On the eastern side of the Ligurian basin the Atlantic water flow from the Balearic basin joins that from the Tyrrhenian Sea (Astraldi and Gasparini 1992) forming the Northern Current, which flows from the Ligurian to the Catalan Sea along the continental slope, adapted to the bathymetry and contouring the NW basin cyclonically (e.g. Allain 1960; Béthoux et al. 1988). Associated to the Northern Current there is a marked shelf-slope front, detectable down to a depth of around 400 m, again separating the relatively low salinity Atlantic water from the more saline open sea waters (Font et al. 1988). This front is strengthened by a surplus of buoyancy due to the local riverine runoff on the coastal side and by the strong evaporation due to the northern winds on the opposite side (Salat and Font 1987). The Northern Current has significant mesoscale activity, which leads to intense meanders, filaments and eddies that can develop and propagate along the Northern Current pathway (Millot 1990; Sammari et al. 1995; Flexas et al. 2002).

Driving Mechanisms for Plankton Production

The plankton productivity in the NW Mediterranean is influenced by a variety of physical factors, acting at both local and regional scales, whose effect in most cases depends on the seasonal cycle. The Mediterranean climate is characterized by a clear seasonal forcing in irradiance which, although subject to considerable interannual variability, because of variable cloud cover, leads to highly reproducible seasonal changes in surface temperature (Duarte et al. 1999). During the year, the upper layer of the water column, containing the photic zone, shifts between an interval of well-mixed water and a strongly stratified one. Winter cooling produces a breakdown of the thermocline and the vertical mixing bring nutrients from deep waters to the photic zone. The subsequent thermocline development in spring, due to increasing solar heating, prevents vertical motion, and then nutrient supply to the surface is interrupted. This cycle is common everywhere in mid-latitudes, but in the NW Mediterranean the stratification period is rather long, and the winter convection may reach the deepest layers (Lacombe et al. 1981). The alternation of stratified and mixing periods confers strong seasonality to primary production (Estrada et al. 1985).

The northern continental shelves (Gulf of Lions in the NW Mediterranean, but also the Northern Adriatic Sea and the Northern Aegean in the central and eastern sectors) are areas of intense vertical mixing and dense water formation in winter due to the strong and persistent continental winds (MEDOC Group 1970; Roether et al. 1996; Schott et al. 1996). The geographical area centered around 42°N 5°E receives the maximum wind stress (Reiter 1975; Jansá 1987) and is involved in deep convection during winter (Prieur et al. 1983). Fluctuations in the intensity of this phenomenon have been related to interannual variations in primary production, partly because stronger mixing would incorporate deeper and richer waters and partly because deep water spreading would occur over a larger area (Estrada 1996). These northwesterly winds are also responsible of a marked surface thermal front perpendicular to the coast, between 41° and 42° N, clearly identifiable in satellite images (López García et al. 1994).

Nevertheless, the stratified period is far from being as oligotrophic as often accepted. During that period, riverine runoff waters may spread over wide areas, due to the stratification, and can supply nutrients to the surface (Blanc et al. 1969; Ribera d'Alcalà et al. 2004). Although the contribution of this source to the total primary productivity is moderate (ca. 10–20 %, Salat et al. 2002) these freshwater inputs are very relevant because they help to locally maintain surface planktonic production in summer, and in addition they play a major role in balancing the water budget with the Atlantic. Continental runoff waters, mostly from the northern rivers, the Rhône and the Ebro, account for around 70 % of the total fresh water input into the western basin (Béthoux 1979).

There are other relevant mechanisms that enhance the productivity in the NW Mediterranean region that are not related to the water column structure. They are associated with the circulation and its mesoscale activity. Sills, changes in the slope orientation, canyons and some relatively shallow seamounts interact with the currents creating upward vertical components at locations that are typically upstream from these topographic features (Alvarez et al. 1996; Palanques et al. 2005). Current-frontal systems, like those of the Atlantic inflow in the Alboran Sea, or the Northern Current in the NW Mediterranean, show high mesoscale activity playing a decisive role in exchange processes between shelf and oceanic waters associated with instabilities or oscillations of the current (Wang et al. 1988; Millot and Taupier-Letage 2005). The generation of mesoscale eddies by frontal instabilities (Flexas et al. 2002; Taupier-Letage et al. 2003; Rubio et al. 2005) promotes vertical motions which support phytoplankton growth (Boucher et al. 1987; Prieur and Sournia 1994; Fielding et al. 2001) and also contribute to enhancing the productivity at the deep chlorophyll maximum level (Estrada 1985; Sabatés et al. 2004). Furthermore, these convergent fronts have been shown to be zones of accumulation of marine snow particles, possibly due to physical accumulation and coagulation of marine production (Gorsky et al. 2002; Stemmann et al. 2008).

Seasonal Patterns

The distinct seasonality of the climate and hydrographic features in the Mediterranean is a major factor determining the structure and functioning of the whole pelagic ecosystem (Duarte et al. 1999), and obviously influence the composition and succession patterns of the zooplankton assemblages. The long tradition on zooplankton research in the Mediterranean has provided an excellent collection of seasonal studies available in the literature, most of them mainly concerning the coastal or neritic areas; in occasions those studies besides the concomitant characterization of the physico-chemical features of the water column, also benefit from simultaneous information on phytoplankton and ciliate abundance and composition (e.g. Ribera d'Alcalà et al. 2004). These lower trophic levels are presumably relevant drivers of seasonality patterns due to their condition of major food items for zooplankton (Saiz and Calbet 2011) and fish larvae (Rossi et al. 2006).

Although located in temperate latitudes, the seasonality in the western Mediterranean differs from the typical cycles illustrated in books for the North Atlantic, in which a spring and autumn bloom drive zooplankton production (Kiørboe 1993). This dissimilarity transmits also into the upper trophic levels, as evidenced by the fact that in the Mediterranean different fish species spawn in succession over the entire year, so the larval peak production is not coupled to the seasonal late winter-early spring production

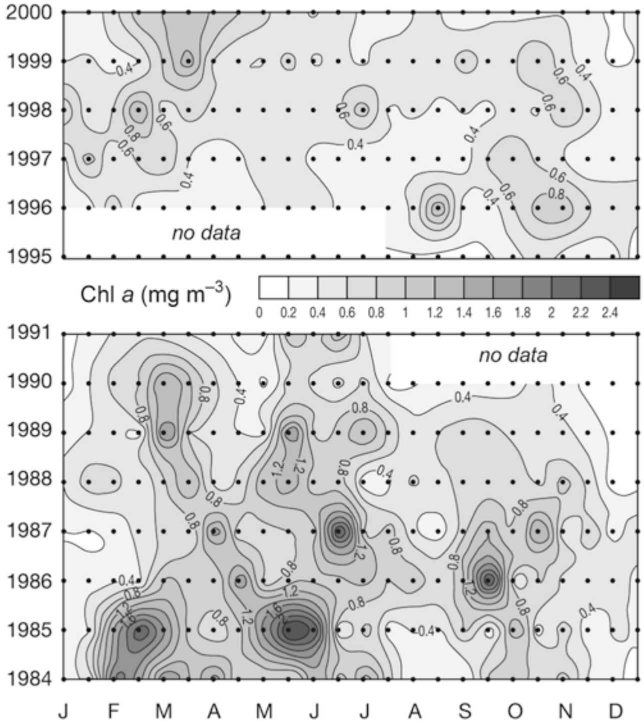

Fig. 11.2 Seasonal and interannual variability of chlorophyll *a* concentration (mg m^{-3}), averaged over the 0–60 m layer, at the station Marechiara off Naples for the period 1984–1991 and 1995–2000 (From Ribera d'Alcalà et al. (2004). With permission of the publisher)

bloom, as the match-mismatch hypothesis postulates (Cushing 1990).

In the Mediterranean water column seasonal stratification typically starts around April, and it is not completely destroyed until late in the year (November–December; Salat 1996; Ribera d'Alcalà et al. 2004). As mentioned before, during the stratified period the events of riverine runoff result in the formation of shallow haloclines spreading over wide areas, with the associated nutrient input, and can boost surface planktonic production over the wide areas they extend (Blanc et al. 1969; Ribera d'Alcalà et al. 2004).

The blooming of phytoplankton in late winter, prior to the thermal stratification of the water column, is a widespread event in the Mediterranean (see Duarte et al. 1999; Ribera d'Alcalà et al. 2004; D'Ortenzio and Ribera D'Alcalà 2009, and references therein) (Fig. 11.2). This winter chlorophyll peak occurs around February–March, and seems to be related to the seasonal presence in January–February of a high-pressure system in the Azores, providing stable water column and clear skies that permit the growth of phytoplankton. This late winter bloom is followed, at least in the northwestern sector and not so frequently in other areas, by a spring-summer bloom (May), confined to the surface layers due to the strong stratification. A third peak in autumn (October–November) is also frequent, that extends, like the winter one, over a deeper mixed layer. High interannual variability can be found in the timing and extent of the seasonal peaks, and in some years one of the peaks might be absent (Ribera d'Alcalà et al. 2004). Regarding ciliates, seasonal patterns are not always so clear and may differ among sites, for instance higher standing stocks are reported in winter in Blanes Bay (Spain) (Vaqué et al. 1997), and Villefranche-sur-Mer (France) (Bernard and Rassoulzadegan 1994), whereas at Naples (Italy) the minimal biomass is found in winter (Ribera d'Alcalà et al. 2004).

To truthfully depict the patterns of variation of zooplankton abundance, biomass and composition through the seasonal cycle, multiannual time-series have been also an essential instrument because allow to study recurrent patterns in zooplankton structure and succession (e.g. Mazzocchi and Ribera d'Alcalà 1995). Some significant differences can be found in the timing and peak abundances of zooplankton in the different areas of the Mediterranean, especially at the species level (e.g. Ribera d'Alcalà et al. 2004; Mazzocchi et al. 2007). Here we will illustrate the most common features of the seasonality scenario for the zooplankton in the coastal/neritic area of the western Mediterranean (Fig. 11.3), and will refer the reader to the original works for more detailed information. The knowledge on the seasonality of the zooplankton of open, deep waters in the Mediterranean basin is still scarce and major efforts are needed.

Many studies in the western Mediterranean describe typically 2–3 seasonal peaks of zooplankton (late winter or spring and late summer) over the year (Champalbert 1996; Calbet et al. 2001). As in the case of phytoplankton, the occurrence, amplitude and timing of peaks are quite variable among years (García-Comas et al. 2011). For instance Fernández de Puelles et al. (2007) reported that the standing stocks of zooplankton were highest in late winter-spring at the Mallorca channel, whereas in other studies, however, the winter standing stocks show the minimum values (e.g. Ribera d'Alcalà et al. 2004; Skovgaard and Saiz 2006). The general pattern followed by the mesozooplankton standing stocks seems to be essentially driven by the dynamics of the copepod community, which on an annual basis dominates the mesozooplankton (ca. 55–65 % of the abundance) and that during winter and spring achieve much higher contributions. At the species level, there is quite a lot of regularity in the seasonal patterns, and a seasonal succession of species assemblages, that appear recurrent and persistent every year, have been described (Mazzocchi and Ribera d'Alcalà 1995; Mazzocchi et al. 2011). Four key species (*Acartia clausi*, *Centropages typicus*, *Paracalanus parvus*, and *Temora stylifera*) seem to be the most abundant ones in the coastal/neritic Mediterranean, accounting for a large share of total copepod abundance from spring to autumn. They display a common succession pattern throughout the Mediterranean, although variations in the timing can be found among sites. First, *Acartia clausi* and *Centropages typicus* peak in

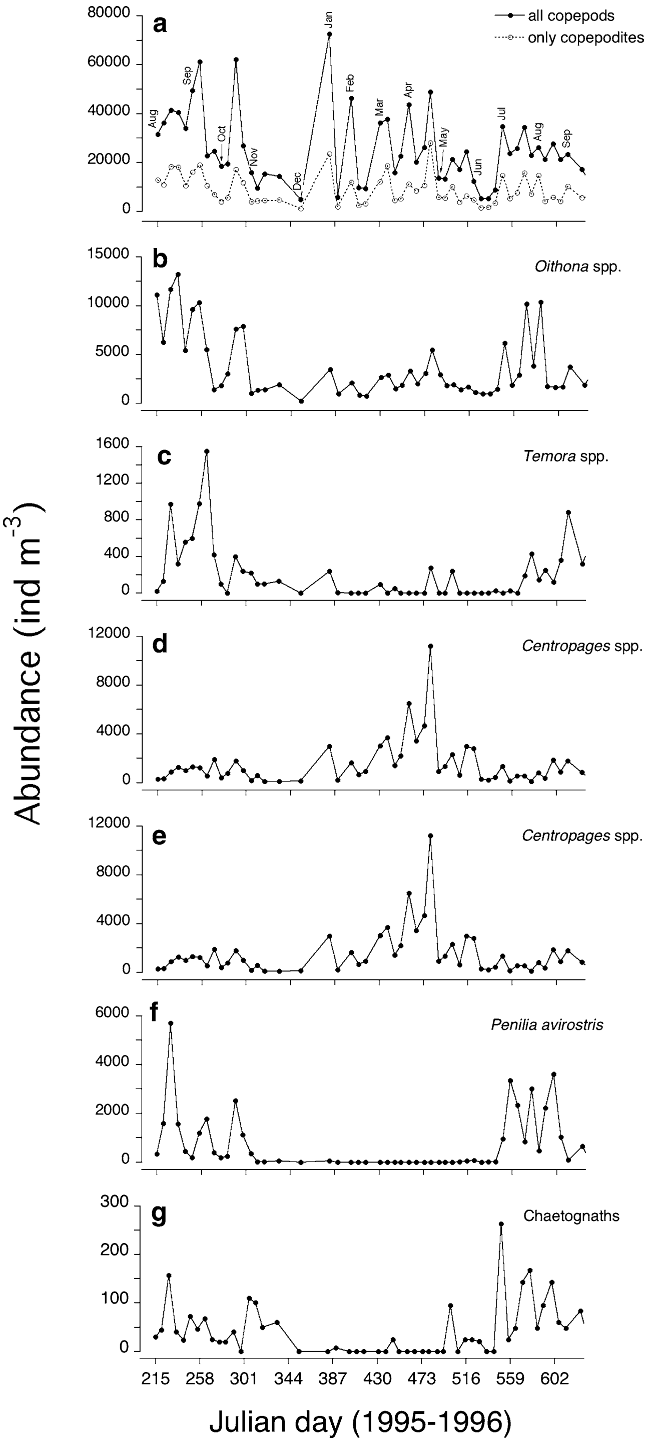

Fig. 11.3 Seasonal variations of several zooplankton groups off Blanes (Catalunya, Spain) (Redrawn and modified from Calbet et al. 2001)

spring-early summer; then *Paracalanus parvus* is important in summer and early autumn, and finally *Temora stylifera* is relevant in later summer-autumn. These populations are multivoltine, and according to Razouls (1974) *C. typicus* and *T. stylifera* have, respectively 7 and 5–6 generations per year in the neritic ecosystem of the Gulf of Lions. The genus *Clausocalanus* and *Oithona*, two of the most abundant genus in all oceans, are also very well represented in the Mediterranean, and a temporal succession of species within the genera has been observed, suggesting ecological differentiation among the congener species (Mazzocchi and Ribera d'Alcalà 1995). It is also worth noticing that the use of large mesh sizes in plankton nets (e.g. 200, 330 μm) has omitted from most studies a very relevant component of the zooplankton community, the smaller forms of metazoan zooplankton, namely copepod nauplii and young copepodites, and adults of small species as well (Calbet et al. 2001). This bias has an obvious influence on our present view of the seasonal patterns of the zooplankton assemblages. In terms of abundance and biovolume, on an annual basis the <200 μm fraction (mainly composed of copepod nauplii) comprised ca. 80 and 21 % of the total community, respectively (Calbet et al. 2001). From a functional point of view, the importance of this size fraction is very relevant due to the inverse relationship between body size and metabolic rates, and their grazing pressure on phytoplankton seems to be similar to the one exerted by the larger (>200 μm) zooplankton (Almeda et al. 2011). When such size fraction is taken into account, the small-sized copepod genus are much more prevalent, in particular *Oithona*, *Oncaea* and *Microsetella* (Calbet et al. 2001; Zervoudaki et al. 2006).

Cladocerans are also a very characteristic and relevant component of neritic zooplankton in the Mediterranean (Della Croce 1964; Vives 1966; Alcaraz 1970; Fernández de Puelles and Molinero 2008; Mazzocchi et al. 2011). They account for ca. 10–20 % of the mesozooplankton standing stock on an annual basis, and are mainly present in surface waters in late spring and, especially, in summer, when can be the major group in the mesozooplankton (Vives 1966; Alcaraz 1970; Fernández de Puelles and Molinero 2008; Mazzocchi et al. 2011). Due to their parthogenetic reproduction and the production of resting eggs, they are characterized by high population bursts (Egloff et al. 1997). The most abundant species is *Penilia avirostris*, which blooms in very stratified waters and can achieve very high numbers (Casanova 1965; Vives 1966; Alcaraz 1970; Thiriot 1972–1973; Calbet et al. 2002a; Atienza et al. 2006, 2008); this cosmopolitan filter feeder can graze efficiently on small flagellates (Atienza et al. 2006) and therefore is well adapted to oligotrophic conditions. As with copepods, seasonal peaks of abundance of *Penilia avirostris* also show some variation in timing throughout the Mediterranean: e.g. June–July in waters off Castellón, Spain (Vives 1966), July–August in Barcelona, Spain (Atienza et al. 2008), and September–October in Banyuls-sur-Mer, France (Thiriot 1972–1973). The other cladoceran species typically appear a bit earlier (Della Croce 1964;

Vives 1966; Alcaraz 1970; Calbet et al. 2001; Fernández de Puelles and Molinero 2008; Mazzocchi et al. 2011). With similar contribution to that of the cladocerans, appendicularians (ca. 10–17 %) are also an important component of neritic zooplankton (Calbet et al. 2001; Ribera d'Alcalà et al. 2004; Fernández de Puelles and Molinero 2008); although present throughout the year, Oikopleuridae seem to be more abundant in summer, whereas the Fritillaria are comparatively more important in autumn (Vives 1966; Fenaux 1968).

Other groups are less well represented in coastal and neritic waters, but also present their characteristic seasonal patterns (Champalbert 1996; Fernández de Puelles et al. 2007). Meroplanktonic larvae can occasionally be very important in coastal and confined areas, and peaks of occurrence are linked to the reproductive cycle of their benthic stages at different times of the year (Vives 1966; Calbet et al. 2001; Almeda et al. 2011). Doliolids are more abundant during the second half of the year (Vives 1966; Braconnot 1971), frequently in coincidence with periods when copepods are scarce and cladocerans (*Penilia avirostris*) are abundant (Ménard et al. 1997). The establishment of shallow haloclines in early summer and late autumn, as a consequence of storms and seasonal river swelling, and the occurrence of periods of calm weather (low winds) seem to favor the seasonal blooming of doliolids (Ménard et al. 1997); likely, these processes might be also relevant for other groups blooming in those periods. Chaetognaths are typically very scarce in winter and the maximum densities are found in August and September, in special for *Sagitta inflata*, the most abundant species in the northwestern Mediterranean (Vives 1966; Andréu 1990). Thaliacea are more common in late winter/early spring associated to the first primary production peak in the Mediterranean (Furnestin 1963; Vives 1966; Ménard et al. 1994). With regard to the Cnidaria, a seasonal maximum peak has been described for medusa and siphonophores in spring and early summer (Goy and Thiriot 1976; Ianora and Scotto di Carlo 1981; Gili et al. 1987; Gamulin and Kršinic 1993; Batistić et al. 2007). During this period of maximum abundance, the coastal communities are dominated by two species, the siphonophore *Muggiaea atlantica* and the medusa *Aglaura hemistoma,* whereas in the open sea, but with much lower abundance, dominate *Chelophyes appendiculata* and *Persa incolorata* (Berhaut 1969; Goy 1987); less abundant species that occur regularly throughout the year may exhibit minor peaks in autumn (Albertini-Berhaut 1971; Gili et al. 1987; Dallot et al. 1988; Andersen et al. 2001b). Not only local productivity peaks (Gili et al. 1988) but also physical factors favoring aggregation can be involved in such seasonal patterns (Graham et al. 2001).

Fish larvae also exhibit a pronounced seasonal variability in both abundance and number of species (Sabatés et al. 2007a), in obvious relation to the spawning cycles of the adults. Most neritic fish species (e.g. Sparidae, Labridae, Blennidae, Mullidae, Serranidae), as well as large migratory tuna, spawn during spring and summer; in winter, when species of relatively cold waters reproduce, the specific composition varies substantially and is less diverse, and larvae of Gadidae and Pleuronectidae are commonly found (Sabatés et al. 2007a). The most abundant commercial fish species, sardine and anchovy, have non-overlapping spawning periods, autumn-winter and spring-summer respectively, and are very well adapted to the productivity mechanisms characteristic of their respective spawning seasons; that is, vertical mixing on the shelf in winter and spreading of continental runoff at surface in spring-summer (Palomera et al. 2007). Their eggs and larvae dominate the ichthyoplanktonic fraction in neritic areas of the Mediterranean during these periods.

As a final remark, it is important to notice that although in the Mediterranean the adverse period is not too extreme compared to higher latitudes, still a certain number of species of zooplankton are not found in the water column year around, or only in very low numbers. The existence of resting stages that allow such species to spend the adverse period in the benthos is probably more common than usually acknowledged (Boero et al. 1996; Marcus and Boero 1998). Such life strategy is very apparent for some groups or species, like for instance the Cnidaria in which the polyps may become encysted as resting hydrorhizae and will recruit at the next favorable season (Boero and Bouillon 1993), or the cladocerans (Egloff et al. 1997). For copepods, the existence of resting and diapause eggs that may reside in the sediment of coastal and neritic environments is well known (Marcus 1996), but the number of studies on this subject in the Mediterranean is very limited (e.g. Ianora and Santella 1991; Marcus and Boero 1998; Belmonte and Pati 2007) and it is difficult to provide an assessment on their role in the population dynamics.

Vertical Structure

Different spatial and temporal scales frame the patterns of vertical distribution of zooplankton, as the result of the interaction of the behavior of the organisms (i.e. diel rhythms of vertical ascend at night and descend during the day, ontogenetic and seasonal migrations) with the physical forcing and physico-chemical-biological vertical structuring of the water column. These phenomena and patterns are common to all oceans and seas, but the marked seasonality in the Mediterranean, with alternating periods of mixing and stratification, strongly affects the vertical distribution of zooplanktonic organisms throughout the year cycle and shows some peculiarities worth mentioning here.

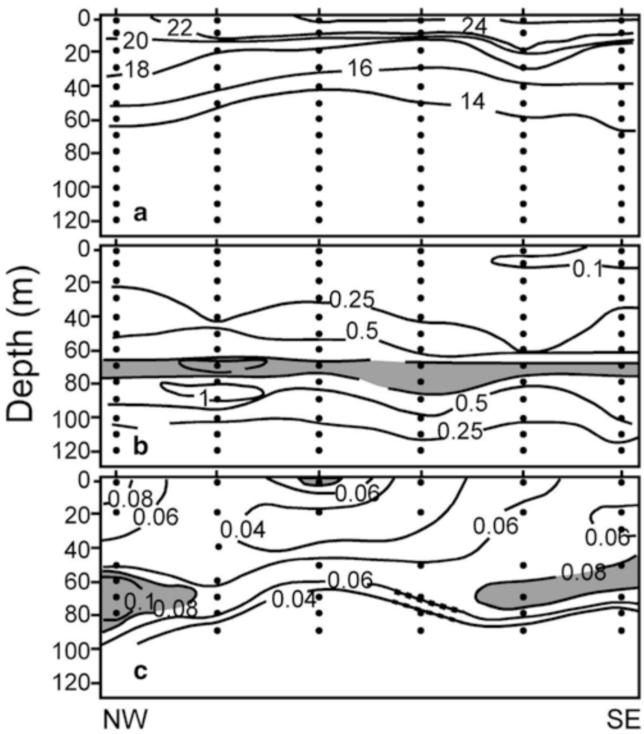

Fig. 11.4 Vertical profiles of (**a**) temperature (°C), (**b**) chlorophyll *a* concentration (µg chl *a* L^{-1}) and (**c**) mesozooplankton biomass (µg-at Nzoo L^{-1}) along a transect from Barcelona through the channel between Mallorca and Menorca, in the Catalan Sea, in summer. Concentrations >1 µg chl *a* L^{-1} and >0.08 µg-at Nzoo L^{-1}, respectively, are highlighted (Redrawn and modified from Alcaraz 1988)

Regarding the epipelagic realm, one of the major features of the vertical structure of the water column in the western Mediterranean is the stratification of the upper water column over a large portion of the year, resulting in the formation of a deep chlorophyll maximum which extends over large areas (Estrada et al. 1993) (Fig. 11.4). When the heat balance overrides vertical mixing, a thermocline starts to develop and deepens during summer down to deeper waters. During that period, nutrients are very scarce in the surface layers, and a deep chlorophyll maximum (DCM) develops associated with the thermocline or just below it, at depths where light is still sufficient for photosynthesis and nutrient inputs from the nutricline can warrant certain phytoplankton growth. It is important to consider that in the western Mediterranean the DCM is not only the result of a higher chlorophyll cell content at low light intensities, but can be the result of a cell maximum as well. The DCM can also correspond to a peak of primary production, although the major center of phytoplankton growth is in the upper layers (Estrada et al. 1985). In such an oligotrophic environment like the Mediterranean, especially during the stratification season, the presence of the DCM could be considered as an "oasis" to sustain secondary production. For this reason, the presence of the DCM during the long stratification period has relevant implications for the functioning and structuring of the pelagic food web in the Mediterranean. In addition the DCM seems to be also rich on ciliates, mainly the heterotrophic ones (Dolan and Marrasé 1995; Calbet et al. 2002a); ciliates are known as a preferred prey for the dominant zooplankter in marine systems, copepods (Saiz and Calbet 2011).

The vertical distribution of epipelagic mesozooplankton in the Mediterranean during summer is characterized by the presence of a zooplankton maximum at approximately the same depths that the DCM during the daytime (70–90 m), whereas at night, following the general pattern of vertical migration observed all over the world, zooplankton ascends to upper layers (25–50 m; Alcaraz 1985) (Fig. 11.4). As pointed out, the fact that epipelagic zooplankton remains during the day at the depth of the DCM and ascend at dusk to upper waters have important ecological implications, since zooplankton may feed not only at night but also during the day while at the DCM (Saiz and Alcaraz 1990). For this reason, the ascent of copepods at night during summer results in an upward flux of recycled nutrients (via zooplankton excretion) to the nutrient limited surface waters. Such recycling would, therefore counteract the loss of nutrients due to the downward vertical flux of particulated organic matter, and would help to sustain primary production in the surface waters. Estimates suggest that the contribution of regenerated nutrients to the phytoplankton requirements can increase 1.5 times due to the night ascend of zooplankton to the surface waters (Alcaraz 1988; Alcaraz et al. 2007). High densities of nauplii and copepodite stages of copepods have been reported associated to the DCM levels (Sabatés et al. 2007b, 2008; Olivar et al. 2010). In turn, larvae of some fish species, such as anchovy, have been found at the DCM during the daylight hours (the feeding period) benefiting from food aggregations at this level, ascending to the surface at night (Olivar et al. 2001; Sabatés et al. 2008) (Fig. 11.5).

This overlapping of the vertical distribution of the bulk of the epipelagic zooplankton biomass and the DCM seems to be a common feature that extends all over the Mediterranean during the stratification period (e.g. see Fig. 4 in Nowaczyk et al. 2011), although frequent exceptions, for instance of bimodal or multimodal distribution can also be found (Andersen et al. 2001b). At the species level such exceptions are not rare and should be interpreted in tight relation to the micro and fine scale structure of the water column and particular behavioral components (e.g. affinities to determined temperature and/or salinity, presence of potential prey or predators), as examples of niche segregation (e.g. vertical segregation of congeneric species of the genus *Clausocalanus*, Peralba and Mazzocchi 2004; see also a similar case for the eastern Mediterranean in Fragopoulu et al. 2001). Although waters above the DCM are nutrient poor, the maximum of phytoplankton productivity during the stratification period is typically well above the DCM, and other potential prey for

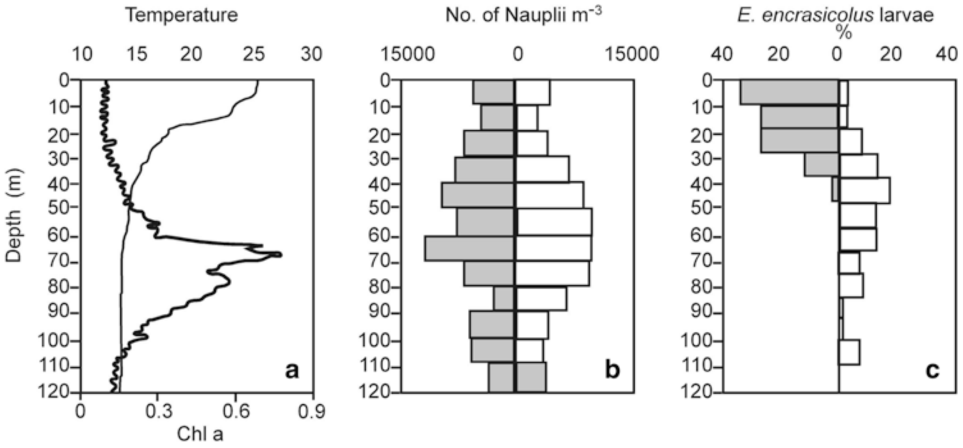

Fig. 11.5 Vertical distribution of (**a**) temperature (°C) and chlorophyll *a* (μg chl a L^{-1}), (**b**) nauplii stages of copepods, and (**c**) *Engraulis encrasicolus* larvae (> 8 mm SL) in the Catalan Sea (July 2003). *White* and *grey* bars are respectively day and night samples (Redrawn from Sabatés et al. 2008)

zooplankton (i.e. mixotrophic ciliates, Dolan and Marrasé 1995) could be more abundant above the DCM, therefore potentially providing a food supply for the zooplankters inhabiting those waters. Unfortunately, there is a lack of fine scale studies on the vertical distribution of zooplankton in the Mediterranean coupled to the distribution of potential prey/predators and hydrographic singularities that could provide further insights into the factors driving the vertical distribution of different zooplankton. At the smallest scales, there are evidences that zooplankton are capable to find and make profit from such patchiness in food distribution (Tiselius 1992; Saiz et al. 1993).

During the winter mixing period, in absence of strong vertical gradients and high algal biomass and primary productivity (Estrada et al. 1999; Morán and Estrada 2005), the vertical distribution of zooplankton abundance and biomass is more homogeneous along the water column (Vives 1966; Alcaraz et al. 2007), and the depth-dependent differentiation of zooplankton assemblages due vertical habitat partitioning observed in summer disappears (Ramfos et al. 2006). In this situation it has been reported that different species of the genus *Clausocalanus* did not show preferential depths distribution and were less segregated, presenting a more homogenous distribution (Peralba and Mazzocchi 2004). Nauplii and copepodite stages of copepods show a wide distribution along the first 100 m of the water column (Sabatés et al. 2007a; Olivar et al. 2010). Vertical distribution of sardine larvae, *Sardina pilchardus*, one the most abundant species during winter, also shows a wide distribution, in coincidence with their main food (Olivar et al. 2001; Sabatés 2004; Morote et al. 2010). Additionally, there seems to be seasonal variations in the intensity and extent of the diel vertical migration of zooplankton, which appears weaker from late summer to winter (Hure 1961).

Nowadays the study of the mesopelagic fauna has renewed a growing interest due to the acknowledge of the relevant role the mesopelagic zone has as a "filter" of the particulate organic matter between the epipelagial and the deep-sea and seafloor, and their significant contribution to export fluxes (Steinberg et al. 2000; Robinson et al. 2010). The western Mediterranean has a long tradition on studies of the deep zooplankton, including macroplankton and micronekton, although the degree of knowledge varies with the geographical area (i.e. Hure and Scotto di Carlo 1974; Vives 1978; Scotto di Carlo et al. 1984; Andersen and Sardou 1992; Andersen et al. 1992, 1998), and references therein). More detailed information has been gathered since the wide availability of multisampling nets since the early 1990s. There appear to be typically three zooplankton strata between 250 and 1,000 m depth during daytime, with ranges between 250–350, 400–550 and 700–800 m, inhabited with characteristic species assemblages with particular trophic relationships and life strategies (Gasser et al. 1998; Yoon et al. 2007). Different behavioral patterns can typically be found among the zooplankton inhabiting those deep waters (composed mainly of large copepods, but also accompanied by macroplankton and microneckton, e.g. euphausiids, pteropods, siphonophores and amphipods), ranging from strong diel migrators to weak or non-migrant species (Andersen and Sardou 1992; Andersen et al. 1998). The fish larvae of Myctophidae are another very relevant component of this community (e.g. Sabatés and Masó 1990; García Lafuente et al. 1998). This ecologically highly successful group of mesopelagic vertical migrators (Olivar et al. 2012) very likely plays a very significant role in the vertical carbon fluxes in the world oceans (Pakhomov et al. 1996), and exhibits high morphological diversity as an a strategy to optimize the utilization of trophic resources in the open-ocean habitat (Sabatés and Saiz 2000; Sabatés et al. 2003). It is also

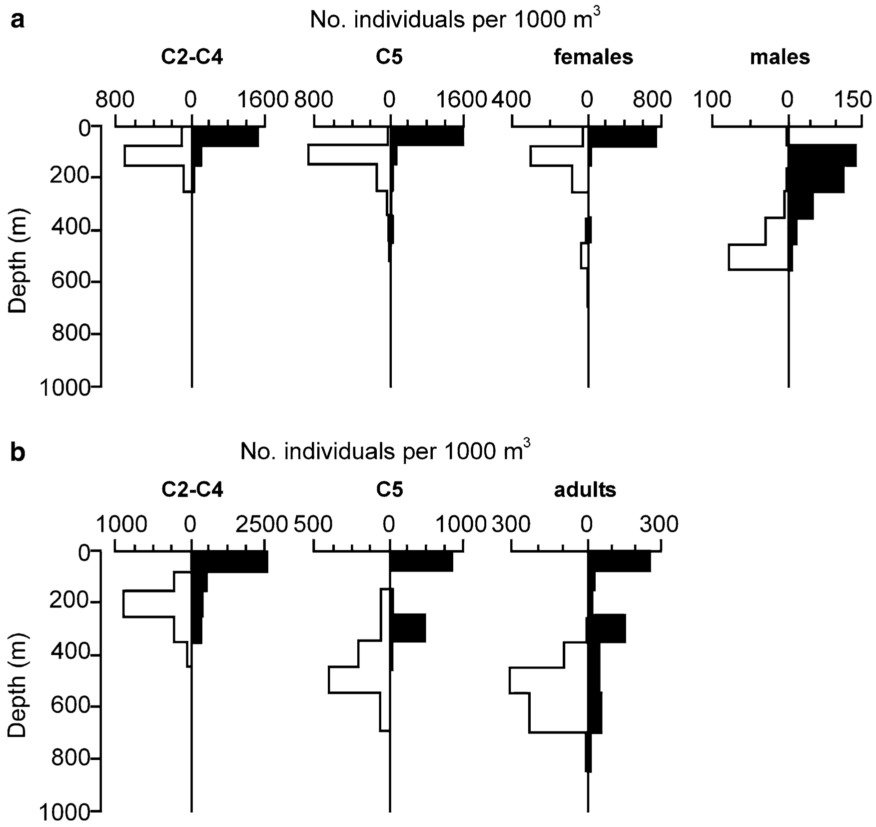

Fig. 11.6 Day (*white bars*) and night (*black bars*) vertical distribution of two mesopelagic copepod species ((**a**) *Neocalanus gracilis*, (**b**) *Euchaeta acuta*) in the northwestern Mediterranean, showing ontogenetic segregation (Redrawn and modified from Andersen et al. 2001a)

worth noticing that most studies dealing with mesopelagic zooplankton in the Mediterranean have employed very coarse mesh nets (i.e. 500 µm), but the very few studies with fine nets (50 µm) carried out in the eastern Mediterranean suggest that small copepods, especially from the poecilostomatoid genus *Oncaea*, can be also a significant and neglected component of those communities (Böttger-Schnack 1994).

Common patterns of ontogenetic vertical segregation of zooplankton (in which the younger stages inhabit less deep waters; i.e. Williams and Conway 1984; Uye et al. 1990), and of seasonal migration (in which the late developmental stages of zooplankton go though the unfavorable season in a resting or diapause state; overwintering: Conover and Huntley 1991; Hagen 1999; oversummering: Wang et al. 2003) found in other seas can also be found in the Mediterranean, although the number of studies dealing with this issue is also scarce (Fig. 11.6). (Andersen et al. 2001a) provides fine examples of the ontogenetic segregation of the day time vertical distribution of the copepods *Neocalanus gracilis*, *Pleuromamma abdominalis* and *Euchaeta acuta* in the Ligurian Sea at the DYFAMED station; at nighttime there seems to be overlapping, although vey likely a finer vertical resolution in the upper 100 m would show also some degree of segregation among stages. Regarding examples of seasonal migration and overwintering/oversummering strategies in the western Mediterranean, there are several reports of downward seasonal migration of large-sized copepods like *Eucalanus monachus*, *Eucalanus hyalinus* and *Calanus helgolandicus* (Hure and Scotto di Carlo 1974; Vives 1978; Gasser et al. 1998; Andersen et al. 2004). Typically these organisms descend to deeper waters (400–900 m) in summer and autumn, and rise to shallower waters in winter spring (Andersen et al. 2004). Such oversummering life strategy is likely related to the avoidance of the less productive season and the warmer surface waters during summer and autumn, and to exploit the peak of productivity in late winter-spring. In comparison with the Atlantic, the triggering of the seasonal descend seems to occur earlier in the year in the Mediterranean (Williams and Conway 1984; Andersen et al. 2001a). Gasser et al. (1998) reported high abundances of *Calanus helgolandicus* CV, with a large oil sac filling out most of their body in the deep waters (700–800 m) of the Ligurian Sea in June, as a signal of the oversummering stage.

Near-Bottom Zooplanktonic Communities

Although the near-bottom zooplankton dynamics is, in comparison with the pelagic one, much less known, their study has acquired an increasing interest in the last years due to its importance as a hot spot of diversity and to its key role in the trophic web (e.g. Cartes et al. 2010). The initial studies using sledges and dredges have been recently complemented with plankton nets attached to bottom trawls and have evidenced the existence of large swarms of euphausiids and mysids close to the bottom (e.g. Cartes et al. 1994; Cartes 1998). The supra-benthic fauna in those habitats, mainly composed of mysids, euphausiids, amphipods and isopods (Bellan-Santini 1990; Cartes et al. 1994; Macquart-Moulin 1998), seems to be well adapted to the variability generated by re-suspension processes caused by the currents near the bottom. Whereas certain groups like the mysids and the amphipods constitute a permanent component of this bottom-living fauna, others (e.g. euphausiids, isopods) perform vertical migrations and their dynamics is more linked to processes occurring in the water column, therefore playing an important role in the benthic-pelagic coupling, Macquart-Moulin 1998; Cartes et al. 2010). Under stratification conditions, in summer and autumn, swarms of the adult stages of the dominant macroplankton species can be found close to the bottom off the shelfbreak slope, likely in relation to the seasonally high abundance of their prey (e.g. the oversummering copepod *Calanus helgolandicus*) in those habitats (Cartes 1998; Cartes et al. 2010).

The study of planktonic organisms collected by sediment traps located near the bottom in the submarine canyons has permitted the discovery of a new deep zooplankton community (Gili et al. 2000). Gelatinous zooplankton, mainly jellies, Copepoda, Holothuria and Polycheta are the dominant groups in the traps and their abundance depend on both re-suspension processes near the bottom and the continuous flux of organic matter from the continental shelf, particularly during spring (Gili et al. 1998, 1999; Pagès et al. 2007; Sardá et al. 2009). The specific composition of the deep-sea canyon fauna highlights their relevance, in particular the jelly species, as an endemic component of the Mediterranean plankton (Casanova 1990) representative of relict species from the Thetis Ocean (Gili et al. 2000).

Horizontal Distribution Patterns at the Mesoscale

The spatial patterns of plankton biomass, productivity and species composition exhibit high variability as a result of the interaction, at a hierarchical spectrum of space and time scales, of the biological components with the physical oceanographic processes and environmental singularities. The existence, as a consequence of the environmental forcing, of spatial gradients in the local rate of population increase or decrease results in the development and persistence of biological spatial patterns (patchiness) in the ocean (Mackas et al. 1985). Although the Mediterranean Sea is considered globally an oligotrophic sea, a substantial amount of hydrographic features and biological heterogeneities can be found which, especially in the western basin, facilitate a certain increase in its potential fertility (Estrada 1996). As a result, large differences in the zooplankton communities between the eastern and western basins are evident, and a decrease in zooplankton abundance has been reported in relation to the strong eastward gradient in productivity and primary production (Mazzocchi et al. 1997; Dolan et al. 2002; Siokou-Frangou 2004; Minutoli and Guglielmo 2009). However, besides this basin scale trends, any attempt at ascertaining the major mesoscale spatial pattern in the Mediterranean is not an easy task, because most of the studies are local and synoptic data are scarce, and in addition the comparisons among areas and studies are flawed by the lack of standardized sampling methods and data treatment (Champalbert 1996). Zooplankton abundance largely depend on the size range of the organisms considered (Calbet et al. 2001; Nowaczyk et al. 2011), thus the use of different sampling mesh-size is a difficulty when comparing different zooplankton datasets. Sampling with finer mesh nets than the standard 200 µm, or with large bottles has revealed that biomass and abundance can increase by 2–20 fold (Andersen et al. 2001b; Calbet et al. 2001; Youssara and Gaudy 2001; Alcaraz et al. 2007).

Like in all oceans, a gradient of zooplankton abundance from coastal waters to the open sea is typically observed in the Mediterranean Sea (e.g. Vives et al. 1975; Champalbert 1996; Gaudy and Champalbert 1998), as a consequence of local eutrophication and river runoff. Physical and biological conditions are extremely variable over the shelf and coastal waters, where episodic pulses of production may occur (Denman and Powell 1984); in comparison, the oceanic region is characterized by a more steady production. As a result, mesozooplankton abundance in offshore waters oscillates within a narrow range and reveals lower seasonal variability than in coastal waters (Scotto di Carlo et al. 1984; Fernández de Puelles et al. 2003b); in addition, the changes in the composition of zooplankton assemblages along such environmental gradients must reflect the peculiarities in ecophysiological response and life history traits suitable to cope with the environmental variability (Runge 1988). Changes in copepod productivity have been observed in relation to the associated changes in the biomass and size spectrum of phytoplankton along this gradient (Saiz et al. 1999; Calbet et al. 2002b). In addition, in the northwestern Mediterranean continental runoff waters from the main rivers of the region, the Rhône and the Ebro, play an important role enhancing primary production of the shelf waters (Cruzado and Veláquez 1990; Salat et al. 2002; Diaz et al. 2008). Associated to these low salinity waters, high copepod densities have been recorded in the Gulf of Lions and near the Ebro delta (e.g. Razouls and Kouwenberg 1993; Sabatés et al. 2008) along with an increase in zooplankton biomass and feeding activity in the outflow plume of the Rhône River (Pagano et al. 1993). These rich zooplankton production areas have been reported to be important spawning grounds of anchovy in the northwestern Mediterranean, favoring larval survival as well as the diet and condition of the adults (Palomera et al. 2007; Banaru and Harmelin-Vivien 2009). Furthermore, over the shelf, topographic irregularities can greatly modify circulation producing complex plankton distributions (Alvarez et al. 1996). Hence, submarine canyons at the continental margin of the NW Mediterranean can interact with the Northern Current and modify the general circulation, generating topographically controlled up- and downwellings and affecting the shelf-slope water exchange (Alvarez et al. 1996; Durrieu de Madron et al. 1999; Palanques et al. 2005). All these processes favour high concentrations of zooplankton and fish larvae near the coast (Sabatés et al. 1989; Sabatés and Olivar 1996).

In the western basin, zooplankton abundance as well as the total biomass display a north–south decreasing gradient in relation to the decrease in primary production and increasing temperatures (D'Ortenzio and Ribera D'Alcalà 2009; Nowaczyk et al. 2011). Changes in the composition, phenology and distribution of zooplankton as a consequence of the latitudinal gradient in temperature between the northern and southern Mediterranean are expected, but comparative studies are scarce (Mazzocchi et al. 2007). In the Catalan coast, the northern sector, which is more directly influenced by strong northerly winds, is generally colder than central and southern parts. Thus, a surface thermal front roughly coincides with the limit of frequent northerly winds (López García et al. 1994). This thermal front has been reported to have a significant effect on zooplankton and fish larval distribution (Atienza 2006; Sabatés et al. 2009).

Numerous studies conducted in the western Mediterranean have highlighted the impact of mesoscale structures such as density fronts on the distribution and diversity of zooplankton, enhancing plankton patchiness and activity, and stimulating trophic transfers towards large predators (Boucher et al. 1987; Ibanez and Boucher 1987; Sabatés et al. 1989, 2004; Gorsky et al. 1991; Saiz et al. 1992; Alcaraz et al. 1994, 2007). The Northern Current (Ligurian Sea and Catalan Sea), the Balearic Current (Balearic Sea) and the Almeria–Oran front (Alboran Sea) constitute transitional zones with overall biological production enhanced by high phytoplankton biomass and primary production (Estrada 1985; Ibanez and Boucher 1987; Estrada and Margalef 1988; Prieur and Sournia 1994; Youssara and Gaudy 2001). Secondary producers have been also shown to be influenced by frontal structures in terms of biomass, productivity or specific diversity (Boucher et al. 1987; Gili et al. 1988; Sabatés et al. 1989; Alcaraz et al. 1994; Prieur and Sournia 1994; Seguin et al. 1994; Gaudy and Champalbert 1998; Youssara and Gaudy 2001; Fernández de Puelles et al. 2004). The higher biomass of zooplankton recorded at oceanic fronts is often explained by a physiological response of the organisms to the frontal environment. However, retention or accumulation of organisms at fronts may also depend on the interaction of the cross-frontal circulations with the differential motion of the organisms (sinking, floating and swimming; Owen 1981; Franks 1992).

In the Ligurian Sea several studies have emphasized the high variability of zooplankton populations linked to geostrophic frontal system (e.g. Boucher et al. 1987; Sournia et al. 1990; Pinca and Dallot 1995; Licandro and Ibanez 2000). The current organizes the hydrological structure of the region into three main distinct zones: a coastal-peripheral zone, a frontal zone, and an offshore central zone with a divergence near the offshore limits of the current jet and convergence inside the frontal zone (Boucher et al. 1987). Nevertheless, this basic hydrological organization may be complicated by other mesoscale structures, such as frontal meanders (Sournia et al. 1990; Prieur et al. 1993) and mesoscale eddies (Taupier-Letage and Millot 1986; Millot 1987), that play an important role in the distribution and concentration of zooplankton (Pinca and Dallot 1995). The main identified zones determine the structure and composition of zooplanktonic communities. High zooplankton densities, particularly copepods, have been reported in relation to the enhanced primary productivity associated with the frontal upward advection and to the secondary circulation (Boucher 1984; Boucher et al. 1987; Ibanez and Boucher 1987; Zakardjian and Prieur 1998) (Fig. 11.7). In addition, the frontal zone may act as a retention area where the enhanced feeding conditions for copepods, probably lead a strong cohort production (Molinero et al. 2008b), although some available information does not support higher copepod productivity (Saiz et al. 2007). Nevertheless, abundance variability of each species may show intense small-scale patchiness, even changing among their successive developmental stages. This arises from complex behavioral, feeding and reproductive strategies in response to environmental organization. This topic was particularly well illustrated by Boucher (1988) for the copepod *Calanus helgolandicus*.

In the Catalan Sea, the role of the Northern Current and its associated front on primary production (Estrada and Margalef 1988; Estrada et al. 1999) and zooplankton distribution and metabolism has also been extensively studied (e.g. Sabatés et al. 1989; Saiz et al. 1992; Alcaraz et al. 1994; Sabatés and Olivar 1996; Masó et al. 1998; Duró and Saiz 2000; Calbet et al. 2002a; Sabatés et al. 2004). In general, the spatial pattern of zooplankton biomass distribution is comparable to that observed by Boucher (1984) and Boucher et al. (1987) across the Ligurian Sea Front. High zooplanktonic biomass and fish larvae concentrations have regularly observed along the shelf-break in relation to the frontal convergence (Sabatés et al. 1989). The front may act as a barrier preventing dispersal of fish larvae towards the open sea (Sabatés and Olivar 1996). However, the patterns observed are subject to

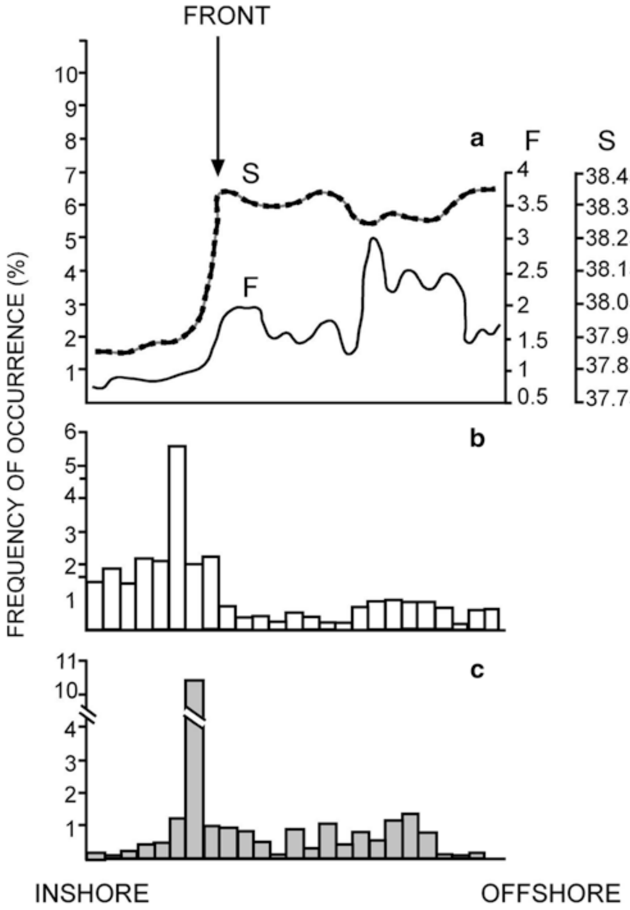

Fig. 11.7 Transect across the density front in the Ligurian Sea. (**a**) Salinity and fluorescence; (**b** and **c**) Relative abundance of, respectively, the calanoid copepods *Centropages typicus* and *Calanus helgolandicus* (Redrawn and modified from Boucher 1984)

considerable spatiotemporal variability, due to frontal mesoscale activity, which can show variations in intensity according to the seasonal variations in the location, strength and narrowness of the front (Sabatés and Olivar 1996; Sabatés et al. 2004). Such variability may reflect differently on zooplankton when considering state variables (i.e. biomass) or functional properties (metabolic activity) as a result of their different time scales (Calbet et al. 1996). Zooplanktonic biomass minima have been reported at the front with high zooplankton densities, particularly copepods, on its oceanic side (Alcaraz et al. 1994; Saiz et al. 1999; Calbet et al. 2002b; Sabatés et al. 2004), similarly to what was observed by Gaudy and Champalbert (1998) at the Ligurian Sea front (Fig. 11.8). These high zooplankton concentrations in the oceanic side of the front are related with peaks in phytoplanktonic biomass in that region (e.g. Estrada and Margalef 1988; Estrada et al. 1993) due to the existence of small convection cells along the front (Boucher et al. 1987) or episodes of cross-frontal ageostrophic circulation (Pinot et al. 1995); such coupling reflects on higher copepod grazing activity and predation pressure on primary producers (Saiz et al. 1992). Furthermore, biomass (organic carbon) and individual size (biomass) are more variable at the front than in the surrounding waters (Alcaraz et al. 2004, 2007). The highly dynamic frontal zone and the high instability induced there by intermittent, non-periodic, mechanical energy inputs would explain the observed variability (Alcaraz et al. 2007). The comparison of the repeated transects in a relatively short period of time, revealed that the front presented a meandering structure with changes in the position, direction and intensity of the current (Sabatés et al. 2004). Mechanisms of convergence/accumulation and divergence/dispersion of zooplankton and fish larvae were reported associated with the current's meandering flow pattern. Thus, the temporal scale at which the frontal system oscillates plays a key role in supplying nutrients to the photic zone on an intermittent basis but also exerts a decisive influence on processes affecting concentration/dispersal of zooplankton (Sabatés et al. 2004). Furthermore, is important to highlight the role of the Northern Current as a transport mechanism of planktonic organisms, in particular anchovy larvae from the spawning grounds of Gulf of Lions, towards the Catalan coast (Sabatés et al. 2007b). In addition to the direct transport by the current, anticyclonic eddies generated by instabilities of the current may entrap and aggregate the anchovy larvae, preventing their dispersion (Sabatés et al. 2007b) (Fig. 11.9).

The Alboran Sea, in the southern sector of the western Mediterranean Sea, is a highly energetic area. Inflow of Atlantic Waters and its geostrophic adjustment, are responsible for the existence of a strong thermohaline front (Tintoré et al. 1988; Prieur and Sournia 1994). The frontal system generates an area of cold, nutrient-rich waters where primary production is enhanced (Prieur and Sournia 1994; Videau et al. 1994). Higher zooplankton biomass and diversity are usually found in the Atlantic waters, as a consequence of the secondary production processes associated to the front, compared with surrounding waters (Dallot et al. 1988; Madin 1991; Seguin et al. 1994; Mills et al. 1996; Youssara and Gaudy 2001). In addition, maximum copepod egg production may occur near the front boundary, due to the existence of favorable feeding conditions (Youssara and Gaudy 2001). Nevertheless, the Atlantic Jet-frontal system has a strong variability at different time and spatial scales (Cheney and Doblar 1982; Parrilla 1984; Font et al. 2002). This time variability induces important changes in the distribution of phyto- and zooplankton. Rodríguez et al. (2001) showed that vertical velocities associated to mesoscale structures determined the phytoplankton size spectrum. Instabilities associated to the front are responsible for the subduction of phyto- and zooplankton to deep layers (Allen et al. 2001; Fielding et al. 2001; Youssara and Gaudy 2001; Andersen et al. 2004). In addition, changes in the Atlantic

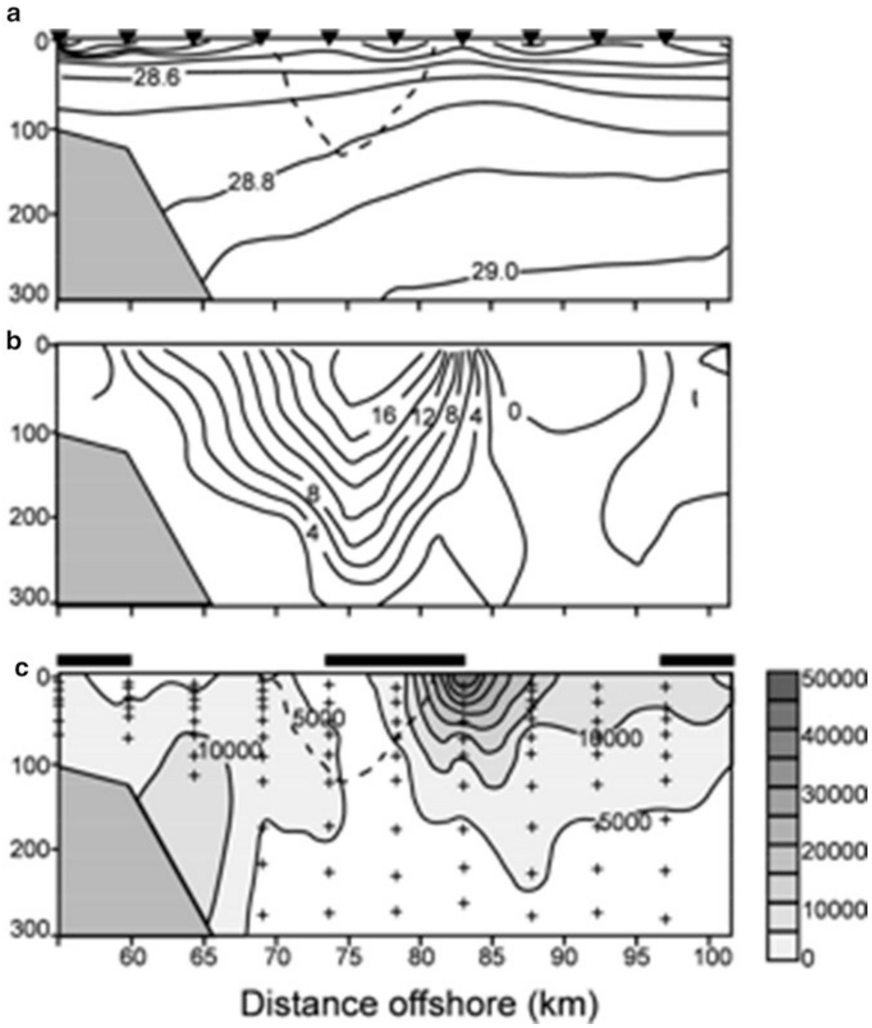

Fig. 11.8 Coastal-open sea transect across the Northern Current and its associated front, in the Catalan Sea (February, 1997). (**a**) Vertical distribution of density; (**b**) Geostrophic velocity (north–south) at 2 cm/s intervals; (**c**) Vertical distribution of copepods (No./100 m3). *Dotted line* in (a) and (c) encloses current velocities higher than 16 cm/s. *Dark segments* on *top* of (c) indicate night period (Redrawn and modified from Sabatés et al. 2004)

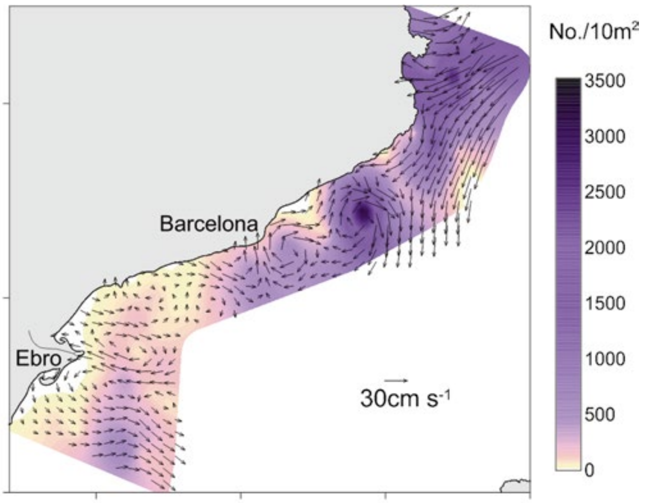

Fig. 11.9 Distribution of *Engraulis encrasicolus* larvae along the Catalan coast (July 2003) overlaid on the geostrophic current fields at 10 m, relative to 600 m. High concentrations of larvae are found in the northern area, associated to the intrusion of the Northern Current, and also inside the anticyclonic eddies originated by instabilities of the Northern Current (Redrawn and modified from Sabatés et al 2013)

Jet– frontal system involve changes in the vertical and horizontal distribution of fish larvae (Rubín 1997; García Lafuente et al. 1998; Vargas-Yáñez and Sabatés 2007). It has been suggested that the northwestern sector of the Alboran Sea is a favorable reproductive habitat for some commercial fish species such as the sardine, *Sardina pilchardus* (García et al. 1988; García Lafuente et al. 1998). Eggs and larvae of sardine are retained off the Málaga coast (i.e., in the geostrophic front area; Rubín et al. 1999) where the upwelling processes (Sarhan et al. 2000) favors high phytoplankton and zooplankton concentrations (Rodríguez et al. 1982; Minas et al. 1991).

Long-Term Changes

The distinctive physical, climatic and ecological features of the Mediterranean make it a very sensitive area to climate change (Lejeusne et al. 2010; Calvo et al. 2011). It is widely accepted that the Mediterranean is already one of the most impacted seas in the world, since climate change interacts synergistically with many other anthropogenic stressors such as fishing, eutrophication, pollution, and introduced exotic species (Turley 1999; Lejeusne et al. 2010). Long-term changes in the hydrographic and meteorological conditions, with warming water, less rainfall, lower wind-speed and progressive acidification have been reported in the Mediterranean (e.g. Béthoux et al. 1999; Rixen et al. 2005; Vargas-Yáñez et al. 2010). These changes appear to be related to atmospheric patterns, such as the NAO, and other mid latitude teleconnection patterns (Vignudelli et al. 1999; Tsimplis and Josey 2001; Rixen et al. 2005). Climate change, through long-term temperature increase, has been demonstrated to affect the boundaries of biogeographic regions, with some warm-water species extending their ranges and colonizing new areas where they were previously absent (Bianchi and Morri 2000; Sabatés et al. 2009; Philippart et al. 2011).

In the Mediterranean, climate change is undoubtedly affecting also the basic biology and ecology of planktonic organisms and the ecosystem functioning (e.g. Molinero et al. 2008a; Conversi et al. 2010; Lejeusne et al. 2010; Martín et al. 2012). However, the magnitude and extension of these changes, and whether or not a common trend can be found is still not clear. This concern about the effects of climate change in the pelagic ecosystem has provided a renovated interest on the use of time-series monitoring studies in order to describe the long-term, natural patterns of zooplankton abundance and composition, and assess their relation to large-scale atmospheric processes and global change. Hence, a recent burst of studies has appeared in an effort to provide new insights on the inter-annual variations in zooplankton standing stocks, assemblage composition and phenological traits in the Mediterranean (e.g. Molinero et al. 2008c; Fernández de Puelles et al. 2009; García-Comas et al. 2011; Mazzocchi et al. 2012), and relate them to basin-scale, regional and local climate forcing related to global change. Due to the key position of zooplankton in pelagic trophic webs, changes in zooplankton communities at decadal and longer-time scales can effect the functioning of the pelagic food web, and may result in severe repercussion for fisheries and other human-related activities (i.e., outburst of gelatinous zooplankton and the human use of beach and swimming activities at sea).

In the western Mediterranean three zooplankton time-series can be considered the most relevant ones, due to their temporal coverage and to the quantity and relevance of the research derived from them: namely the Point B station of Villefranche-sur-Mer in the Ligurian Sea (started in 1966), the Marechiara Station off Naples in the Thyrrenian Sea (started in 1995), and the Baleares Station off Mallorca Island, in the Catalan/Balearic Sea (started in 1994). Here we will summarize the more recent findings derived from their analyses, and refer the reader to the original works and some very recent reviews (Siokou-Frangou et al. 2010; Berline et al. 2012) for more comprehensive information. When doing such exercise, it is important to take into consideration the diversity of environments, sampling strategies (frequency, nets employed,…), taxonomic resolution, etc., encompassed in those time-series, which often can make difficult a straightforward comparison. These issues will be taken into consideration afterward.

The Time Series at Station Point B off Villefranche-sur-Mer

The station Point B is located at the entrance of the Bay of Villefranche-sur-Mer at ca. 80 m depth, on a narrow coastal shelf of the Ligurian Sea influenced by the Northern Current and by a submarine canyon nearby. This is the longest zooplankton time-series in the Mediterranean, sampled weekly (five times a week) since 1966 (Fig. 11.10). Plankton was collected with vertical hauls performed with a Juday-Bogorov net (330 μm mesh size), coupled with additional samples for macroplankton taken with a 690-μm Régent net. The 330 μm-mesh series was discontinued in 2003, but a new collection series started in 1995 using a 200-μm WP-2, which better covered the size range of copepods. In their thorough analyses of zooplankton data during the 1966–1993 period at station Point B, targeted into a few relevant copepod species and several jellyfish and chaetognaths, Molinero et al. (2005a, 2008a, 2008c) found that the effects of local climate variability, especially above certain threshold, translated into changes in the winter water temperature and the degree of water column stratification, which eventually resulted in an increase on jellyfish populations during the mid-late 1980s. According to these authors, the higher frequency of jellyfish outbreaks in the northwestern Mediterranean may significantly alter the functioning of the pelagic ecosystem, evidenced by significant decreases in both copepod (by predation) and chaetognaths (by competition for prey) standing stocks in the Ligurian Sea since the late 1980s (Molinero et al. 2005a, 2008a, c). Such changes may cause a disruption of the functioning of the planktonic ecosystem, affecting both directly and indirectly fish recruitment and dynamics. The climatological and hydrological forcing at regional and local scales responsible for those effects on the zooplankton in the Ligurian Sea appeared to be linked, in last instance, to the long-term changes in the North Atlantic climate. A further analysis of the same Point B series of samples by García-Comas et al. (2011), including ten more years of data (up to 2003) and encompassing not only some target species, but the whole standing stocks of different broad zooplankton groups (e.g. copepods, chaetognaths, appendicularians, etc.) (Fig. 11.10), showed that the previously observed patterns did not hold completely when the study period was prolonged. Even when comparing the same series of years, the increasing trend of jellyfish abundance from the late 1980s, reported by Molinero, differed

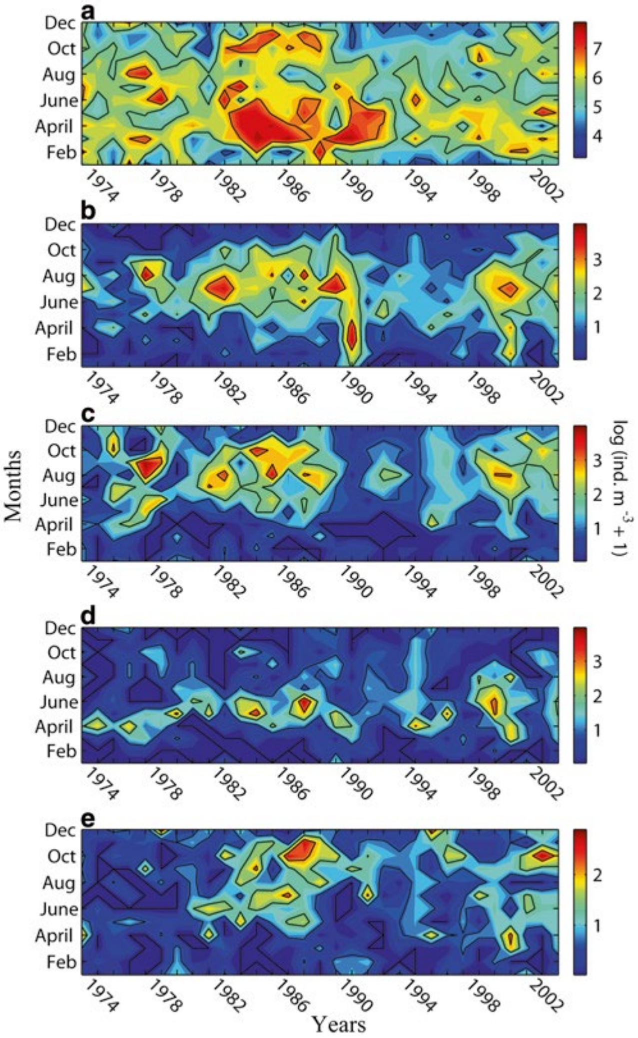

Fig. 11.10 Seasonal and interannual variability of several zooplankton groups at the station Point B off Villefranche-sur-Mer from 1974 to 2003. (**a**) Copepods; (**b**) Decapod larvae; (**c**) Chaetognaths; (**d**) Siphonophores; (**e**) Jellyfish (From García-Comas et al. (2011). With permission of the publisher)

from the observations of García-Comas et al. (2011) with a decrease in total medusae stocks from 1989. In this last study, all the considered zooplankton groups showed similar long-term patterns over the 30-year period of study, and evidenced a certain synchrony with that of environmental factors, following almost-decadal periods (García-Comas et al. 2011). It appears, then, that the trends observed by Molinero for some target species and the proposed regime shift in 1987 for the Mediterranean in synchrony with changes in the Atlantic ocean and the Baltic and Black Seas (Molinero et al. 2008c; Conversi et al. 2010) are challenged when more years are included in the analysis and the bulk of zooplankton standing stocks are considered (García-Comas et al. 2011). Furthermore, the influence of the North Atlantic climate, as represented by the NAO index, on the local hydrological and climatological factors was only evident until the early 1990s. García-Comas et al. (2011) suggested that the link between climate forcing and zooplankton, would be mediated not by a raise of water temperature and thermal stratification, as proposed by Molinero, but by episodes of strong winter mixing, associated to cold and low precipitation (higher salinity) periods, which would augment the nutrient input in the photic zone enhancing phytoplankton productivity, therefore through bottom-up effects increase zooplankton stocks. Contrarily, the recent analysis of the parallel time series taken with a 200-µm WP-2 at Point B during the period 1995–2005 by Vandromme et al. (2011), which also include phytoplankton (chlorophyll) biomass data, seems to support a top-down control of zooplankton on phytoplankton.

The Time Series at Station Marechiara Off Naples

The station Marechiara (off Naples, Italy) is located at a depth of ca. 75 m, in a coastal site hydrodynamically very active, influenced by the land runoff from the nearby populated area, and by intrusions of oligotrophic offshore waters, similar to the open Tyrrhenian Sea (Ribera d'Alcalà et al. 2004; Mazzocchi et al. 2011). Sampling started on 1984 (biweekly sampled), was discontinued temporally between 1991 and 1995, and then continued since 1995 (weekly). Zooplankton is collected by vertical tows with a Nansen net provided with 200-µm mesh size. Mazzocchi et al. (2011, 2012) present the more recent update and analysis of long-term changes in mesozooplankton standing stocks and composition at the site (samples analyzed until 2006). Mesozooplankton standing stocks show relatively low variability over the years (average annual mean: 1,700 ind m^{-3}), with a period of negative anomalies between 1995 and 2002. At the species level, the most abundant zooplankton species displayed high interannual variability (Fig. 11.11), but no remarkable long-term trend could be evidenced, with a few exceptions (e.g. decreased abundance of the copepods *Acartia clausi* and *Centropages typicus* in summer). Despite the extensive variability in hydrographic features and autotrophic communities evidenced at the study site over the years, robust and persisting (over time) zooplankton species assemblages can be distinguished in association with the seasonal cycles of hydrographic and biological features. Although in some cases interannual variations of those assemblages could be associated to environmental long-term trends (e.g. a significant warming trend in summer temperature, a decreasing trend in the autotrophic community), no clear, common patterns were found and the copepod and zooplankton assemblages were notably persistent. It appears that the variability associated

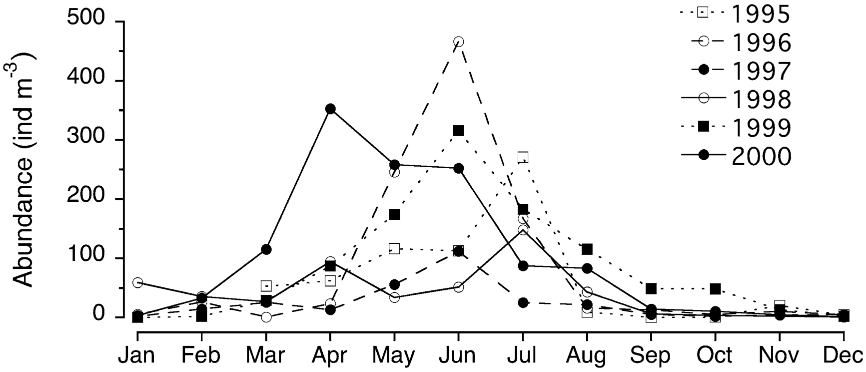

Fig. 11.11 Phenological variation in the occurrence of the calanoid copepod *Centropages typicus* at the station Marechiara off Naples (Redrawn and modified from Mazzocchi et al. 2007)

to changes during the seasonal cycle is much larger than the interannual variations so far observed in the monitoring series.

The Time Series at the Baleares Station off Mallorca

The zooplankton time series at the Baleares station, located at the Mallorca channel in the Catalan/Balearic Sea consists of samples taken every 10 days since 1994 with a Bongo-20 fitted with 250 μm mesh size (Fernández de Puelles et al. 2007); an additional 5-year period (1994–1999) included two other stations sampled monthly across the shelf and additional finer mesh size (Fernández de Puelles et al. 2003a, b). The Mallorca channel is a very relevant area for the meridional water exchange in the western Mediterranean, and is subject to intense mesoscale variability and water masses mixing as the result of being exposed to intrusions of water masses from either the Northern Current (saltier and colder), or from recent, fresher and warmer, Atlantic waters (Pinot et al. 2002). This particular location acts as an excellent observatory to assess how large-scale climate patterns affecting the northern hemisphere and in particular the North Atlantic (i.e. NAO) can act as drivers of regional meteorological variability and hydrographic patterns in the Catalan/Balearic Sea, and therefore influence the north western Mediterranean zooplankton communities (Fernández de Puelles et al. 2007; Fernández de Puelles and Molinero 2008). At seasonal scale, during winter the surface waters of the Mallorca channel mainly show the characteristics of the Northern Current waters, whereas in summer and autumn the warmer and less saline recent Atlantic waters exert a stronger influence (Pinot et al. 2002). Such changes reflect in the standing stocks of zooplankton in the area, in particular copepods, that happen to be higher during the first part of the year, when the Northern Current waters, more productive, have stronger influence (Fernández de Puelles et al. 2003b). The high interannual variability in zooplankton abundance in the Mallorca channel appears to be driven by the large-scale atmospheric forcing in the North Atlantic Ocean, which may reflect in the alternation on the intensity of the influence of Northern Current and Atlantic waters in the area, but also on differential local cooling processes during mild versus cold winters (Fernández de Puelles et al. 2003b). These effects are evidenced by a strong negative relationship between water temperature and zooplankton standing stocks (also conspicuous when dealing with particular taxonomic groups), in special for those periods with strong anomalies (>1 SD) in the North Atlantic climatological indices considered (Fernández de Puelles et al. 2007; Fernández de Puelles and Molinero 2008).

General Remarks

A comprehensive picture of the long-term changes in the zooplankton communities in the western Mediterranean as a whole, and of the influence that large-scale atmospheric processes and global change might have on them, as can be deducted after reading the descriptions above, is not a simple issue. Several considerations have to be taken into account when drawing general conclusions. For instance, their extension in time and the presence of gaps in the sampling are important factors to ponder, because often the number of years (samples) processed is still too short for proper and robust assessment of interannual variability in relation with large-scale atmospheric forcing. Furthermore, in a recent and thorough effort by Berline et al. (2012), which includes also the zooplankton time-series in the Adriatic and Eastern Mediterranean, the authors failed to find significant correlations between climate indices and local temperature or zooplankton abundance, and concluded that probably the monitoring sites are too strongly influenced by local forcing (either climatic and/or anthropogenic) to evidence larger-scale forcing, although synchronous behaviors can be observed among monitoring sites. The peculiarities of the site (i.e. the Baleares station located in neritic waters in the Mallorca channel, main area for meridional water transport in the western Mediterranean; the Point B station near Villefranche-sur-Mer, close to a submarine canyon; the Marechiara station, in a neritic area close to a populated city like Naples) certainly must be considered in order to disentangle the hidden patterns in the typically variable biological data and to extrapolate the observations to other areas. As Mazzocchi et al. (2012) noticed, one should be cautious when coastal sites are used to assess the impact of climate change because these highly variable environments are inhabited by zooplankton species well adapted to cope with variable environmental conditions, and therefore less prone to show dramatic changes. Unfortunately, long-term monitoring sites in open deep waters, free of coastal influences and less sensitive to changes in circulation patterns, are expensive in terms of cost and human-power and are lacking in the Mediterranean.

Another source of uncertainty in the analysis of the time-series data is the taxonomic resolution employed. In this regard, Berline et al. (2012) pointed out that the use of broad taxonomic groups in their study (e.g. copepods, cladocerans, chaetognaths) instead of the species level could have easily masked changes in species composition, phenology, etc. This is consistent with the fact that when standing stocks of broad taxonomic groups are considered, the ranges of variability, either interannual (e.g. Baleares station: in the period 1994–2003, the annual mean abundance of copepods ranged from 454 to 655 ind m^{-3}, with a coefficient of variation of 12 %, Fernández de Puelles et al. 2007), or seasonal (e.g. Baleares station: in the period 1994–2003, the monthly mean abundance of copepods ranged from 347 to 723 ind m^{-3}, with a coefficient of variation of 23 %, Fernández de Puelles et al. 2007) appear rather moderate. At the single species level, Molinero et al. (2005b) reported phenological and abundance changes during the period 1966–1993 at the Point B station in Villefranche-sur-Mer for two significant components of the copepod assemblages in the western Mediterranean, the species *Centropages typicus* and *Temora stylifera*, which could be related to large-scale climate forcing (NAO index). However, in a more ambitious study Mazzocchi et al. (2007) focused on the same species *Centropages typicus* but encompassing several observational sites in both the western and the eastern Mediterranean, only at two locations (Marechiara off Naples and Point B off Villefranche-sur-Mer) the long-term phenological changes in *Centropages typicus* populations could be related to the NAO index, and the response differed between sites. The large size of the Mediterranean basin, encompassing several degrees of longitude and latitude, and its location under the influence of mid-latitude and tropical regimes, is probably responsible for the diversity in patterns observed and the degree of influence of long-term atmospheric forcing related, which would be linked not only to the North Atlantic climate but to other climate regimes as well (Lionello et al. 2006; Martín et al. 2012; Mazzocchi et al. 2012). The range of variation in environmental factors than can be coped with is much narrower when considered at the species level that when the whole community is considered, and hence changes due to climate variations should be first detected at the species level. Mazzocchi et al. (2011) also cautions that although dominant species might not show conspicuous signals of long-term changes, the presence or absence of rare species might be a better proxy to first evidence subtle changes in zooplankton communities. This is the case for the Gulf of Naples, where the disappearance of rare copepod species such as *Acartia margalefi* and *Paracartia latisetosa* (which have disappeared in other areas of the Mediterranean as well), and the more frequent intrusion of offshore copepods at the monitoring site have been reported (Mazzocchi et al. 2012). In this regard, the recent implementation of automatic and semiautomatic zooplankton counting, sizing and identifying methods and technologies (Alcaraz et al. 2003; Grosjean et al. 2004; Gorsky et al. 2010) has helped to speed up the processing of large number of samples and standardize data (e.g. García-Comas et al. 2011; Vandromme et al. 2011), although at the cost of a much lower taxonomic resolution that would be required to detect such changes in rare species. Nevertheless, in order to assess the magnitude of the alterations in the whole planktonic food-web structure and dynamics due to climate change and the implications for the export of carbon to upper trophic levels, the whole assemblage or community might be more relevant (García-Comas et al. 2011).

Jellyfish Blooms and Changes in Fauna

Increases in jellyfish populations have been reported for many pelagic marine ecosystems worldwide (Mills 2001; Purcell 2005) and the Mediterranean is not an exception (Benovic and Lucic 2001; Boero et al. 2008a). Although proliferations of jellyfish, and other gelatinous zooplankton, are a natural phenomenon in coastal and oceanic Mediterranean waters (CIESM 2008) they seem to have become more frequent over the past few years. Many hypotheses have been proposed to explain these blooms throughout the world, which are also applicable to the Mediterranean: climate change, eutrophication, overexploitation, aquaculture and species invasions (Purcell et al. 1999, 2007; Mills 2001). Proliferations of gelatinous zooplankton may therefore be indicative of considerable changes in the functioning of marine ecosystems and have a wide range of ecological implications, including alteration of plankton assemblages through both, top-down and bottom-up effects (Mills 2001; Purcell 2005).

Qualitative scientific records of jellyfish populations and proliferations date from more than 200 years ago in the Mediterranean (Goy et al. 1989; Kogovsek et al. 2010), and despite their heterogeneity and scarcity these data suggest a

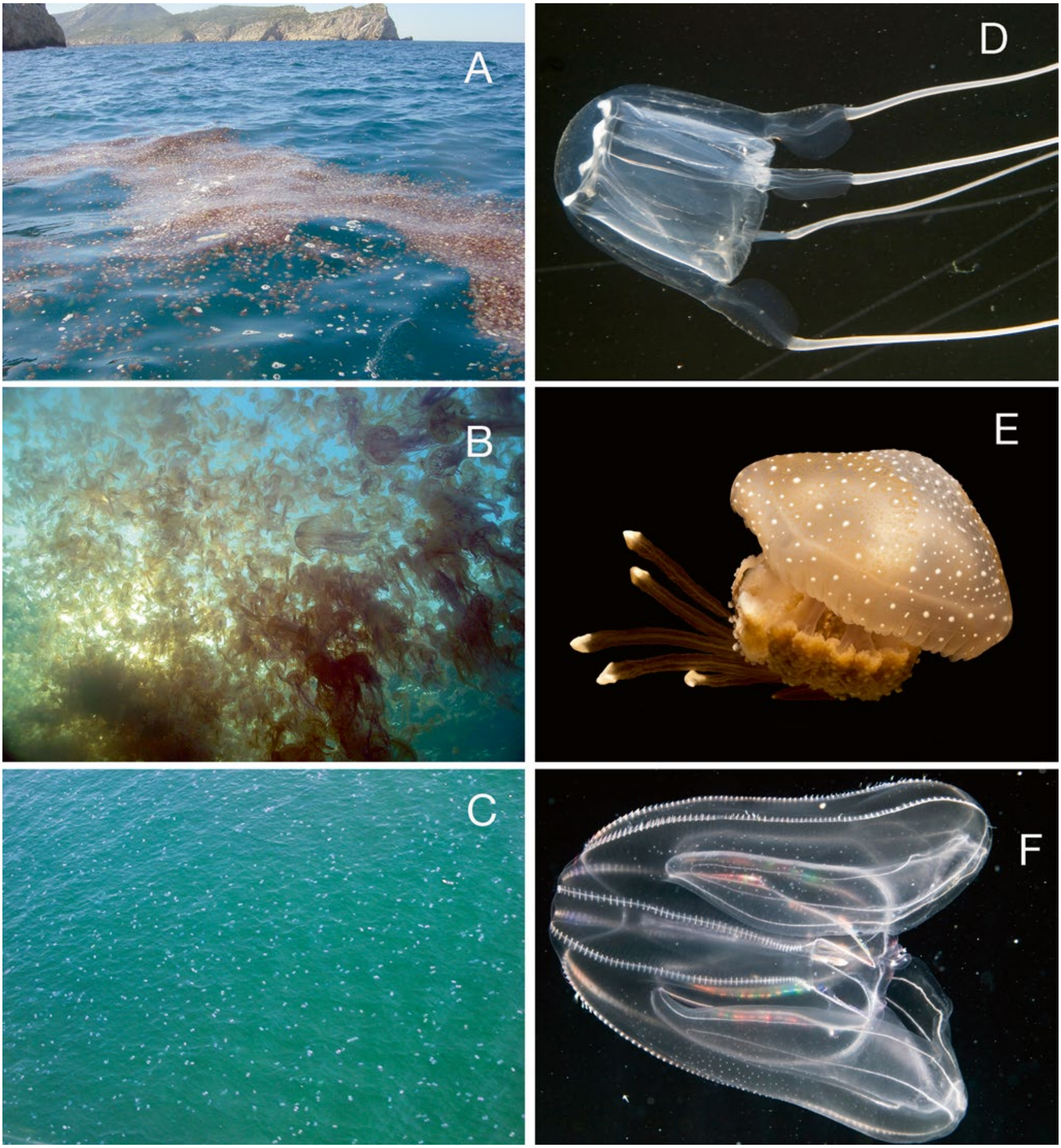

Fig. 11.12 *Left panels*: Three examples of jellyfish proliferations. Swarms of *Pelagia noctiluca* in surface waters of the Balearic Islands in (**a**) June and (**b**) July and (**c**) swarm of *Rhizostoma pulmo* in the Catalan Coast in July. *Right panels*: Three examples of recent invasive species in the Mediterranean (**d**) the jelly *Carybdea marsupialis*, (**e**) the jelly *Phyllorhiza punctata* and (**f**) the ctenophore *Mnemiopsis leidyi* (Photographs of David Diaz (a), Giampiero Mancini (b), Agencia Catalana de l'Aigua (c), Eduardo Obis (d–f))

periodicity in the blooms. The most spectacular events are those of *Pelagia noctiluca* (Fig. 11.12). High densities of *P. noctiluca* have been observed regularly over the past 12 years in the Adriatic and in the whole Mediterranean (Malej and Malej 2004). Goy et al. (1989) reported a periodic occurrence of *P. noctiluca* blooms related to climatic factors, such as low rainfall, high temperatures and high atmospheric pressure. The analysis of data of recent decades, however, suggests that the intensity, timing, and distribution of *P. noctiluca* population outbreaks seem to be driven by recent climatic and hydrological conditions in the Mediterranean (Daly Yahia et al. 2010; Licandro et al. 2010). The common jellyfish *Aurelia aurita* and *Rhizostoma pulmo* are regularly present in the Adriatic Sea, but recently their proliferation has become frequent, especially in the northern coasts (Malej and Malej 1992; Ramšak and Stopar 2007). A similar phenomenon occurs in the Catalan coast where large jellyfish swarms at the beaches caused a great number of swimmers stung (Gili et al. 2010). The presence and arrivals of jellies along the Catalan beaches have been explained in base to local climatic conditions linked to changes in wind and rain regimes (Rubio and Muñoz 1997; Gili and Pagès 2005).

Recent works pointed out that long-term variability of gelatinous zooplankton is strongly affected by climate fluctuations. From the study of the few existing plankton data series and semi quantitative multiyear records in the northwestern Mediterranean, Molinero et al. (2008a) showed that increases of gelatinous plankton were associated with positive phases of the NAO after 1980, with warm and stable water column providing a suitable environmental conditions for their development (see section "Long-term changes" for further discussion). The recent study by Licandro et al. (2012), from the same area, showed that the standing stock of calycophoran siphonophores did not show any significant change during nearly three decades, with the annual maximum in spring. Nevertheless, major changes in the community composition were reported since the middle 1980s, with the decrease of the dominant species *Muggiaea kochi* allowing the increase of the congeneric *Muggiaea atlantica* and *Chelophyes appendiculata.* These community shifts were related to hydroclimatic changes, being salinity, temperature and water stratification the main factors associated with these changes. These results are in line with previous observations of Riera et al. (1986) and Buecher (1999).

Besides the direct effects of climate change, increases in gelatinous zooplankton have also been correlated with overfishing (Lynam et al. 2004; Purcell 2012). Jellyfish and fish interact both as predators and competitors of each other (Brodeur et al. 1999; Pagès 2001), as jellyfish and other gelatinous plankton are consumers of fish eggs and larvae (Lynam et al. 2005; Sabatés et al. 2010). Most of the energy that once circulated through fishes is now processed by other predators, such as pelagic gelatinous carnivores, that fill a gap within the trophic system by the decrease in fish stocks (Mills 2001; Purcell 2012). Other important evidences of the human impact on jelly outbreaks have been demonstrated in coastal lagoons in the Mediterranean (Benovic et al. 2000; Pagès 2001) and other coastal regions related (Purcell et al. 1999). In these areas, the intensive use of fertilizers due to the increment of agricultural activities have resulted in eutrophication, which has favored some species with endosymbiotic algae, such as *Cotylorhiza tuberculata*. Moreover, the increase of available hard substrates (e.g. damns, artificial reefs, shells from bivalve aquaculture) have enhanced the chance for suitable planula settlement and subsequent ephyra production (Pagès 2001; Holst and Jarms 2007). In general, the proliferation of artificial structures associated with the exponential increase of shipping, aquaculture and other coastal industries and defense structures, could, thus, be a major driver of the global rise of jellyfish blooms in Mediterranean coastal areas (Duarte et al. 2013). Thus, a progressive increase in the presence of jellyfish swarms during the next years in the Catalan coast has been proposed as consequence of the interaction between environmental changes and anthropogenic pressures (Calvo et al. 2011).

The long-term water temperature increase has also affected the boundaries of biogeographic regions, with some thermophilic species extending their ranges and colonizing new areas where they were previously absent (Laubier 2003). The northward migration of species with an affinity for warm waters has been reported in different Mediterranean regions for fish and benthic organisms (Francour et al. 1994; Astraldi et al. 1995; Bianchi and Morri 2000; Sabatés et al. 2006). The increase of thermophilic biota in the Mediterranean Sea would involve changes in both indigenous (meridionalization) and non-indigenous (tropicalization) species (Boero et al. 2008b).

Regarding plankton, strong biogeographical shifts in copepod assemblages in relation to the water temperature increase have been observed in the North Atlantic, involving a northward extension of warm water species and a decrease in the number of cold water species (Beaugrand et al. 2002). However, in the Mediterranean such clear examples for plankton are still scarce. Very likely the changes will be first detected in the northern coldest regions and common species will be less sensitive due to their wide distribution in the whole basin. For instance, in the Northern Adriatic, changes in the specific composition of copepods have been reported in relation to the temperature increase. The relative abundance of southern species, i.e. *Diaixis pygmoea, Oithona similis* and *Oithona nana,* has increased in the last years while, on the contrary, relic cold-water species, such as *Pseudocalanus elongatus,* have decreased (Fonda Umani and Conversi 2008). Moreover, Mazzocchi et al. (2012) reported that rare copepod species, for instance *Acartia margalefi* and *Paracartia latisetosa*, have changed drastically their presence in the Thyrrenian Sea and other parts of the Mediterranean, but the mechanism behind these changes are not clear. More clear examples, in parallel with the northwards expansion of pelagic fish species (i.e. *Sardinella aurita* and *Pomatomus saltatrix*) due to sea warming, can be found in the ichthyoplankton (Sabatés et al. 2009, 2012) (Fig. 11.13).

Other changes in zooplankton biota in the Mediterranean are related to the increase of non-indigenous invasive species, phenomenon known as tropicalization. The availability

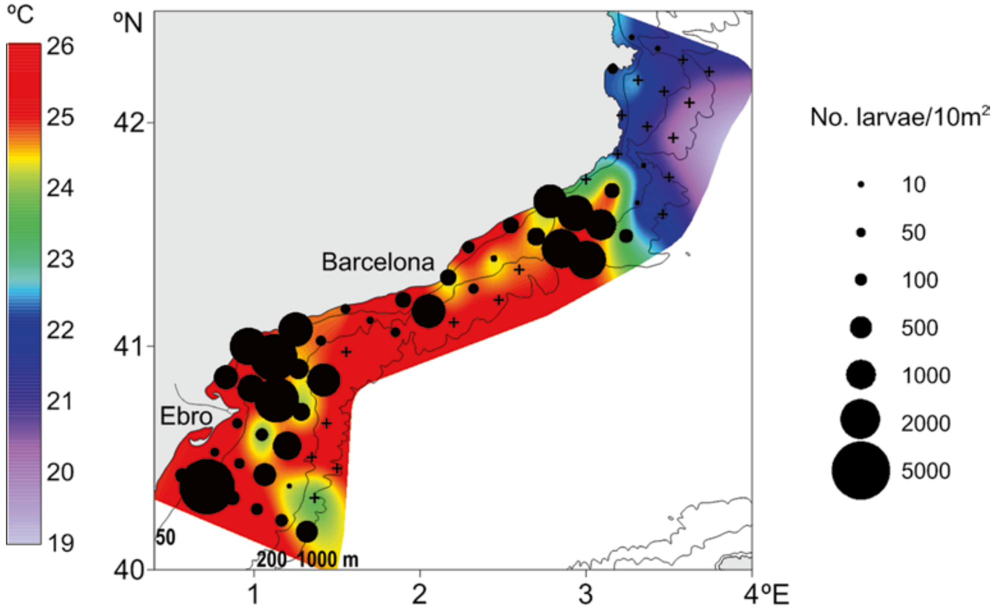

Fig. 11.13 Distribution of *Sardinella aurita* larvae along the Catalan coast (July 2003) overlaid on sea surface temperature. The northern limit of the larval distribution is bounded by the thermal front associated to the intrusion of the Northern Current (Redrawn and modified from Sabatés et al. 2009)

of proper conditions for both tropical and temperate species makes the Mediterranean a perfect sea for biological invasions (Boero et al. 2009). In addition, the seasonality in the Mediterranean is a key factor that facilitates the coexistence of many species (Coma et al. 2000) including those species that resist or remain as resting stages or in dormancy (Boero et al. 1996). Today, more than 500 non-indigenous species are listed from the Mediterranean Sea (Galil 2007), mostly benthic and of tropical and subtropical origin (Zenetos et al. 2010). The best known invasive species are the Lessepsian ones, entering from the Red Sea to the Mediterranean by the Suez Canal (e.g. Kovalev 2006, and references therein). In some cases, these Lessepsian species have become problematic, for example the Sciphomeduse *Rhopilema nomadic,* forming stable populations in the eastern basin (Spanier and Galil 1991). In addition to the entrance of new species from both Suez and Gibraltar (the Atlantic flow never stopped), the Mediterranean is also experiencing the transport of exotic species by ships, both as fouling or in the ballast waters (Lotan et al. 1992). The appearance of the calanoid copepod *Acartia tonsa* (Gaudy and Viñas 1985) and the cyclopoid copepod *Oithona davisae* (Saiz et al. 2003) in the Mediterranean are likely examples of such transport. Another recent example of the introduction of foreign species is the presence and increase in the western Mediterranean of the invasive ctenophore, *Mnemiopsis leidyi* (Fuentes et al. 2009) (Fig. 11.12). The success of the introduced *M. leidyi* has been mainly attributed to the reduced competition due to overfishing of zooplanktivorous fish populations and the lack of predators (Siapatis et al. 2008). Another important invasive species is the Scyphomedusae *Phyllorhiza punctata* with a relative well-documented history of invading tropical and subtropical environments over the last years (Galil et al. 1990; Boero et al. 2009). The proliferation of the cubomedusa *Carybdea marsupialis* in the western Mediterranean Sea have been related to the increase in water temperature and to the enhanced chances for polyp settlement in artificial substrata (Bordehore et al. 2011).

In summary, the historical process of species distribution changes, migrations, colonization, and invasions has given rise to a puzzle of species that conform the actual Mediterranean biodiversity. It is evident that the Mediterranean has always been changing (both physically and biologically). Nevertheless, nowadays, like most marine ecosystems worldwide, the Mediterranean is highly impacted by several human-mediated threats. These major disturbances, in addition to species introductions and climate change, may severely impact the natural balance of planktonic communities and, therefore, have repercussions to the whole ecosystem.

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