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Plankton in the open Mediterranean Sea: a review

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Abstract

We present an overview of the plankton studies conducted during the last 25 years in the epipelagic offshore waters of the Mediterranean Sea. This quasi-enclosed sea is characterized by a rich and complex physical dynamics that includes unique thermohaline features, particular multilayer circulation, topographic gyres, and meso- and sub-mesoscale activity. Recent investigations have basically confirmed the long-recognised oligotrophic character of this sea, which enhances along both the west-east, and the north-south directions. Nutrient availability is low, especially for phosphorous (N:P up to 60), although limitation may be relaxed by inputs from highly populated coasts and from the atmosphere. Phytoplankton biomass as chl-*a*, generally displays low values (less than $0.2\,\mu\mathrm{g chl}-a\mathrm{l}^{-1}$) over large areas, with a modest late winter increase. A large bloom (up to $3\,\mu\mathrm{g l}^{-1}$) throughout the late winter and early spring is only observed in the NW area. Relatively high biomass peaks are also recorded in fronts and cyclonic gyres. A deep chlorophyll maximum is a permanent feature for the whole basin (except during the late winter mixing). It progressively deepens from the Alboran Sea (30 m) to the easternmost Levantine basin (120 m). Primary production reveals a similar west-east decreasing trend and ranges from 59 to $150\,\mathrm{gC m}^{-2}\mathrm{y}^{-1}$ (in situ measurements). Overall the basin is largely dominated by small-sized autotrophs, microheterotrophs and egg-carrying copepod species. The phytoplankton, the microbial (both autotrophic and heterotrophic) and the zooplankton components reveal a considerable diversity and variability over spatial and temporal scales, the latter less explored though. Examples are the wide diversity of dinoflagellates and coccolithophores, the multifarious role of diatoms or picoeukaryotes, and the distinct seasonal or spatial patterns of the species-reach copepod genera or families which dominate in the basin. Major dissimilarities between western and eastern basins have been highlighted in species composition of phytoplankton and mesozooplankton, but also in the microbial components and in their relationships. Superimposed to these longitudinal differences, a pronounced biological heterogeneity is also observed

in areas hosting deep convection, fronts, cyclonic and anti-cyclonic gyres or eddies. There, the intermittent nutrient enrichment promotes switches from a small-sized microbial community to diatom-dominated populations. A classical food web is ready to substitute the microbial food web in these cases. These switches, likely occurring within a continuum of trophic pathways, may greatly enhance the flux towards high trophic levels, in spite of an apparent heterotrophy. Basically, the system seems to be top-down controlled and characterised by a multivorous web, as shown by the great variety of feeding modes and preferences and by the significant and simultaneous grazing impact on phytoplankton and ciliates by mesozooplankton.

> *"La Mediterrània, o almenys la seva zona pelàgica, seria comparable a una Amazònia marina." (Margalef, 1995)*
> (The Mediterranean, or at least its pelagic zone, would be like a marine version of the Amazon forest.)

1 Introduction

The Mediterranean Sea (MS) is the largest quasi-enclosed sea on the Earth, its extension being similar to that of the largest semi-enclosed (e.g., the Gulf of Mexico) and open (e.g., the Caribbean Sea) marginal seas of the extant ocean (Meybeck et al., 2007). The MS' size, location, morphology, and external forcing allow for a rich and complex physical dynamics that includes: i) unique thermohaline features ii) particular multilayer circulation iii) topographic gyres, and iv) meso- and sub-mesoscale activity. Nutrients and chlorophyll-*a* (chl-*a*) pools rank the basin as oligotrophic to ultra-oligotrophic (Krom et al., 1991; Antoine et al., 1995). Oligotrophy seems to mainly due to the very low concentration of inorganic phosphorus, which is assumed to limit primary production (Berland et al., 1980; Thingstad and Rassoulzadegan, 1995, 1999). Additional features of the MS are i) the decreasing west-east gradient in chl-*a* concentration, as shown by color remote sensing (D'Ortenzio and Ribera d'Alcalá, 2009) as well as by in situ data (Marie et al., 2006, and references therein), and ii) a relatively high number of bioprovinces (sensu Longhurst, 2006), with boundary definition mostly based on the distribution of benthos and necton (Bianchi, 2007). The MS is also a site of intense anthropic activity dating back to at least 5000 years BP, whose impact on the marine environment have still to be clearly assessed and quantified. All these peculiar and contrasting characteristics should likely be reflected in the structure and dynamics of plankton communities. Numerous investigations have been conducted on the fluxes of the main elements, as linked to the biological pump. Studies on structure and dynamics of plankton communities in the open MS have increased in the last decades.

A first synthetic overview of the pelagic MS ecosystems was provided by the collective efforts reported in Margalef (1985) and Moraitou-Apostolopoulou and Kiortsis (1985). Most of those contributions focused on bulk parameters (e.g., chl-*a*, primary productivity, mesozooplankton biomass) and organismal distributions. In the following years, the discovery of picoplankton (e.g., Waterbury et al., 1979) and the consequent increased attention for the role of microheterotrophs within the pelagic food web provided new angles for the understanding of oligotrophic seas such as the MS (Rassoulzadegan, 1977; Hagström et al., 1988). Numerous research efforts starting from the nineties were hence devoted to constrain carbon and nutrient fluxes and to provide insight on the key players of the MS pelagic food web (e.g., Lipiatou et al., 1999; Thingstad and Rassoulzadegan, 1999; Tselepides and Polychronaki, 2000; Monaco, 2002; Mazzocchi et al., 2003; Krom et al., 2005). An increasing number of studies have focused on relevant biological processes and/or vital rates (e.g. Calbet et al., 1996; Estrada, 1996; Saiz et al., 1999; Moutin and Raimbault, 2002), while the hypothesis of phosphorous limitation has inspired studies on the pelagic food web as affected by phosphorus enrichment (Thingstad et al., 2005). Physical-biological coupling due to mesoscale dynamics has been addressed more frequently during the last decades (e.g., Champalbert, 1996; Alcaraz et al., 2007). Clearly these studies have provided new insights in the MS plankton in terms of its components, besides a more extended geographic coverage.

The present review aims at providing an updated and integrated picture of the Mediterranean plankton in the offshore epipelagic waters (0–200 m) as it emerges from studies conducted during the last 25 years. The key issues addressed in the review are: i) the plankton components, from the virus, bacteria and picoautotrophs, up to mesozooplankton, with a prevalent focus on the key players, i.e., with a species-oriented approach; ii) their mutual interactions within the pelagic realm, with the aim of corroborating or improving the existing descriptions of the planktonic food web structure (Thingstad, 1998; Sommer et al., 2002) and depicting the principal carbon producers. A review could be helpful, among others, for the assessment of global change impact on MS ecosystems. In addition, as detailed in the following sections, the main forcings on the basin and their scales display peculiar features. As a consequence, non-trivial responses might be triggered in plankton communities, which could be of significant interest for a wider than Mediterranean community.

2 Physical and chemical framework

Physical dynamics is a crucial driver of the seasonal cycle of production in the pelagic environment (Mann and Lazier, 2006, and references therein). Here we use the term of physical dynamics in a broad sense, which includes both marine and atmospheric processes. The latter are particularly important in the MS because, besides ruling the general circulation, they contribute to the fluxes of elements into the basin. As compared to the open ocean or other internal seas, the inputs from land play a greater role in the MS, due to its higher coastal-length to basin-surface ratio and its connection with one of the proportionally largest catchment areas (Meybeck et al., 2007).

The bathymetry (Fig. 1) highlights a key feature of the MS, i.e. the connection with the neighbouring ocean and between the deep sub-basins through shallow or very shallow straits (e.g., Gibraltar, Dardanelles, Sicily, etc.), which preclude exchange of deep water masses. Nonetheless, the deep layers are efficiently oxygenated in the present MS, because deep waters are regularly formed independently in the western and eastern sub-basins and renewal occurs at yearly pace (Hopkins, 1978).

The present MS is a concentration basin (freshwater loss exceeds freshwater inputs), which forces an anti-estuarine circulation, with saltier and denser water exiting the basin at Gibraltar and a compensating entrance of the fresher Atlantic water. As the unbalance between evaporation and precipitation plus runoff (the E-P-R term) increases towards east, the eastern basin is anti-estuarine respect to the western basin. This creates a single open thermohaline cell, encompassing the upper layer of both basins, with a dominant west-to-east surface transport and a east-to-west intermediate transport (e.g., Pinardi and Masetti, 2000). North-westerly wind stress prevails over the whole basin in winter, with a rotation towards north-east, whereas east quadrants in the western MS in summer enhance the W-to-E transport. The wind stress pattern, the morphology of the basin and the bottom topography produces a somewhat regular pattern in the distribution of eddies and gyres, which are mainly anticyclonic in the southern regions and cyclonic in the northern ones (Pinardi and Masetti, 2000).

The Atlantic Water entering the basin is often referred to as Modified Atlantic Water (MAW) to account for the progressive eastward change in its T-S properties. The MAW adds a haline component to the thermal contribution to stratification in large areas of the SW MS decreasing the winter mixed layer depth (D'Ortenzio et al., 2005).

From a dynamical point of view, the entrance of MAW into the basin produces a system of highly energetic anticyclonic structures in both the Alboran Sea and in the Algerian basin, where the Algerian current generates anticyclonic eddies (Fig. 2) with lifetimes from several months up to three years (Puillat et al., 2002, and references therein). One of the most striking features associated with the MAW is the North Balearic Front in the NW MS, which separates two subregions with drastically different regimes. Also associated with MAW is the jet across the Straits of Sicily, which is the dominant connecting surface flow among the two MS sub-basins. In the Aegean Sea, at the north-eastern edge of the MS, the modified Black Sea Water flows in through the Dardanelles Strait. A strong thermohaline front (the North Eastern Aegean Front) is formed in the area where the less saline (~30) and colder water meets the saltier (~38.5) and warmer water of Levantine origin (Zervakis and Georgopoulos, 2002).

The general circulation of the MS is also characterized by the presence of permanent or semi-permanent sub-basin gyres, which are mostly topographically controlled (Robinson and Golnaraghi, 1994). The most relevant among them are the cyclonic Rhodos Gyre (NW Levantine Sea) and the South Adriatic Gyre, with convective events during winter leading to the formation of intermediate and deep water masses, respectively. Another quasi permanent gyre, which is mostly wind driven and displays strong seasonality, is located in the North Tyrrhenian Sea (Artale et al., 1994), with a coupled anti-cyclonic twin on its southern edge (Rinaldi et al., 2009). In the southern part of the basin, in addition to the Algerian eddies, quasi permanent anticyclonic structures populate the eastern MS, e.g., Ierapetra (south of Crete Island), Mersa Matruh (north of the Egyptian coast), Shikmona (south of Cyprus) and Cyprus Eddy (south-west of Cyprus (Fig. 2). Local deep convection events occur periodically in the deep troughs ($>1000 m$) of the North Aegean Sea and in the deep basin of the South Aegean sea. Finally, in the Gulf of Lion (NW MS), a large scale cyclonic circulation and the extreme atmospheric forcing, especially in winter, force intense convective events, which eventually reach the bottom. Based on an analysis of wind driven surface Ekman transport, intermittent coastal upwelling events are also likely to take place in selected regions of the MS, namely the Alboran, Balearic, Straits of Sicily, East Adriatic and North-East Aegean Sea (Agostini and Bakun, 2002).

The two terms affecting the vertical flux of nutrients to the photic zone that allows new production are the depth of the mixing and the subsurface nutrient concentrations. A synthetic view of the mixed layer depth in different seasons is reported in Fig. 3. Main features are: i) the presence of few sites where maximum depth of mixing is greater than 200 m. Sub-basin cyclonic gyres and the large cyclonic area of the NW MS are likely the only sites where the doming of isopycnals may enhance vertical transport of nutrients due to winter convective events; ii) clear differences among regions in the time when the mixed layer reaches the maximum depth; iii) a different duration of the stratification season among different areas, with variable thickness of the layer, i.e., of the location of the pycnocline.

As for the second term, the inventory of surface and subsurface nutrients is represented in Fig. 4, where the average winter concentrations of nitrates at 10 and 100 m depths are shown. The two maps include the effect of the processes represented in Fig. 3, but also highlight the role played by the cyclonic structures sketched in Fig. 2. In addition, Fig. 4 shows the very strong west-east gradient in the subsurface nutrient concentration. Nutrient concentrations in coastal upwelling areas are lower than those found in other upwelling systems (Fig. 4), probably because the temporal scale of the upwelling events is very short. Therefore in those areas it should not be expected to observe a striking difference in biological production as compared with other active areas of the basin. By contrast, in situ observations and modeling studies suggest that mesoscale and submesoscale processes may affect biological activity in the MS, in the proximity of: i) active frontal regions (North Balearic-Catalan, Almeria-Oran, North-East Aegean Sea Fronts), ii) deep convection areas (Gulf of Lion, South Adriatic Gyre, Rhodos Gyre), and/or iii) sites where coastal morphology and intense wind stress generate a strong input of potential vorticity leading to energetic filaments (Bignami et al., 2008). The latter process, previously detected only through Sea Surface Temperature anomaly, is frequently observed also in high resolution remote sensing chl-*a* maps (Iermano et al., 2009). Such a feature may contribute to disperse coastal inputs toward the open sea, along with plankton. In fact, in addition to the mechanisms of vertical transport, a significant role in the MS is played by external inputs from the coasts, although only three major rivers are present, namely the Po River in North Adriatic Sea, the Rhone in the Gulf of Lion and the Nile in the South-East Levantine Sea, the latter with a dramatically decrease in transport over the last decades. More important at times is the deposition of aerial dust, which however is difficult to quantify correctly because atmospheric inputs are only monitored at a few sites located along the coasts. Despite the associated uncertainties, budget calculation (Ribera d'Alcalá et al., 2003; Krom et al., 2004) and, more recently, isotopic data (Krom et al., 2004; Sandroni et al., 2007; Schlarbaum et al., 2009) suggest that atmospheric inputs support a significant amount of new production, especially in the E MS. In particular, phosphorus addition from atmosphere may account for up to 40% of primary production and nitrogen addition might fulfill the nitrogen requirement for all the export production, at least in the E MS (Kouvarakis et al., 2001; Markaki et al., 2003).

Atmospheric inputs are certainly a crucial term in the functioning of the basin. A relevant biogeochemical feature in the MS is the very high N/P ratio in its deep layers. Processes leading to this feature are still controversial, but the high N/P ratio of atmospheric inputs indicates that they are among the contributing factors to the anomalous ratio recorded in Mediterranean waters (Markaki et al., 2008, and references therein).

Markaki et al. (2008) reported also that between 30 and 40% of the N and P input to the basin is in organic form highlighting the role of atmospheric inputs also as a source of organic matter. This adds to riverine inputs. Ludwig et al. (1996) estimated that approximately 0.8×10^{12} $\text{mol}\,\text{y}^{-1}$ of organic carbon may enter the basin from rivers as a result of erosion processes on the land. Therefore inputs from atmosphere and land contribute not only nutrients to support primary production but also reduced carbon potentially respirable. To complete the picture on respirable carbon not produced inside the basin we have also to account for the net DOC input through Gibraltar, which is in the order of 0.3×10^{12} $\text{mol}\,\text{y}^{-1}$ (Dafner and Bryden, 2001). Assuming a conservative OC/ON ratio of ten for the atmospheric inputs, its contribution is in the order of 0.35×10^{12} $\text{mol}\,\text{y}^{-1}$ of organic carbon. Those very rough figures, which are likely on the lower edge of real numbers because of the underestimated impact of anthropogenic activity, amount to $\sim1.5\times10^{12}$ $\text{mol}\,\text{y}^{-1}$ of allochthonous organic carbon entering the upper layer of the water column. It is well known that intermediate and deep layers of the basin display high oxygen utilization rates (Christensen et al., 1989; Roether and Well, 2001), which were further enhanced during the years of the Eastern Mediterranean Transient (Klein et al., 2003; La Ferla et al., 2003, and references therein). High oxygen utilization rates have generally been attributed to DOC oxydation (Christensen et al., 1989; Ribera d'Alcalá and Mazzocchi, 1999; La Ferla et al., 2003), part of which may originally derive directly or from reprocessing of allochthonous carbon.

In synthesis, MS displays lower nutrient values in the internal pool, especially for P, than the ocean at similar latitudes. In addition, vertical transport is effective in bringing them to the photic zone only in restricted areas: where convection is sufficiently deep, in a small number of frontal regions and in the few upwelling sites. This enhances the role of the inputs from the boundaries (atmosphere and coasts) in sustaining the new production of the basin and the whole Mediterranean food web.

3 Phytoplankton

3.1 Biomass and primary production

The first order response to the above described physical and chemical features is the distribution of phytoplankton biomass as chl-*a* (Fig. 5), which displays generally low values (less than 0.2 μgchl – al^{-1}) over large areas, with the exception of a large bloom observed throughout the late winter and early spring in the Liguro-Provencal Region. Pronounced phytoplankton blooms, though spatially limited, are also recorded in the Alboran Sea and in the area of the Catalan-North Balearic front. Wind affecting winter mixing and coastal upwelling, along with the presence of cyclonic structures, are considered to be the most relevant physical factors allowing the build-up of phytoplankton biomass through the induced increase of nutrient availability. An exception to this mechanism is the high biomass in the Alboran Sea, where the mesoscale dynamics (front) associated with the inflow of Atlantic water plays a major role. More confined high biomass spots are located near the coasts, especially in proximity to large river mouths or to extended continental shelf (e.g. Adriatic and North Aegean seas – the latter associated with the local front).

Both satellite data and in situ values measured across the MS reveal a west-east increasing oligotrophy gradient. The integrated chl-*a* concentration in May–June 1996 (Dolan et al., 1999) showed a west to east decline of a factor of about 7 (from 0.48 to 0.07 mgCm^{-3}). A similar trend was observed in June 1999 (Ignatiades et al., 2009) and in September 1999, when however the easternmost stations were not sampled and the decline was smoother (Dolan et al., 2002; Marie et al., 2006). The eastward latitudinal decrease is generally rather gradual and continuous across the WMS, with a sharp change at the transition between the two sub-basins and much smaller gradient if any, in the EMS. In addition to the west-east decrease, a decreasing chl-*a* gradient from north to south is also evident from both satellite data and in situ studies in both the eastern and the western basin (e.g., Morel and André, 1991; Barlow et al., 1997), with the exclusion of higher values along the Algerian coasts. These gradients clearly reflect the physiography of the basin and the related circulation patterns.

An intriguing picture was issued by grouping sites with a similar seasonal cycle and dynamics of chl-*a* values based on the whole SeaWiFS data set (D'Ortenzio and Ribera d'Alcalá, 2009). Seven bioprovinces (sensu Longhurst, 2006) resulted from the analysis (Fig. 6), which displayed markedly different patterns in the seasonal cycle. The first province, mostly concentrated north of the North Balearic front (no. 5 in the figure), presents a unique pattern, with a late winter-early spring bloom lasting more than three months, typical for temperate areas, and a biomass increase up to 6 fold the background values. Other provinces show a typical subtropical cycle, with biomass maxima centered in January but extending from December to early March. These provinces (nos. 1, 2 and 3) include the EMS, the area across the Algerian coasts, the areas affected by northerly continental winds (North Adriatic and North Aegean seas), and areas possibly affected by dust input, mainly represented in the southeastern part of the basin. The annual range of phytoplankton biomass in these provinces is much smaller, with maxima 2.5 fold the background values. Two provinces (nos. 6 and 7) seem to be driven by river runoff and continental shelf dynamics. The last province (no. 4), including e.g. the South Adriatic Sea, the Ionian Sea and the central part of the western basin, is the most interesting. It apparently combines features for the temperate and subtropical mode: the autumn bloom, typical of temperate regions, is followed by a progressive deepening of the thermocline and/or by the subsequent vertical transport due to cyclonic or mesoscale frontal dynamics (D'Ortenzio and Ribera d'Alcalá, 2009).

The relatively few in situ studies conducted in different periods of the year in the same area confirm the patterns obtained from satellite data, showing seasonality in biomass accumulation and production processes. At the station DYFAMED in the Ligurian sea, the only offshore Mediterranean site regularly investigated over more than a decade, the maximum values (up to 3 μgl^{-1}) are observed in late winter-early spring (Vidussi et al., 2001; Marty et al., 2002). Similarly high peak values are recorded in the Catalan front area (ca. 2 μgl^{-1} , Estrada, 1991; Estrada et al., 1993, 1999), whereas those in the Alboran Sea are still higher (4.3 μgl^{-1}, Mercado et al., 2005 and 7.9 μgl^{-1}, Arin et al., 2002). Notably, the spring peak values in the latter two areas were in many cases detected in deep waters in response to local doming of nutrient-rich waters caused by the Atlantic current (Arin et al., 2002; Mercado et al., 2005). Both a strong chl-*a* signal in late winter-spring and summer-autumn minima have been detected in many areas, but the values and ranges are different between the two MS sub-basins The maxima in the eastern basin rarely exceed 0.5 μgl^{-1} (Yacobi et al., 1995; Gotsis-Skretas et al., 1999), and the minima are as low as 0.003 μgl^{-1} (e.g., Herut et al., 2000). Exceptions are the peak values of 1.34 μgl^{-1} in the frontal zone of the North East Aegean Sea in April (Zervoudaki et al., 2007) and 3.07 μgl^{-1} in a small-scale cyclonic area of the Northern Levantine Sea in March 1992 (Ediger and Yilmaz, 1996). The South Adriatic and the Ionian seas show intermediate peak values (Boldrin et al., 2002; Nincevic et al., 2002). An autumn increase is generally undetected (Psarra et al., 2000; Marty et al., 2002), although this could be due to the inadequate temporal sampling scale. Indeed, a high frequency study conducted in a NW MS site, relatively close to the long term station DYFAMED, showed a two-threefold variability in bulk phytoplankton parameters (e.g. total chl-*a* and primary production) over a one-month period in the transition from summer to autumn 2004 (Andersen et al., 2009; Marty et al., 2009).

Low sampling frequency could also explain the high interannual variability, often of the same magnitude of the seasonal variability, shown for the Cretan Sea (Psarra et al., 2000) and for the Alboran Sea (Claustre, 1994; Mercado et al., 2005). Effects of climate variations are instead clearly seen in some areas of the basin which have been monitored more regularly over the years. For example, higher winter temperature and low wind intensity caused a decrease in biomass in oligotrophic coastal waters off Corse (Goffart et al., 2002), whereas an increase in biomass and production is reported for the long-term Ligurian Sea station DYFAMED in recent years, probably due to more intense winter mixing driven by circulation and wind (Marty, personal communication). At the basin scale, chl-*a* variability in the MS appears to be related to main climatic patterns of the northern hemisphere, namely, the East Atlantic pattern, the East Atlantic/Western Russian pattern, the North Atlantic Oscillation, the East Atlantic Jet and the Mediterranean oscillation (Katara et al., 2008).

Most of the times peak chl-*a* values ($>2\,\mu\mathrm{g\,l}^{-1}$) were localized in subsurface waters. This was the case for the Alboran Sea (Arin et al., 2002; Mercado et al., 2005) the Catalan-North Balearic front (Estrada, 1991; Delgado et al., 1992; Estrada et al., 1999), and for a cyclonic area of the North Levantine Sea (Ediger and Yilmaz, 1996). The highest value ever measured in offshore MS ($23\,\mu\mathrm{g chl}-a\mathrm{l}^{-1}$) was found in a 6 m thick subsurface layer around 54 m depth in the Almeria-Oran frontal area in late November 1987 (Gould and Wiesenburg, 1990). In addition to these deep biomass accumulations in very dynamic areas, a deep chlorophyll maximum (DCM), generally not exceeding $1.5\,\mu\mathrm{g chl}-a\mathrm{l}^{-1}$, is a permanent feature for the whole basin over the entire annual cycle, with the exception of the short period of the late winter mixing. The DCM progressively deepens from west to east (Fig. 7) from 30 m in the westernmost area (Dolan et al., 2002), to 70 m in the South Adriatic Sea (Boldrin et al., 2002), down to 120 m (Christaki et al., 2001; Dolan et al., 2002). This eastward deepening is probably related with lower productivity and hence higher seawater transparency in the Levantine Sea, but the level of DCM may vary notably between cyclonic and anticyclonic areas (Ediger and Yilmaz, 1996). In the westerm MS the depth of the DCM is strongly affected by the Atlantic water inflow and by the consequent physical dynamics along the vertical axis (Raimbault et al., 1993).

The distribution of biomass is clearly reflected in primary production rates (Table 1). Satellite data range from 130 to 198 $\mathrm{gC\,m}^{-2}\mathrm{y}^{-1}$ over the years 1997–2001 (Bricaud

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et al., 2002; Bosc et al., 2004), with values for the EMed generally in the lower portion of the range. Estimates from in situ incubation in previous decades were as low as 80–90 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$ (Sournia, 1973). More recent measurements get closer to satellite-based estimates, e.g. in the Gulf of Lion (140–150 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$, Conan et al., 1998), but remain consistently lower in other areas such as the Cretan Sea (59 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$, Psarra et al., 2000). A clear eastward reduction in primary production is reported in the results from a late-spring (May-June) transmediterranean cruise (Moutin and Raimbault, 2002), when maxima close to 1 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ in the south western basin and minima between 150 and 250 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ at several stations of the Levantine Sea were measured (Fig. 8). Interestingly, estimates obtained in spring in other areas reflect the same spatial pattern and are within the same ranges as those shown by Moutin and Raimbault (2002). Comparably high values (up to 1 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$) were reported in the Catalan front area in March (Moran and Estrada, 2001), and in the Alboran Sea in May-June (Lohrenz et al., 1988). At the DYFAMED station in the Ligurian Sea primary production rates were 240–716 $\mathrm{mg\,C\,m^{-2}}$ (in 14 h) (Vidussi et al., 2001) but reached values as high as 1.8 $\mathrm{g\,C\,m^{-2}\,d^{-1}}$ in April (Marty and Chiaverini, 2002). Measurements at other sites of the EMS, namely in the South Adriatic Sea (Boldrin et al., 2002) and in the North East Aegean Sea (Ignatiades et al., 2002; Zervoudaki et al., 2007), also match the low values recorded by Moutin and Raimbault (2002).

Spatial and seasonal variability of primary production values can be high (Table 1), especially in very dynamic areas like the Alboran Sea (Macías et al., 2009) or the Catalan Sea (Granata et al., 2004). Interannual variability of primary production may also be high, mainly depending on the depth of the winter mixing (Estrada, 1996). In spite of light limitation, the contribution of subsurface and DCM can be significant, reaching in some cases 30% of the total production of the water column (Estrada et al., 1985).

All in situ and satellite values of primary production reported above are estimates for gross primary production and include a significant portion of recycled production. New primary production is much lower, in the order of 4.5 $\mathrm{mol\,C\,m^{-2}\,y^{-1}}$ (1 mol C≡12 g C) and 1.5 $\mathrm{mol\,C\,m^{-2}\,y^{-1}}$ for the western and the eastern basin, respectively (e.g. Bethoux, 1989), which add up to 3.6×10^{12} and 2.1×10^{12} mol y^{-1} of new carbon produced in the two basins. Comparing those figures with the very rough estimate of allochtonous carbon inputs for the whole basin (1.5×10^{12} mol y^{-1}, see Sect. 2), we confirm that external inputs besides sustaining new production, actually introduce organic carbon at rates comparable with new production rates, with relevant implications which will be discussed in Sect. 6.

3.2 Community structure and composition

At a first sight, the emerging picture from many studies shows the dominance of the picophytoplankton as the fingerprint of the MS and of its overriding oligotrophy. As mentioned above, the peculiar and notably diversified physical structure of the Mediterranean is reflected in the presence of areas of higher nutrient availability and intense biological activity. Some of these areas are, for example, the permanent mesoscale structures such as the Alboran gyres and the Catalan front and the sites of deep-convection, such as the North Balearic area, the South Adriatic and the Rhodos cyclonic gyres (see the above sections). In those areas, different planktonic associations are found, in which cyanobacteria and picoeukaryotes often coexist or alternate with diatoms, dinoflagellates and other flagellates belonging to different algal groups. The strong seasonality ruling the basin also creates optimal conditions for the alternation of phytoplankton populations dominated by different functional groups and species. Finally, the DCM provides a still different set of environmental conditions where distinct phytoplankton populations are found. In most areas, these diversified patterns in species distribution can only be deduced from scattered studies.

This highly dynamic patchwork of populations that are different over the temporal and spatial scale contrasts the situation of other oligotrophic seas generally reported to host rather stable phytoplankton (e.g. Goericke, 1998; Venrick, 2002). The information available is too heterogeneous to allow tracing large scale patterns in species distribution that can parallel the spatial patterns in biomass and production depicted in the previous section. However, from the few studies conducted across the basins it appears that spatial differences in phytoplankton populations are not simply quantitative. For example, chemotaxonomic studies showed that in late spring 1996 prymnesiophytes and 19-BF containing taxa (mainly chrysophytes and pelagophytes) decreased eastward while cyanobacteria, did not vary significantly across the basin (Dolan et al., 1999). Indeed, longitudinal biomass patterns in September 1999 seemed to be mainly caused by a decrease in microplankton and nanoplankton rather than by picoplankton (Dolan et al., 2002) (Fig. 9). In the early summer of the same year, an eastward increase in the diversity of dinoflagellates and mainly of coccolithophores was reported across the basin, whereas an opposite trend was evident for diatoms (Ignatiades et al., 2009). Finally, significant latitudinal differences were evidenced in chemotaxonomic markers of the different phytoplankton groups in summer 1993 across the WMS basin, when nanoflagellates were more important in the northern stations as compared to the southern ones (Barlow et al., 1997).

In the following, we present a brief account of the main microalgal groups in the MS in different conditions. The rationale behind an appraisal by species groups is that, given the differences in ecophysiological characteristics among the various groups, insights can be gained from their distribution on the prevalent environmental conditions. On the other hand, the different groups depicted below are included in completely distinct trophic pathways, and can hence provide information on the fate of autotrophic production.

3.2.1 The smallest fraction (prochlorophytes, *Synechococcus*, picoeukaryotes)

Like in most oligotrophic and subtropical oceanographic regions, (Takahashi and Bienfang, 1983; Takahashi and Hori, 1984; Li, 2002), in the MS low biomass values are generally associated with the dominance of cyanobacteria, prochlorophytes and tiny flagellates (Yacobi et al., 1995; Dolan et al., 2002; Ignatiades et al., 2002; Casotti et al., 2003; Brunet et al., 2007; Tanaka et al., 2007). As an average on the whole basin, this smallest fraction of the phytoplankton, which is generally ignored in routine light microscopy counts, contributes for 59% of the total chl-*a* and 65% of the primary production. However the values widely vary depending on the locations, depths, seasons as well as on the method used and size fraction considered (Magazzù and Decembrini, 1995). In the eastern Basin, values up to 80% of total biomass were reported for waters off Israeli coast (Berman et al., 1984) and in the Straits of Sicily during the summer (Brunet et al., 2006). With the exception of the highly dynamic mesoscale structures, picoplankton dominates the upper water layers of the Eastern Basin through most of the year, e.g., in the southern part of the Levantin Basin in autumn (Yacobi et al., 1995), in the Straits of Sicily in July (Brunet et al., 2007), in the Cyprus eddy in May (Tanaka et al., 2007), in the Ionian Sea in April/May (Casotti et al., 2003) and in the Aegean Sea (Ignatiades et al., 2002). Picoplankton is often dominant also in the DCM, both in the western basin, e.g. at DYFAMED (Marty et al., 2002) or in the Aegean Sea (Ignatiades et al., 2002).

Among picoplankton, *Synechococcus* and *Prochlorococcus* can reach abundances up to 10^4 cells ml^{-1} (Zohary et al., 1998; Christaki et al., 2001). At the NW Mediterranean station DYFAMED, *Synechococcus* is dominant in the upper layers in stratification periods when, despite the pronounced oligotrophy, it is apparently responsible for maximum photosynthetic efficiency (Pb) values probably due to its capacity to cope with low nutrient conditions (Marty and Chiaverini, 2002). Like in other oceans, prochlorophytes are instead found most often in deeper layers in stratified conditions (Yacobi et al., 1995), while they become abundant at surface over the autumn/winter (Fig. 10, Marty et al., 2002). In the EMS also, *Prochlorococcus* presents a typical distribution with a very sharp maximum concentration near the bottom of the euphotic zone (Zohary et al., 1998; Partenski et al., 1999; Christaki et al., 2001). However, prochlorophytes have also been found to be abundant in surface waters in summer (Vaulot et al., 1990). This contradictory distribution can be explained by the existence of two distinct ecotypes of *Prochlorococcus* (Moore et al., 1998), showing preferences for high-and low-light conditions, respectively. Both types, substituting one another along the water column, have been identified in the MS (Brunet et al., 2007).

In addition to prokaryotes, quite a high diversity of eukaryotes may be found within the picoplanktonic fractions, among which prasinophytes, pelagophytes, prymnesiophytes and chrysophytes. Tiny ($<3\,\mu$m) autotrophic and heterotrophic flagellates in the order of 10^3–10^4 cells ml^{-1} have been reported to be the dominant component in cell numbers among flagellates when these are enumerated using epifluorescence counts (Christaki et al., 2001). Several non-colonial picodiatoms (e.g., some *Chaetoceros*, *Thalassiosira*, *Minidiscus*, *Skeletonema* and some cymatosiracean species) have also found to be abundant in some cases (Delgado et al., 1992, Percopo and Zingone, unpublished data), although their small size may prevent their identification even at the class level.

Picoeukaryotes in some cases have shown specific distribution patterns, mainly gleaned from their specific pigment signatures. For example, in the Straits of Sicily, the $<3\,\mu$m fraction in summer stratified oligotrophic conditions (0.010–0.60 μg chl-*a* l^{-1} below 50 m) was dominated by picoeukaryotes, largely prymnesiophytes, which gradually replaced the prokaryotes that were dominant in the upper layers (Brunet et al., 2007). Pelagophytes have been found to be important in deep waters at several places, e.g., in the Alboran Sea (Claustre et al., 1994) and in other areas of the western MS (Barlow et al., 1997), as well as in the Straits of Sicily (Brunet et al., 2006, 2007).

In general, it is difficult to interpret the apparent differences in the distribution and relative contribution of eukaryotes to picoplanktonic biomass, mainly because of the few and scattered data and of the rather low and different taxonomic resolution provided by the various identification methods (e.g. flow-cytometry, epifluorescence, electron microscopy and chemical taxonomic methods). However, recently developed molecular methods not only add evidence of the actual abundance and diversity of tiny eukaryotes but also allow tracing their seasonal succession (McDonald et al., 2007) and fine distribution (Fig. 11; Marie et al., 2006; Foulon et al., 2008). A more extensive application of these methods in oceanography will contribute to build up knowledge on the specific ecological role of the least known component of the MS phytoplankton.

3.2.2 The nanoplankton

The size component smaller than 20 μm, commonly defined as nanoplankton, is mainly constituted of small flagellates (generally $<5 \mu$m) and dinoflagellates, mostly naked species, in addition to a limited number of small solitary diatom species. Single cells of colonial diatoms are often also smaller than 20 μm, but they are treated separately because of their larger functional size and quite distinct ecological role. Small nanoflagellates are the dominant group in terms of cell numbers most of the year in oligotrophic MS waters (Decembrini et al., 2009; Revelante and Gilmartin, 1976; Malej et al., 1995; Totti et al., 1999). Similarly to the $<3 \mu$m eukaryotic fraction, a long-standing lack of taxonomic resolution for this heterogeneous group has lead to the view that it does not vary significantly in quality and quantity over time and space, probably because it is kept in check by equally fast-growing predators (Banse, 1995; Smetacek, 2002). However, there are several indications that nanoflagellates do vary in space and time, and may also significantly contribute to blooms, e.g., in the Catalan Sea (Margalef and Castellví, 1967) or at DYFAMED (Marty et al., 2002). From pigment signatures, prymnesiophyceans often represent a large part of them most of the year and at several places (Latasa et al., 1992; Claustre, 1994; Bustillos-Guzmán et al., 1995; Barlow et al., 1997; Zohary et al., 1998). Among the few mentioned taxa there are the species of the genus *Phaeocystis*, which may form large, recognisable colonies (see the section on microplankton below), but are not easily detected when they are in the flagellate stage. Among prymnesiophytes, the coccolithophores deserve a special mention, as they show a high diversity in the MS (Cros and Fortuno, 2002). The widespread species *Emiliania huxleyi* is generally the dominant coccolithophore, although it does not seem to form such spectacular blooms as those revealed by satellite images, e.g., in the North Sea. Coccolithophores have been found to constitute large part of the population in autumn and winter, e.g., in the Rhodos gyre area (64%, Gotsis-Skretas et al., 1999; Malinverno et al., 2003), in the Aegean Sea (Ignatiades et al., 1995), South Adriatic and Ionian Sea (Rabitti et al., 1994). A consistent fraction of coccolithophores was reported also in winter offshore the Catalan Front (Estrada et al., 1999), or in spring in the Aegean Sea (Ignatiades et al., 2002) and maximum fluxes were recorded in winter-spring in the central EMS (Ziveri et al., 2000). In a June 1999 transmediterranean study, coccolithophores were found to be more diversified and abundant at eastern stations than at western ones (Ignatiades et al., 2009).

Cryptophytes, often only detected by their marker pigment alloxanthin, are generally more abundant when diatoms are also abundant, e.g. in winter and spring at the station DYFAMED (Vidussi et al., 2001; Marty et al., 2002) or in the Cretan Sea (Gotsis-Skretas et al., 1999). In this group, species names often mentioned in light microscopy investigations should all be reconsidered, as most species can only be recognised in live samples or using electron microscopy (Cerino and Zingone, 2007).

As for small dinoflagellates, they mainly include naked autotrophic and heterotrophic species which are poorly known and are not identifiable in light microscopy. In addition, their pigment signature may overlap with that of other flagellate groups. All information about these nano-dinoflagellates derives from microscopic counts, based on which they are less abundant than flagellates but much larger and hence more important in terms of biomass, especially in late spring and summer. In the eastern basin, dinoflagellates were reported to be dominant in different seasons and especially in stratified conditions (Berland et al., 1987; Gotsis-Skretas et al., 1999; Totti et al., 2000; Psarra et al., 2000; Ignatiades et al., 2002), although the flagellates $<5\,\mu$m were not enumerated in these cases. Some small thecate species such as *Prorocentrum* (*P. minimus*, *P. balticum*), *Heterocapsa* or *Scrippsiella*-like species are also part of this component, but they are generally not abundant in MS offshore waters.

3.2.3 The colonial and large diatoms

The general rule that the contribution of picoplankton and nanoplankton decreases along with the increase of chl-*a* concentration (Li, 2002) is also valid for the MS. The presence, and at times the dominance, of colonial diatoms that are part of the size fraction larger than 20 μm (microplankton) belonging to several genera (*Asterionellopsis*, *Chaetoceros*, *Thalassiosira*, *Thalassionema/Thalassiothrix*, *Pseudo-nitzschia*) is associated with relatively dense biomass accumulation that in the MS is typical of very different situations, namely i) the winter bloom, ii) the deep convection, gyre and front areas, and iii) the summer-autumn DCM.

A diatom increase is evident at many sites of the WMS (Marty et al., 2002; Claustre et al., 1994) and EMS (Gacic et al., 2002; Wassmann et al., 2000) in February-March, confirming the consistent anticipation of the vernal bloom as "the unifying signature" of the basin (Margalef and Castellví, 1967; Duarte et al., 1999). However these events are very ephemeral in offshore waters. For example, a diatom increase is regularly recorded at DYFAMED in February–March (Fig. 10), but an actual bloom is missed by the monthly measurements of primary production (Marty and Chiaverini, 2002). No diatom bloom was detected either during a February cruise in the Adriatic Sea (Totti et al., 1999), whereas in January and in March diatoms reached 58 and 37%, of the $>5\mu$m fraction of the phytoplankton, respectively, in the Cretan Sea (Gotsis-Skretas et al., 1999), and 88% at shelf stations (Psarra et al., 2000). Notably, massive sedimentation events are often recorded in the Mediterranean Sea in winter (Miquel et al., 1994; Stemmann et al., 2002), suggesting that these diatom blooms are scarcely exploited by zooplankton populations (Duarte et al., 1999; Ribera d'Alcalá et al., 2004), but are rather a resource for the zoobenthos of the underlying bottom (López et al., 1998; Zupo and Mazzocchi, 1998), for which winter is not a resting period (Coma et al., 2000), probably as an adaptation to the recurrent food rain from above (Duarte et al., 1999; Calbet, 2001).

In addition to the winter bloom, diatoms also dominate, and for longer periods, in deep convection areas. There, mixing largely exceeds the critical depth but blooms are possibly allowed by brief periods of quiescence. Colonial species belonging to the genera *Pseudo-nitzschia* and *Chaetoceros* largely dominated in spring in deep convection areas of the North Balearic sea (Zingone and Sarno, unpublished data). In the Otranto Straits, high concentrations of healthy *Chaetoceros* were found as deep as 500 m (Vilicic et al., 1989). Apparently, diatoms in highly dynamics areas are only associated with the highest biomass values. For example, prymnesiophytes and prokaryotes instead of diatoms dominated in March in the Cyprus eddy, with moderately high chl-*a* concentrations (59 mg m^{-2} at the core and 45.5 mg m^{-2} at the boundary) (Zohary et al., 1998).

Colonial, bloom forming diatoms belonging to the genera *Chaetoceros*, *Thalassiosira*, *Proboscia*, *Rhizosolenia*, *Leptocylindrus* are generally the main contributors also to high chl patches in the very dynamic environments associated with fronts and gyres (Fiala et al., 1994; Arin et al., 2002; Ignatiades et al., 2002; Zervoudaki et al., 2006, 2007). These structures, which are seen both in the WMS and EMS (see the above section), have been defined the "oasis" of the Mediterranean desert (Claustre et al., 1994). The biological phenomena that they drive are spatially heterogeneous, strictly depending on water mass dynamics and show a very high temporal dynamics, besides a marked interannual variability (Mercado et al., 2005).

Diatom-dominated chl-*a* peaks are often found in subsurface waters (Arin et al., 2002), as in the exceptional case of a monospecific blooms of a *Thalassiosira* (probably *Th. partheneia*) forming gelatinous colonies (~10^{6} cells l^{-1} and 23 μg chl-*a* l^{-1}), which was detected at 54 m depth in the Almeria-Oran front area (Gould and Wiesenburg, 1990). The formation and dynamics of these deep accumulations are strictly linked to the frontal circulation (e.g., Raimbault et al., 1993) and therefore are quite different from those characterizing the development of the seasonal DCMs.

A significant contribution of diatoms to the DCM has been reported from many areas of the MS, e.g. the Catalan Sea (Margalef, 1969), Southern Adriatic Sea (Boldrin et al., 2002) and Cretan Sea (Gotsis-Skretas et al., 1999). The frequent finding of the same species that are typical of the high production situations described above, supports the hypothesis that the DCMs are sites of active growth, rather than of passive accumulation. Here diatoms are found in association with picoplankton or, at times, markedly dominating the subsurface populations (e.g. Decembrini et al., 2009). The relative importance of diatoms may vary greatly over the time and across sites (Estrada and Salat, 1989; Estrada et al., 1993). In one of the few cases of across-basin studies at the species level (Ignatiades et al., 2009), diatoms seemed to be by far less abundant in the Levantine basin DCM as compared to the stations in the western basin (Fig. 11). Interestingly, in the summer DCM at the station DYFAMED, diatoms are associated with the highest chl-*a* concentrations and sit under a layer occupied by prochlorophytes and nanoflagellates, whereas *Synechococcus* dominates in the above oligotrophic waters (Marty and Chiaverini, 2002). This vertical zonation, similar to that reported in the Atlantic waters (Claustre et al., 1994), points at a tightly structured system, within which the distinct phytoplankton components may have different ecological roles.

While colonial *Chaetoceros* species are a rather constant feature of diatom-dominated DCMs, the accompanying assemblages seem to vary from area to area. For example, *Pseudo-nitzschia*, *Rhizosolenia* and *Thalassiosira* were reported in the Catalan-Balearic DCM (Latasa et al., 1992), while *Leptocylindrus danicus*, *Pseudo-nitzschia delicatissima*, *Thalassionema nitzschioides* were found in the Southern Adriatic Sea (Boldrin et al., 2002). To the east, *Bacteriastrum*, *Hemiaulus*, *Thalassionema*, *Thalassiothrix* were found south of Crete in July (Berland et al., 1987), whereas *P. delicatissima*, *Dactyliosolen fragilissimus*, and *Thalassiothrix frauenfeldii* were found north of Crete in June (Gotsis-Skretas et al., 1999). Finally, in the Southern Tyrrhenian Sea the DCM was dominated only by *Leptocylindrus danicus* in June 2007 (Percopo and Zingone, unpublished data). These differences in species composition are relevant but, to assess their actual consistency and ecological significance, more observations are needed. Overall, the intermittent and most probably undersampled pulses of diatom growth in deep waters might contribute explaining the mismatch between the relatively few reports of diatoms in phytoplankton samples and the high amount of biogenic silica found in surface sediments and sediment traps (Kemp et al., 2000).

While the above-mentioned colonial species often appear in relatively high concentrations, other large-sized diatoms are found at lower concentrations in the offshore MS waters. These large diatoms have been indeed reported as responsible for a substantial and underestimated fraction of primary production in oligotropic waters characterized by a strong seasonal thermocline and nutricline in areas outside the MS

(Goldman, 1993) however they have a patchy or sparse distribution and are generally not sampled properly. Among them are some of the large *Rhizosolenia* species, which may form migrating mats in other oceans (Villareal et al., 1996), and together with species of the genus *Hemiaulus*, may host the diazotrophic cyanobacteria *Richelia intracellularis*, thus playing a role in nitrogen fluxes in the pelagic ecosystems (Villareal, 1994; Villareal et al., 1996). However, diatom-diazotroph associations do not seem to form large-scale blooms off the Israeli coast, possibly because of P-limitation in those waters (Zeev et al., 2008).

3.2.4 Other microplankton species

The diversity of microplanktonic dinoflagellates is very high in the MS (Marino, 1990; Gómez, 2006), although their importance in terms of biomass is rather low and their ecological role is still to be assessed. Indeed, quantitative information is very fragmentary for this group, which has often been aggregated with the small dinoflagellates. In the size fraction higher than 20 μm, dinoflagellates are generally more abundant than diatoms, with the exception of the cases of high productivity mentioned above (Marty et al., 2009). The species most commonly reported are those of the genera *Gymnodinium*, *Gyrodinium*, *Ceratium*, *Protoperidinium*, *Oxytoxum*, which are generally associated with warm and stratified waters (Estrada, 1991). Very few are the cases when the percentage contribution of species of this group is high. One such case is *Oxytoxum* spp. reaching 12% of total cell counts in the Alboran Sea (Lohrenz et al., 1988). Indeed, as for diatoms, the larger-sized species are not sampled properly most of the time, and can also escape capture because they are can effectively swim. Like in the case of the largest diatoms, the role of this component can be relevant despite its low abundances. Some of them, e.g., in the genera *Ornithocercus*, *Histioneis* and *Citharistes*, can host endosymbiotic cyanobacteria that would allow their existence, under severe nitrogen limitation (Gordon et al., 1994).

Species of the widespread genus *Ceratium* may be mixotrophic (Smalley and Coats, 2002), occupy selected depths (Tunin-Ley et al., 2007), and constitute good biological indicators of warming in the MS (Tunin-Ley et al., 2009). Finally, *Protoperidinium* spp. and several athecate dinoflagellates in the genera *Gymnodinium*, *Gyrodinium* and *Lessardia* are truly phagotrophic and may constitute a main part of the microzooplankton (Sherr and Sherr, 2007), but their importance in the offshore Mediterranean has rarely been assessed (see Margalef, 1985). Finally the silicoflagellates *Dictyocha* and *Distephanus* are also a constant although scarce component of offshore MS plankton, their abundance reaching the highest values in surface waters in winter (Totti et al., 2000) or in deeper waters in spring-summer (Lohrenz et al., 1988; Estrada et al., 1993).

In addition to dinoflagellates and silicoflagellates, a few flagellates that can form large colonies are also part of the offshore microplankton at least in some phases of their life cycle. One of these is the key species *Phaeocystis* cf. *globosa* (often reported in the Mediterranean Sea under the name of the congeneric, cold-water species *P. pouchetii*), which can form spherical colonies reaching a few millimeter diameter. The species has occasionally been recorded as abundant in the Catalan Sea (e.g., Estrada, 1991) where its importance is apparently increasing over the last years (Margalef, 1995). Another interesting species is the prasinophyte *Halosphaera viridis*, which has been found down to 1000 m in autumn-winter (e.g., Kimor and Wood, 1975) but then rises to shallow water in spring. Such extensive migrations could account for considerable upward recycling of carbon and nutrients (Jenkinson, 1986). Unfortunately, like in the case of large dinoflagellates and diatoms, there are not many data on the distribution of these interesting microplanktonic taxa in offshore waters, due to the limited usage of net samplers in recent phytoplankton studies.

4 Heterotrophic microbes and viruses

In the MS the hypothesis of phosphate limitation of primary production, firstly demonstrated by Berland et al. (1980), and the remarkably pronounced gradient of P depletion from west-to-east (Krom et al., 1991; Thingstad and Rassoulzadegan, 1995, 1999), have inspired numerous studies dealing with microbial processes. Recent technological and conceptual breakthroughs are beginning to allow us to address biological complexity in terms of diversity and open new perspectives in integrating microbial loop processes into predictive models of ecosystem functioning. Here we describe the different components and processes within the microbial food web focusing on heterotrophic microbes, including the viral shunt, in the Mediterranean open sea waters. Based upon data published over the last 25 years, we attempt to establish some large-scale patterns of abundance and activities for viruses, bacteria and protists along the Mediterranean west-east gradient.

4.1 Viruses

The net effect of viruses relevant to the pelagic food web is the transformation of particulate organic matter (the host) into more viruses, and returning biomass into the pools of dissolved and colloidal organic matter – "the viral shunt". Studies on viruses in the open MS are few, even less than in other marine areas. To date, most Mediterranean work has examined viral control on bacterial accumulation rather than characterization of the viral community. The studies have revealed viral abundances in the surface waters which vary from $0.08 \pm 0.01 \times 10^7$ to $1.6 \pm 4.8 \times 10^7$ viruses ml^{-1}, while lower values occur in deeper waters (Fig. 12, Table 2). In the MS as elsewhere, viral abundances increase from the oligotrophic to more eutrophic waters. Existing data (Table 2) also suggests that while viral abundance correlates with chl-*a* concentration (n=46, r=0.409, p<0.05), a tighter relationship exists between viral and bacterial abundances (n=46, r=0.549, p<0.01) implying that bacteria are more probable virus hosts than phytoplankton cells. Viral concentrations are related to both bacterial abundances (n=24,

r=0.520, $p<0.05$) and bacterial production (n=24, r=0.421, $p<0.05$). The low correlations between viral and bacterial abundance reflect in part the fact that the virus to bacteria abundance ratio (VBR) in the upper 200 m layer of the MS varies between 5 and 50 (Fig. 12). The wide range of this ratio, suggests that viruses may belong to different types of host organisms, and/or that viral concentrations are temporally variable with different samplings reflecting different phases of infection and release from host cells.

Comparing the WMS and EMS, viral and bacterial abundances to the west appear to be more tightly coupled than to the east (Fig. 13 and Table 3). However, these trends have to be taken cautiously, because the number of samples for the EMS are relatively few, and differences between slopes are not statistically significant (t-student, t_{value}=2.3; p=0.17). Viral infection accounts for less than 20% of bacterial mortality in the Catalan Sea thus being definitely less important than mortality due to grazing by protists (Guixa-Boixereu et al., 1999a,b). However, virus-induced mortality can occasionally prevail over grazing by heterotrophic nanoflagellates, for example at higher bacterial abundances in coastal waters (Weinbauer and Peduzzi, 1994). In a gradient from eutrophic to oligotrophic waters of the Adriatic Sea, viral production was higher in eutrophic areas and viral decay rates were not balanced by viral production rates over short time scales (Bongiorni et al., 2005).

Alonso et al. (2002) characterized 26 bacteriophages of the viral community found in the Alboran Sea. Most of them belonged to two of the three tailed families of the order Caudovirales; phages were grouped in 11 classes on the basis of protein patterns and sizes of viruses were between 30 nm to >100 nm. Different morphotypes of bacteria hosted viruses of different sizes. Thus, virus between 30 and 60 nm mainly infected rods (74%) and spirillae bacteria (100%), while viruses between 60 to 110 nm were mostly found inside cocci (65.5%).

4.2 Bacteria

The first study in the open Mediterranean examined the ultra-oligotrophic waters of the Levantine Sea (Zohary and Robarts, 1992) and showed that bacterial abundance, at 3×10^8 cells$\,l^{-1}$, clustered around the lower threshold of the world ocean (Cho and Azam, 1990). In the MS, while bacterial numbers are quite stable and bacterial production is low (Table 4) there are important variability aspects to consider: (i) the west-east gradient of increasing bacterial production (Christaki et al., 2001; Van Wambeke et al., 2000, 2002), and (ii) the enhanced metabolic activities and production related to specific hydrologic discontinuities, such as currents, eddies and frontal areas (Fernàndez et al., 1994; Moran et al., 2001; Van Wambeke et al., 2004; Zervoudaki et al., 2007). Interestingly, the slopes of log-log linear regressions for bacterial biomass and bacterial production obtained for WMS and EMS (Fig. 14a) are not significantly different ($t_{\mathrm{value}}=-0.22$; $p=0.85$) with both slopes being smaller than 0.4, thus suggesting top-down control on bacteria (Billen et al., 1990; Ducklow, 1992).

Following the general pattern of increasing oligotrophy eastward, bacterial production is several times lower in the eastern than in the western basin (Turley et al., 2000; Van Wambeke et al., 2000, 2002). However, the relationship between bacterial production and primary production is quite similar in the EMS and WMS. Updating Turley et al. (2000) data set (Table 3), plots of log bacterial production (BP) and log primary production (PP) for the WMed and the EMed display similar positive slopes ($t_{\mathrm{value}}=-0.22$; $p=0.87$) (Fig. 14b). The significant positive relationship between BP and PP suggests that primary production is an important source of DOC fuelling bacterioplankton.

A crucial factor that might limit bacterial production in the MS is the availability of inorganic nutrients, especially phosphorus. A nutrient control on bacterial production, as well as on bacterial adaptations to cope with the oligotrophy of the open MS, have been experimentally approached in a number of studies. During a Lagrangian experiment, phosphate addition to ultra-oligotrophic surface waters of the Levantine Sea, caused an unexpected ecosystem response: a decline in chl-*a* concentration and an increase in bacterial production. It has been hypothesized that while phytoplankton was concurrently N and P limited, bacterial growth was mainly limited by phosphorous (Pitta et al., 2005; Thingstad et al., 2005; Zohary et al., 2005). However, while phosphorus is usually the limiting nutrient, nitrogen and carbon limitation or co-limitation also occurs, and the type of limitation can vary with depth (Sala et al., 2002; Van Wambeke et al., 2000, 2009). It seems that the bacterioplankton of the oligotrophic Mediterranean live in a dynamic equilibrium in which slight changes in grazing pressure, competition and nutrient concentrations can shift the communities from limitation by one nutrient to another (Sala et al., 2002). Indeed, over time scales of a few hours, large shifts in abundance, production, and portions of particle-attached or free-living bacteria have been documented (Mével et al., 2008).

The metabolism of natural communities of bacterioplankton has been studied in terms of enzymatic activity and dissolved amino-acid (DFAA) uptake; these parameters are indicators of the uptake of dissolved organic matter by bacteria and the factors possibly influencing uptake (Karner and Rassoulzadegan, 1995; Van Wambeke et al., 2000, 2004; Christaki et al., 2003; Misic and Fabiano, 2006). For example, in a longitudinal study across the MS, alkaline phosphatase activity was used as indicator of bacterial P-limitation (Van Wambeke et al., 2002). Alkaline phosphatase turnover times less than 100 h were documented and corresponded to situations of P limitation of bacterial production. In a study conducted in the Aegean Sea, ectoaminopeptidase activity was weakly related to bacterial production, but tightly coupled with respiration rates of amino acids; moreover, the percentage of respiration of DFAA was relatively high (50±18%) (Christaki et al., 2003). The authors hypothesized that bacteria used the amino acids added in the samples to meet energy requirements for cell maintenance rather than biomass production.

Surprisingly little information exists on bacterial respiration (BR) and bacterial growth efficiency (BGE=BP/[BP+BR]) and furthermore, the studies are limited to the WMS. However, the studies underline the importance of BR to total plankton community respiration. The mean portion of BR to community respiration was 65% in the NW MS

(Lemée et al., 2002), and an average value of 52% (range 41 to 85%) was recorded closer to the coast (Navarro et al., 2004). It is noteworthy that BR as a percent of total community respiration increased with the percentage of high DNA bacteria. Bacterial respiration rates ranged from ~0 to 3.64 μmolO_2 l^{-1} d^{-1} (Lemée et al., 2002; Navarro et al., 2004).

Generally BGE tends to be low in oligotrophic systems, perhaps because most of the DOC pool is recalcitrant and inorganic nutrients are scarce (del Giorgio et al., 1997). In the MS an accumulation of DOC in the surface waters has been hypothesized as resulting from nutrient limitation of bacterial activity, specifically BGE (Thingstad and Rassoulzadegan, 1995; Gasol et al., 1998). Indeed, in the Almeria-Oran geostrophic front and adjacent Mediterranean waters BGE was estimated to be 7% (Sempéré et al., 2003). Conversely, in a study over a year in the NW MS, Lemée et al. (2002) report that BGE ranged widely, from 0.1 to 43%. These authors underline that they could not identify any regulatory mechanisms of BGE and respiration over this period.

Preliminary microbial diversity studies from Mediterranean samples revealed a considerable diversity of unknown prokaryotes (e.g., Pukall et al., 1999). Community fingerprinting by 16S rDNA restriction analysis applied to WMS offshore waters showed that the free-living pelagic bacterial community was very different from that living on aggregates (Acinas et al., 1997, 1999) and similar results were obtained in the EMS (Moesender et al., 2001). A study of the bacterial assemblages carried out offshore Barcelona using the DGGE (denaturing gradient gel electrophoresis) technique showed that diversity index followed a seasonal dynamics, but bacterial assemblages were relatively similar over 10's of kilometres suggesting that coastal areas might be characterized by rather homogeneous communities (Schauer et al., 2000). Distinct communities, stable over the time-scale of a month were found in different depth strata between 0 and 1000 m by Ghiglione et al. (2005, 2008) in the NW Mediterranean. In terms of temporal stability, a rather stable taxonomic composition of bacterioplankton was reported over time for Blanes Bay (Alonso et al., 2002; Schauer et al., 2003).

4.3 Protists

4.3.1 Heterotrophic nanoflagellates

In open MS, heterotrophic nanoflagellates (HNF) are usually dominated by small cells (≥80% less than 5 μm) with total abundances between 10^5 and 10^6 cells l^{-1} (Zohary and Robarts, 1992; Christaki et al., 1999, 2001, Tables 3 and 4). Nanoflagellate bacterivory is important, accounting from 45 to 87% of daily bacterial production in an East-West Mediterranean transect (Christaki et al., 2001). Spatially variable bacterivory rates were reported for the NW Mediterranean, ranging from <10 to 100% of bacterial production with bacterial consumption positively correlated with the presence of High-DNA bacteria (Vaqué et al., 2001). In the Aegean Sea, bacterivory by HNF and mixotrophic nanoflagellates roughly balanced bacterial production (Christaki et al., 1999).

Although the number of papers reporting HNF abundance and their grazing activity is limited (Table 4), they provide a quite good spatial coverage of the open Mediterranean, and overall suggest that bacterivory is the dominant cause of bacterial mortality. According to the model of Gasol (1994), the plot of the relationships between log HNF abundance (HNF, ml^{-1}) and log bacterial abundance (ml^{-1}) suggests that HNF are resource, or bottom-up, controlled by bacteria (Fig. 14c). A tight coupling of HNF and bacterial concentrations supports the view that bacteria are top-down controlled as we have suggested above (Fig. 14a).

Little is known about HNF diversity in the Mediterranean; Massana et al. (2004) constructed genetic libraries of picoeukaryotes from surface coastal picoplankton. Four libraries were constructed from Blanes Bay (NW Mediterreanean); they belong to the MAST-4 group (marine stramenopiles).

4.3.2 Ciliates

Ciliate abundance in the Mediterranean Sea at different sites and in different seasons displays a remarkably high variability. For example, in the Catalan Sea in June, the highest values of about 850 cells l^{-1} were found at the DCM whereas in the Ligurian Sea in May average surface layer values (5–50 m) were $\sim 3.3\times10^{3}$ cells l^{-1} with a maximum of $\sim 10^{4}$ cells l^{-1} (Peréz et al., 1997). These high values contrast with those for the Aegean Sea, where ciliate abundance were always lower than 5×10^{2} cells l^{-1} (Pitta and Giannakourou, 2000). Lower concentrations in the EMS, compared to WMS, are not the general rule. Pitta et al. (2001) reported a 2-fold decrease in ciliates concentration from west to east. However, a decline in concentrations along the west-to-east oligotrophy gradient has not been found to be always true for ciliates standing stock (e.g., Dolan et al., 1999). It could be that the relationship between ciliate abundance and chl-*a* concentration is stronger in the WMS than in the EMS indicating a better coupling with phytoplankton stock in the WMS (Fig. 15). However, differences between slopes are not statistically significant ($t_{\mathrm{value}}=1.7$; $p=0.23$) probably, due to the restricted data set for the eastern part (Table 3).

Since most of the primary production in the Mediterranean is due to nano- and picophytoplankton (see phytoplankton section of this review) one can expect that ciliates are likely important grazers (Rassoulzadegan, 1978; Rassoulzadegan and Etienne, 1981). Ciliate grazing impact can be about 50% of the primary production in the Catalan Sea and ciliate maximum abundance was found near the DCM (Dolan and Marrasé, 1995). In the Ligurian Sea, Peréz et al. (1997) estimated that ciliates could graze from 8 to 40% of primary production. The importance of ciliates as primary production consumers seem to be higher in the EMS (Dolan et al., 1999; Pitta et al., 2001).

In the MS, as in all marine systems, planktonic ciliates are dominated by the order Oligotrichida (Lynn and Small, 2000). Within that order, the aloricate naked forms are the main group (Margalef, 1963; Travers, 1973; Rassoulzadegan, 1977, 1979). An important aspect of ciliate ecological diversity is linked to their trophic type as well as their size, since both affect their role within the food web. As a percentage of total ciliates, the mixotrophs can vary between <10% to almost 100% (Verity and Vernet, 1992; Bernard and Rassoulzadegan, 1994). Dolan et al. (1999) have found that large mixotrophic ciliates were more abundant, both in absolute and relative terms, in the

EMS than in the WMS. In a later study across the Mediterranean Sea, Pitta et al. (2001) confirmed that pattern reporting that mixotrophs represented 17% and 18% in abundance and biomass, respectively and they were from 3 to 18 times more abundant in the EMS (although with lower total ciliate abundance) than the WMed. In the Ligurian Sea nano- and micro-mixotrophic ciliate contribution to total oligotrich biomass and abundance ranged from 31 to 41% and from 42 to 54%, respectively and they were mainly located at the level of the DCM (Peréz et al., 1997) In a comparative study of the ciliates in the North and the South Aegean Sea, mixotrophs contributed to total abundance from 17 to 24% in the South and from 21 to 54% in the North, and in terms of integrated biomass the values varied from 13 to 27% and from 18 to 62% in the South and North, respectively (Pitta and Giannakourou, 2000). Mixotrophs were dominated by distinct morphotypes as well. Cells smaller than 18 μm dominated in the South Aegean, whereas in the North Aegean, receiving the outflow of the Black Sea, the mixotrophic fauna was characterized by a relative abundance of cells of 18 to 50 μm size.

Patterns of taxonomic diversity have been investigated with regard to tintinnid ciliates. Along a west-east Mediterranean Sea longitudinal transect sampled in June, while the concentration of tintinnids varied little, their number of species and genera as well as their diversity indices increased eastward. Diversity parameters correlated positively with the DCM depths and negatively with the chl-*a* concentration. In a later study, the west-east variation of the tintinnid diversity was parallel to shifts in the chl-*a* size-diversity estimate (Dolan et al., 2002). In contrast, Pitta et al. (2001) did not observe any obvious west-east trend in tintinnid diversity but noted rather a peak in species richness in central stations.

While the importance of microzooplankton (ciliates and dinoflagellates) is well established in marine ecosystems only one field study has provided estimates of ciliate growth in the WMS (0.19–0.33 d^{-1}, Peréz et al., 1997). To our knowledge there is virtually no quantitative data on heterotrophic dinoflagellates for the open MS.

5 Mesozooplankton

5.1 Standing stock

An overview of the distribution of mesozooplankton standing stock in epipelagic Mediterranean waters highlights a general paucity in most regions, which reflects the oligotrophic character of the basin (Fig. 16, Table 5). Superimposed to this overall picture, a west-to-east decrease emerged from the surveys accross the basin conducted in June and September 1999 (Dolan et al., 2002; Siokou-Frangou, 2004, Fig. 17), and in June 2008 (Minutoli and Guglielmo, 2009). Sampling with finer mesh nets than the standard 200 μm, or with large bottles, which has been rarely conducted in the open MS, has revealed that biomass and abundance can increase by 2–20 fold when the smaller metazooplankters (~50–200 μm) are considered, but they also highlight west-east differences (Böttger-Schnack, 1997; Kršinic, 1998; Youssara and Gaudy, 2001; Andersen et al., 2001; Zervoudaki et al., 2006; Alcaraz et al., 2007).

Mesozooplankton abundance and biomass display patterns at sub-basin scale that roughly follow hydrological features, similarly to the distribution of primary producers, discussed in the previous sections. In the Alboran Sea, the sustained productivity caused by processes linked to the Atlantic Water inflow results in high zooplankton dry mass (18 mg m^{-3}) and copepod abundance (up to 5000 ind. m^{-3}) in the upper 200 m of the Almeria-Oran frontal area (Seguin et al., 1994; Thibault et al., 1994). Interestingly a great spatial variability of biomass values (5.5 to 25 mg m^{-3}) was observed in this region among sites positioned within different water masses and hydrological features and at a distance of 15–20 miles (Fig. 18). Increased mesozooplankton standing stock values are associated with the fronts in the Balearic, Catalan, and Ligurian Seas (Sabatés et al., 1989; Pinca and Dallot, 1995; Mc Gehee et al., 2004; Alcaraz et al., 1994; Licandro and Icardi, 2009). The hydrographic features of the frontal system in the Catalan Sea determine not only the prevailing structural (e.g., biomass) and metabolic (e.g., respiration, excretion) properties of zooplankton in the area but also their variability in different seasons (Alcaraz et al., 2007). The zooplankton abundance

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in the Straits of Sicily seems to be enhanced by intermittent upwelling (Mazzocchi et al., 1997). In the very oligotrophic EMS, the strong thermohaline front between the inflowing modified Black Sea water and the Aegean Sea water harbors the highest mesozooplankton standing stock in the epipelagos (0–100 m) of the eastern basin (up to 3875 ind. m^{-3} and 26.73 $\mathrm{mg\,m}^{-3}$ dry mass, Siokou-Frangou et al., 2009). The permanent or semi-permanent cyclonic gyres of the EMS (e.g., the Rhodos Gyre and the gyre South-West of Crete Island) revealed higher mesozooplankton abundance than the neighboring anticyclonic gyres (Mazzocchi et al., 1997; Christou et al., 1998; Siokou-Frangou, 2004).

In the open MS, the bulk of epipelagic mesozooplankton is concentrated in the upper 100 m layer and sharply decreases downward (Scotto di Carlo et al., 1984; Weikert and Trinkaus, 1990; Mazzocchi et al., 1997). It is in this upper region of the epipelagic layer that zooplankton play a major role in the biological processes, based on their linkage with phyto- and microzooplankton in the euphotic layer (Longhurst and Harrison, 1989). The generally decreasing vertical pattern of mesozooplankton abundance may be interrupted by small-scale increase at the level of the DCM, where high mesozooplankton biomass can be associated with high diatom concentrations (Latasa et al., 1992), and copepod feeding has been found to be enhanced (Saiz and Alcaraz, 1990). However, studies are too scanty to allow for a clear appraisal of the role of mesozooplankton in relation to DCM in the MS.

In the annual cycle, offshore mesozooplankton oscillate within a narrow range of abundances and reveal a seasonal variability that is modest in comparison to coastal waters. Peaks occur in February–March and in May offshore Mallorca Island (Fernández de Puelles et al., 2003), and in April in the Tyrrhenian Sea (Scotto di Carlo et al., 1984). Notwithstanding differences in the amplitude, a synchronous timing of the annual cycle along coastal-offshore gradients is reported at different sites, for mesozooplankton communities (e.g., Fernández de Puelles et al., 2003) and some copepod species, such as *Temora stylifera* and *Centropages typicus* (Di Capua and Mazzocchi, 2004). With the *caveat* that most data are from neritic areas, the few copepod species investigated at basin scale, such as *Calanus helgolandicus* and *C. typicus*, exhibit similar timing of seasonal cycle throughout the MS (Bonnet et al., 2005; Mazzocchi et al., 2007).

A time-series covering at monthly frequency a decade (1994–2003) offshore Mallorca Island constitutes the single interannual study of mesozooplankton in the open MS. Copepod variability in the area was related to winter North Atlantic Oscillation and the highest abundances coincided with the lowest NAO index in 1996 (Fernández de Puelles et al., 2007).

5.2 Composition

Epipelagic mesozooplankton in the open MS are highly diversified in terms of taxonomic composition. However, their patterns of spatial and temporal distribution over the annual scale reflect mainly the variability of copepods, which contribute as the major group both in terms of abundance and biomass. The dominance of small copepods (mostly ≤1 mm in total length) in terms of both numbers and biomass represents the major feature of the structure of mesozooplankton communities at basin level. In samples collected with coarser mesh nets (333 μm), the 0.5–1 mm size fraction contributes 45–58% to the total mesozooplankton abundances in the open EMS (Koppelmann and Weikert, 2007).

A few small-sized and specious genera of calanoids (*Clausocalanus* and *Calocalanus*, together with *Ctenocalanus vanus*) and cyclopoids (*Oithona*, oncaeids, corycaeids) account for the bulk of copepod abundance and biomass in epipelagic layers of the MS (Seguin et al., 1994; Siokou-Frangou et al., 1997; Saiz et al., 1999; Andersen et al., 2001; Youssara and Gaudy, 2001; Gaudy et al., 2003; Fernández de Puelles et al., 2003; Mazzocchi et al., 2003; Riandey et al., 2005; Licandro and Icardi, 2009, Fig. 19). These copepods cover a wide range of diversity not only in terms of taxonomy and morphology but also in life history traits and behaviour, which greatly affect their modes of interacting with the surrounding environment, including their reactions to the presence of prey and predators (Paffenhöfer, 1998). For example, *Calocalanus* and *Ctenocalanus* cruise slowly and create feeding currents, likely collecting more efficiently non-moving phytoplankton cells, as reported for *Paracalanus* (Paffenhöfer, 1998), that has similar swimming behavior. In contrast, *Clausocalanus* moves continuously without creating feeding currents and it captures cells that enter a restricted volume just in front of copepod's head (Paffenhöfer, 1998; Mazzocchi and Paffenhöfer, 1999; Uttieri et al., 2008). Oithonids stand still most of the time perceiving hydromechanical signals from moving preys with their rich array of long setae (Paffenhöfer, 1998; Svensen and Kiørboe, 2000; Paffenhöfer and Mazzocchi, 2002). Oncaeids and corycaeids swim primarily with a jerky forward motion (Hwang and Turner, 1995) and have peculiar mouth appendages, that allows scraping food items within particle aggregates, such as discharged appendicularian houses and marine snow (Alldredge, 1976; Ohtsuka et al., 1993). All these distinct behaviours point at different functional roles in the epipelagos, with the occupation of distinct niches even in apparently homogeneous open oligotrophic waters.

Further differences in ecological traits ad/or feeding habits are suggested by the distinct although partially overlapping distributions of different congeneric species of the above mentioned genera along the water column and/or over the seasons (Böttger-Schnack, 1997; Fragopoulu et al., 2001; Kršinic and Grbec, 2002; Peralba and Mazzocchi, 2004; Zervoudaki et al., 2007; Peralba, 2008), as also observed in the tropical Atlantic (e.g., Paffenhöfer and Mazzocchi, 2003). Although their populations largely overlap, the peaks of *Clausocalanus paululus*, *C. pergens*, *C. arcuicornis* and *C. furcatus* succeed each other from winter to autumn in the open Tyrrhenian Sea (Peralba and Mazzocchi, 2004) as well as in the Ionian Sea and in the Straits of Sicily (Mazzocchi, unpublished data), similarly to what observed in coastal waters (Mazzocchi and Ribera d'Alcalá, 1995). In the Ionian and South Aegean seas, the dominant *C. furcatus* and *Oithona plumifera* in the autumn are replaced by *C. paululus* and *O. similis* in the spring (Siokou-Frangou et al., 1997; Mazzocchi et al., 2003; Siokou-Frangou et al., 2004). In the eastern basin and in autumn, *O. plumifera* is abundant in the 0–50 m layer whereas *O. setigera* dominates in the 50–100 m layer (Siokou-Frangou et al., 1997). The comparison of individual activity and motion behavior between *C. furcatus* and *O. plumifera* has revealed substantial differences in their sensory and feeding performances, which apparently allow them to coexist (Paffenhöfer and Mazzocchi, 2002). The overall picture emerging from the diversified characters of the small copepods, prevailing in the open MS, indicates that they may exploit efficiently the whole spectrum of resources available in the epipelagos.

West-to-east differences in the community structure revealed by the percentage contribution of some genera or species to total copepod numbers might reflect differences in species biogeography and be also indicative of different trophic features and paths in the systems. *Centropages typicus* is mentioned among the dominant species in the WMS (Pinca and Dallot, 1995; Saiz et al., 1999; Fernández de Puelles et al., 2003; Gaudy et al., 2003), in the Adriatic Sea (Hure et al., 1980), and in the North Aegean Sea (Siokou-Frangou et al., 2004, Fig. 19). By contrast, *Calocalanus* spp. (e.g., *C. pavo*, *C. pavoninus*), oncaeids (e.g., *Oncaea "media"* group, *O. mediterranea*), corycaeids (e.g., *Farranula rostrata*), and *Haloptilus longicornis* contribute more to total copepod abundance in the eastern than in the western basin (Weikert and Trinkaus, 1990; Siokou-Frangou et al., 1997; Mazzocchi et al., 2003; Ramfos et al., 2006).

The occurrence of large calanoids, such as *Calanus helgolandicus*, in the open MS is much less important than in the North Atlantic (Bonnet et al., 2005, and references therein). This species inhabits mainly intermediate and deep layers of the North-West MS, Adriatic Sea, and North Aegean Sea, and ascents to epipelagic waters in late winter-spring (e.g., Bonnet et al., 2005; Siokou-Frangou, unpublished data). Its presence was extremely rare in the Levantine Sea until an outstanding abundance was recorded in June 1993 (15.6×10^3 ind. m^{-2} in 4000 m water column), probably in relation to changes in the deep circulation induced by the Eastern Mediterranean Transient (Weikert et al., 2001). Seasonal and vertical patterns similar to those of *C. helgolandicus* are reported for the large *Subeucalanus monachus* in the Alboran, Ionian and Levantine seas (Weikert and Trinkaus, 1990; Siokou-Frangou et al., 1999; Andersen et al., 2004). This suggests that these two large calanoids are vicariant species that can co-occur but peak in different areas of the MS. *C. helgolandicus* was found in high density patches at the frontal zone in the open Ligurian Sea, in association with high phytoplankton concentrations (Boucher, 1984). *S. monachus* was very abundant in the Rhodos Gyre during the spring of 1992 when the upwelling of waters rich in nutrients leaded to high phytoplankton biomass dominated by large diatoms (Siokou-Frangou et al., 1999). The other mesozooplankton groups that contribute to community diversity in the open MS present much lower abundances than copepods (Gaudy, 1985).

Among crustaceans, cladocerans, which are a very abundant component of zooplankton in coastal waters, expand their occurrence beyond the continental slope only in narrow neritic areas at their maximum abundance observed in summer (Saiz et al., 1999; Riandey et al., 2005; Isari et al., 2006). In open waters of the Straits of Sicily and the EMS during autumn, cladocerans accounted for only 0.3% of total zooplankton with a scattered distribution among and within regions (Mazzocchi et al., 1997). Interestingly in the South Aegean Sea, *Evadne spinifera* contributed 6% to mesozooplankton abundance in September (Siokou-Frangou et al., 2004). Ostracods, which are not numerous in the mesozooplankton communities at temperate latitudes (Angel, 1993), increase gradually with depth. Their contribution to total zooplankton numbers varies from ~2% in the upper 50 m to ~11% in the 200–300 m layer, and they present a remarkably consistent distribution in different Mediterranean regions (Scotto di Carlo et al., 1984; Mazzocchi et al., 1997; Isari et al., 2006). The ostracod highest abundances are recorded in the winter period in neritic waters, likely in relation to temperature conditions and the minimum abundance of the potential predators (Brautovic et al., 2006).

Gelatinous zooplankton represent an important group of various organisms that play different and relevant roles in the pelagic communities as efficient filter-feeders or voracious predators. However, they are generally underestimated because standard sampling devices utilized for mesozooplankton damage or destroy their fragile bodies and are therefore inappropriate for their quantitative estimation. The pelagic filter-feeder tunicates, and especially salps, are known to occur in periodic dense swarms and sometimes outbreak for days to weeks (Bone, 1998; Ménard et al., 1994). It seems however, that salps form smaller swarms in the MS than in other oceans, which could be related to the oligotrophic nature of this sea (Andersen, 1998). Doliolids and salps together accounted for 4% of total zooplankton abundance in the Catalan Sea in June (Saiz et al., 1999) and only 0.04–1.3% in the EMS in October-November (Mazzocchi et al., 1997). However, doliolids made up to 9% of total zooplankton in the North Aegean Sea in September (Isari et al., 2006). Appendicularians represent a more constant component in open-waters zooplankton. Given their high population growth rate under favourable conditions (Gorsky and Palazzoli, 1989), their abundances seem to depend on the selected sampling area and time. Indeed, they accounted for 8% of abundances in spring in the open Catalan Sea (Saiz et al., 1999) and from 1 to 8% in the Ionian Sea in spring 1992 and 1999 (Mazzocchi et al., 2003). The range of their relative abundances was very wide among several regions of the eastern MS in the autumn of 1991, from 1% in the West Levantine Sea up to 23% at a station in the Rhodos Gyre area (Mazzocchi et al., 1997). Among the highest contributions should be that recorded in the Ligurian Sea in December (38%) when *Fritillaria* was the dominant genus (Licandro and Icardi, 2009).

Among the carnivorous gelatinous zooplankton, chaetognaths are more abundant and contribute more than siphonophores (Mazzocchi et al., 1997; Isari et al., 2006), but the latter group can easily be underestimated due to the net sampling that limits their accurate quantification (Lucic et al., 2005). In the EMS in autumn, the most abundant chaetognaths are *Sagitta enflata*, *S. bipunctata*, *S. minima* and *S. serratodentata* (Kehayias, 2003).

Mesozooplankton community structure in the open MS seems to be affected by mesoscale circulation and hydrodynamic features similarly to what reported above for the standing stock. In the Alboran Sea, the copepods *Centropages typicus* and *Clausocalanus furcatus* revealed a preference for the frontal area (Youssara and Gaudy, 2001). In the North East Aegean frontal region, two distinct copepod assemblages inhabit the areas occupied by the modified BSW and by the Aegean Water, respectively, due to the strong salinity differences (up to 8) (Zervoudaki et al., 2006; Siokou-Frangou et al., 2009). An interesting aspect regarding the influence of mesoscale features is revealed when studying simultaneously cyclonic and anticyclonic eddies. In the Algerian basin, the eastern edge of an anticyclonic eddy seemed to be favorable for *Paracalanus/Clausocalanus*, *Calocalanus*, and *Calanus*, due to the downward entrainment of chl-*a* down to 200 m. Chaetognaths were more abundant in the center of the above structure. On the other hand, in the neighboring cyclonic eddy, the highest abundance of filter-feeders (ostracods, cladocerans, doliolids and salps) was attributed to enhanced trophic conditions (Riandey et al., 2005). Dissimilarities in copepod assemblages between cyclonic and anticyclonic gyres in the EMS in the autumn of 1991 were recorded only in the subsurface layer (50–100 m). The cyclonic gyres were characterized by the copepods *C. pergens* and *Ctenocalanus vanus*, while the anticyclonic ones were dominated by *C. paululus*, *Mecynocera clausi* and *Lucicutia flavicornis*; differences were attributed to the higher chl-*a* values of the cyclonic gyres compared to the anticyclonic ones (Siokou-Frangou et al., 1997). In the hydrodynamically very active area of the Ligurian Sea, zooplankton assemblages seem to be distinguished due both to physical environment and animal behavior (Pinca and Dallot, 1995). In the same area, high density spatial sampling revealed species-specific patterns in the copepod spatial distribution. The copepods *C. helgolandicus*, *C. typicus*, *Oithona* spp., and *Oncaea* spp. were associated with the frontal zone; *Acartia* spp. and salps had a scattered distribution while *Clausocalanus*/*Paracalanus* did not show a clear pattern. The cross-shore zooplankton distribution appeared strongly influenced by both the Northern Ligurian current and the Ligurian front (Molinero et al., 2008).

5.3 Mesozooplankton production

Most studies on mesozooplankton production in the MS are limited to coastal species and sites and based mainly on the egg production method; their results are hardly applicable to open water conditions, dominated by copepod species such as *Clausocalanus*, *Oithona* and Oncaeidae, whose reproductive biology is very poorly known.

Data of mesozooplankton production in the open epipelagic MS are restricted in space and time. In the Gulf of Lion, the Catalan Sea and the North-East Aegean Sea, which are less oligotrophic regions within the MS, copepod production ranged from 19 to 58 $\mathrm{mg\,C\,m^{-2}\,d^{-1}}$ over the seasons. The values are much lower in the North and South Aegean Sea, in accordance with the remarkable oligotrophy of these areas (Table 6).

For the egg-carrying *Oithona* and Oncaeidae, and the egg-carrying species belonging to the genus *Clausocalanus*, only a few studies were conducted in the open MS (Zervoudaki et al., 2007; Peralba, 2008). As the egg-carrying strategy implies lower egg production but also lower egg mortality in comparison to egg broadcasting (Kiørboe and Sabatini, 1995), these species can maintain quantitatively limited but persistent populations in a wide range of trophic conditions. Indeed the cosmopolitan and abundant *Oithona similis* has very low and similar egg production rates (~2 $\mathrm{eggs\,f^{-1}\,d{-}1}$) in the North Aegean Sea (Zervoudaki et al., 2007) and in the more eutrophic North Atlantic Ocean (Castellani et al., 2005), without significant seasonal differences in both seas. By contrast, for the broadcast-spawners *C. typicus*, *Temora stylifera* and *Clausocalanus lividus*, egg production rates recorded in the Catalan Sea are lower than the maximal rates reported for the same species in the literature. This indicates that their production is limited by the oligotrophic conditions of the region (reviewed in Saiz et al., 2007). Unfortunately, no information is available so far on the reproduction of the *Calocalanus*, and a few data have been provided only recently for *Ctenocalanus vanus* in the Red Sea (Cornils et al., 2007).

5.4 Mesozooplankton and their prey

The horizontal patterns of mesozooplankton in the open MS are similar to those of autotrophic biomass and production (e.g., the west-to-east decrease) and, to a less extent, to those of microheterotrophs, suggesting a good coupling between mesozooplankters and their prey. This coupling was also observed at smaller scale in the frontal areas of the Ligurian, Catalan and North Aegean Seas (Saiz et al., 1992; Alcaraz et al., 1994; Pinca and Dallot, 1995; Alcaraz et al., 2007; Zervoudaki et al., 2007). However, sometimes the areas of the maximum zooplankton abundance do not coincide with those of the highest phytoplankton concentration (e.g., in the Catalan Sea, Calbet et al., 1996), and the contrast might be attributed to factors other than nutrition such as zooplankton mortality due to predation.

Only rarely have the natural diet and feeding performances been measured in the open MS. In situ measurements evidenced that mesozooplankton grazing impact on phytoplankton could be significant. In the Gulf of Lion, the grazing impact of zooplankton on primary production was estimated to be important both in winter (47%) and spring (50%) (Gaudy et al., 2003). In the very oligotrophic South Aegean Sea, copepod grazing impact on the primary production by cells $>3\,\mu$m was estimated to be 14% in March and 35% in September (Siokou-Frangou et al., 2002). The grazing impact would be even higher had these estimates included copepod nauplii and the small copepodites as well as groups with high growth rates such as appendicularians (Saiz et al., 2007). In the North-East Aegean Sea, small copepods (*Oncaea* spp., small *Clausocalanus* species, *Paracalanus parvus*) showed a considerably higher grazing impact on phytoplankton production (almost 100% during September) as compared to larger copepods (*C. helgolandicus*, *C. typicus*) (Zervoudaki et al., 2007). The above results are in agreement with the statement by Calbet (2001) that in oligotrophic environments zooplankton should exert a tighter control on autotrophs than in productive systems. However, data available for the open MS are still too few to provide a conclusive evidence.

Despite the significant consumption of the autotrophic production by copepods, ciliates seem to be their preferable food items (Wiadnyana and Rassoulzadegan, 1989). In different regions of the world oceans and in the coastal MS, copepods have been reported to consume preferentially ciliates *vs* autotrophic food (reviewed by Calbet and Saiz, 2005). Indeed in the North-East Aegean Sea and in April, clearance rates of some copepods (*C. helgolandicus*, *C. typicus*, *P. parvus*, *O. similis*, *Oncaea* spp.) were one order of magnitude higher on ciliates than on chl-*a*-containing cells. Moreover, copepods seemed to consume almost the entire ciliate production, but only part of the available primary production, suggesting that probably not all autotrophs provided adequate food supply in terms of quality and/or size (Zervoudaki et al., 2007). This prey preference of copepods could affect significantly ciliates abundances, exerting a strong top down control of their populations. This control was hypothesized as the major factor for the low standing stock of ciliates across the entire MS (Dolan et al., 1999; Pitta et al., 2001). The observed uncoupling between mesozooplankton and microheterotroph standing stocks in the North Aegean Sea could be due to the same factor (Pitta and Giannakourou, 2000).

Rare measurements of feeding rates seem to confirm the results of studies conducted in the laboratory or in coastal areas, i.e., the ingestion rates depend on food quantity and quality. During the spring bloom in the Alboran Sea, copepod ingestion rates on natural particle mixtures varied between 0.5 and $5.8\times10^6\,\mu\text{m}^3\,\text{mg}^{-1}\,\text{h}^{-1}$, with the highest values measured in the layer with chl-*a* maximum concentration (Gaudy and Youssara, 2003). Copepod feeding can be selective even in presence of a more homogeneous food assemblage; at DYFAMED site, copepod filtration rates rose from 0.54 to $1.89\,\text{ml}\,\text{copepod}^{-1}\,\text{h}^{-1}$ when diet switched from mixotrophic to heterotrophic nanociliates (Peréz et al., 1997). Most of the in situ studies have provided evidence that mesozooplankton feeding can change in relation to the type of food prevailing at one time. Apart from the examples given above, in offshore waters of the Northwest Mediterranean, communities dominated by the same four copepod genera (*Clausocalanus*, *Paracalanus*, *Oithona*, and *Centropages*) fed on phytoplankton in June, when cells $>10\,\mu$m occurred, while they relied on microzooplankton or detritus in October, when small cells ($<10\,\mu$m) dominated, or under pronounced oligotrophic conditions (Van Wambeke et al., 1996). In the Gulf of Lion, the mesozooplankton communities were very similar in taxonomic composition during winter and spring, but differed in their feeding performances. In winter, the autotrophic food was sufficient to support low zooplankton biomass, while heterotrophic food richer in protein sustained the enhanced secondary production in spring (Gaudy et al., 2003). A seasonal shift was also observed in the Catalan Sea, where copepod species were strongly coupled with the autotrophic biomass in conditions of phytoplankton bloom (dominated by cells $>5\,\mu$m) in March, and on heterotrophs in late spring and early summer where autotrophs abundance was lower (Calbet et al., 2002).

These switches in feeding preferences and performances might result from a real plasticity of a group/genus in response to different food conditions. However, it is also possible that this apparent flexibility masks neglected differences among congeneric species that are very similar morphologically but have different needs for food quantity and quality. This second case can be hypothesized for *Clausocalanus pergens* and *C. paululus* by observing their distribution in different regions of the MS and the Atlantic Ocean (Peralba, 2008). Both species are widespread in epipelagic waters of the open MS in late winter-spring, but the former prevails in presence of phytoplankton blooms (e.g., in the North Balearic Sea) and the latter in oligotrophic regions (e.g., the Ionian Sea), suggesting a separation of their trophic niches (Peralba, 2008). Unfortunately, information on the natural diets of the dominant *Clausocalanus*, *Oithona*, *Oncaea* species are almost lacking. Differences in the trophic regime seem to account for the variability of distribution and abundance of *Centropages typicus* in different regions of the MS. This species is common and abundant in coastal and neritic areas, while in open waters it contributes significantly to copepod assemblages only during spring bloom conditions, i.e., in the Gulf of Lion, Ligurian Sea, and North Aegean Sea (Andersen et al., 2001; Calbet et al., 2007; Siokou-Frangou et al., 2004). This distribution indicates a relatively modest adaptability of *C. typicus* to fluctuations in food availability (Calbet et al., 2007), despite its capacity of feeding on a wide spectrum of prey types.

Given the oligotrophic status of the MS, prey availability could affect mesozooplankton. Food limitation was suggested to occur in the Catalan Sea, since mesozoooplankton ingestion rates were correlated with food availability but were lower than in experimental studies (Saiz et al., 2007). Similarly, in the North-East Aegean Sea, the chl-*a* concentration in spring and early autumn was well below the saturation level of copepod clearance, indicating that the animal growth was probably food limited or that they were feeding on heterotrops (Zervoudaki et al., 2007). In addition, food limitation could lead to competition among mesozooplankters in the open MS. However, the possibility to exploit different food sources may allow the co-occurrence of various and numerous taxa, as suggested by experiments conducted with doliolids and small copepods in the coastal Catalan Sea (Katechakis et al., 2004). Experiments providing information on the grazing impact of other mesozooplankton groups (e.g., appendicularians, doliolids, salps, ostracods) on autotrophs and microheterotrophs are lacking for the open MS. As for the rare studies on the feeding impact of carnivorous zooplankton, the predation pressure exerted by chaetognaths on copepod standing stocks appears overall negligible in the Catalan Sea (<1%, Durò and Saiz, 2000), whereas it varied from 0.3–7.8% in several areas of the eastern MS (Kehayias, 2003).

6 Planktonic food webs in the Mediterranean epipelagos

After the first report of a food web dominated by small-sized plankton in the Ligurian Sea (Hagström et al., 1988; Dolan et al., 1995) several studies showed that the microbial food web is dominant in large parts of the oligotrophic MS (Christaki et al., 1996; Thingstad and Rassoulzadegan, 1995; Turley et al., 2000; Siokou-Frangou et al., 2002, among the others).

The widespread P deficit of the Mediterranean waters led Thingstad et al. (2005) to investigate on how P limitation could shape microbial food web and influence carbon flow in the very oligotrophic Levantine Sea. The fast transfer of the added P to the particulate form, along with an unexpected slight decrease in chl-*a*, led the authors to postulate two possible scenarios: i) the relaxation of P limitation due to the P addition was exploited only by bacteria, which could utilize DON as source of nitrogen, thus outcompeting N limited autotrophs. The heterotrophic biomass would then have been quickly channeled toward larger consumers, mesozooplankton included, with a sharp increase in copepod egg production (bypass hypothesis). ii) The relaxation of P limitation produced a "luxurious" accumulation of P in both bacteria and picophytoplankton (presumably less in the latter) with a P enriched diet for grazers, which stimulated the observed increase in egg production (tunneling hypothesis). In either scenario emerges a community which would not always manifest its response to nutrient inputs as autotrophic biomass accumulation, especially when the input is biased towards one or the other element. The latter is confirmed by Volpe et al. (2009) after an in depth analysis of color remote sensing images of phytoplankton response to dust storms on the whole basin. Further, this strongly supports the view that the planktonic web in that region is tightly controlled by the heterotrophic component.

The leading role of heterotrophs, in the MS, as it emerges from a plankton standing stock prevalently heterotrophic and dominated by microbes, is the dominant situation in the basin. Heterotrophic/autotrophic biomass ratios vary from 0.5 to 3.0 in the west MS (Christaki et al., 1996; Gasol et al., 1998; Pedrós-Alió et al., 1999) and from 0.9 to 3.9 in the Aegean Sea, with higher values more frequently found in the oligotrophic regions and during the stratified period (Siokou-Frangou et al., 2002). The spatial trend is consistent with this pattern, with ratios increasing along a longitudinal transect from the Balearic Sea to the East Levantine Sea (Christaki et al., 2002). As a result, the distribution of biomass among the food web compartments would be represented by an "inverted pyramid" or "squared inverted pyramid", as it was depicted in the Aegean Sea (Siokou-Frangou et al., 2002), a picture common in oligotrophic oceanic waters (Gasol et al., 1997).

The above outlook suggests two different scenarios for the Mediterranean epipelagic food webs: i) the system is net heterotrophic, with a dominance of heterotrophic bacteria and protists not only in biomass but also in rates. Bacteria would outcompete autotrophs in P uptake and bypass the autotrophic link, relying on allochthonous C (Sects. 2 and 3.1), which would be used with more or less efficiency, according to the season, area etc. ii) the system is in balance between production and consumption and the "inverted pyramid" may reflect either seasonally biased sampling, (for instance Casotti et al. (2003) reported a higher biomass of autotrophs than that of microheterotrophs in the central Ionian sea in spring), and/or higher turnover rates in autotrophs than in heterotrophs. The latter would be in contrast with the conceptual representation by Thingstad and Rassoulzadegan (1995) and with several observations in the basin (Sect. 4).

Despite the dominance of the microbes and picoautotrophs in the MS offshore waters, prevalence of nano- and micro-autotrophs has been observed after intermittent nutrient pulses in highly dynamic mesoscale physical structures and frontal areas, as well as in areas being in contact with extended and at times highly productive coastal systems (Adriatic and North Aegean seas) (Sect. 2). Such pulses are spatially limited and concentrated, in contrast to the nutrient inputs deriving from the atmosphere, which are spread over large spaces and diluted. Because of the pulses intermittency, their impact is likely underestimated. They determine a considerable variability of the food web structure along trophic gradients, which change not only in space but also in time, going from marked oligotrophy (recycling systems) to new production systems (Legendre and Rassoulzadegan, 1995). In the Ligurian Sea, the deep vertical mixing induced by strong winds during May 1995 resulted in high primary production dominated by diatoms and in increased copepod abundance compared with the followed stratification period-early June 1995 (Andersen et al., 2001).

The central divergence of the Northwest MS is another area of enhancement of the classical food web activity (Calbet et al., 1996) providing food to the higher trophic levels, from zooplankton (Pinca and Dallot, 1995) up to large mammals (Forcada et al., 1996).

New production occurs also at the DCM (with frequent presence of diatoms) close to the nutricline over a broader time interval, but its overall weight on the production of the basin is poorly constrained. If DCM hosts a significantly different planktonic web is still an open question (e.g. Estrada et al., 1999).

A first order picture would then be that microbial food web is the prevailing way of functioning of the MS offshore waters, with few exceptions where larger, bloom forming phytoplankton would initiate the “classical” food web. However this simplification is becoming less and less robust with new findings on nutritional potential of marine organisms. What were considered as heterotrophic bacteria when estimated with normal counts, turned out to include groups capable of diversified metabolic strategies (Moran and Miller, 2007; Van Mooy and Devol, 2008; Zubkov and Tarran, 2008) and the MS should not be different in this respect. Flagellates, ciliates and dinoflagellates are mixotrophic (Sects. 3 and 4) and their contribution is significant in the EMS (Sect. 4). Metazoans display also a wide range of feeding modes and food preferences. Among copepods, the genera more abundant in the MS are known to exploit a large variety of food resources, including fecal pellets (e.g., *Oithona*, González and Smetacek, 1994; Svensen and Nejstgaard, 2003) and marine snow (e.g., oncaeids, Alldredge, 1976; Ohtsuka et al., 1993). Appendicularians, which are capable to feed on pico- and small nanoplankton (Deibel and Lee, 1992), constitute a by-pass from the lower trophic levels to fishes (Deibel and Lee, 1992), contributing to a more efficient food web as that described in the oligotrophic North Aegean Sea (Siokou-Frangou et al., 2002).

The variable grazing impact on larger than 5 μm primary producers by mesozooplankton, despite the prevalence of ciliates as their food items, both during mixing and stratified seasons (Sect. 5) indicate in MS a flexible and possibly efficient connection between both autotrophs and microheterotrophs and the higher trophic levels. All this suggests that in the MS is characterized by a "multivorous food web" (sensu Legendre and Rassoulzadegan, 1995), including a continuum of trophic pathways spanning from the herbivorous food web to the microbial loop and dynamically expanding or contracting along with seasons, areas and transient processes. The high diversity in species, feeding and reproduction modes, and consequently in functional roles, might support a more efficient energy transfer to the higher trophic levels.

Most of the studies describing phytoplankton biomass dynamics in the MS (Sect. 3) have stressed the bottom up constraints to phytoplankton growth and accumulation to justify the generally low standing stocks of autotrophs. On the other hand Thingstad et al. (2005) have shown that purely heterotrophic processes may produce, even in the extreme oligotrophy of the EMS, a rapid transfer to higher levels, which suggests an efficient top-dow control.

We are then confronted with two possible depictions: i) the low standing stocks of autotrophs due to low dissolved nutrients testifies a strong oligotrophy that determines a low standing stock also of intermediate and top predators (bottom-up control); ii) the low standing stock of autotrophs could instead result from a very effective top down control that propagates along the food web, ultimately reaching the top predators (see Sects. 4 and 5). In this latter case the stock of grazers would be larger, and fishery richer than expected on the sole basis of measured chl-*a*nd nutrients concentrations, generating the so called Mediterranean paradox (Sournia, 1973; Estrada, 1996). We can thus hypothesize that the intricate and very flexible food web (e.g. Paffenhöfer et al., 2007) helps in keeping at a minimum the carbon loss versus deeper layers (POC export is very low in the MS, e.g., Wassmann et al., 2000; Boldrin et al., 2002 and references therein) and predators could optimally profit of carbon produced and transformed within the system, thus being the ultimate controllers of plankton abundance in the MS. The paradox would become even less paradoxical if one takes into account the external inputs to the basin, which would reinforce the view of the MS as a coastal ocean.

7 Perspectives

Despite the numerous investigations of the last decades, the emerging picture of plankton dynamics in the MS is far from being satisfying, neither at the spatial nor at the temporal scales. Except for the satellite images, some areas, especially in the southern part of both basins, are still insufficiently known. The temporal variability at short, seasonal and interannual scale also calls for more intensive sampling: in addition to the DYFAMED site, other long term offshore stations should be initiated in key geographical locations to investigate seasonal patterns, fluxes of the major components, and responses of the planktonic biota to anthropogenic and climatic changes.

Not all the components of the pelagic system have been addressed with comparable efforts, also because of the lack of appropriate sampling and identification tools. The diversity and distribution patterns of autotrophic and heterotrophic prokaryotes, viruses, and eukaryotes which are the major component of the MS epipelagos are still largely underestimated. The few molecular studies realised since the late 90s have shown their great potential in advancing our knowledge on the microbial component of the sea. Different communities likely characterize the spatial and temporal texture of this diversified basin, playing distinct roles in terms of energy transfer and food web structure. The proper identification of their components is a prerequisite for our understanding of the functioning of the Mediterranean pelagic realm.

The intriguing picture of heterogeneity emerging from this review points at a difference between the pelagic Mediterranean and other oceanic sites, which might be explained considering the small scale and the enclosed nature of this basin. This "miniature ocean" surrounded by populated coasts, hosting a surprising and still largely underestimated variety of planktonic organisms linked together by dynamic and plastic trophic pathways is an intruiguing system. The relatively close proximity with land intensifies the effect of climatic changes and anthropic-driven impacts such as increased nutrient fluxes and/or overfishing might affect the biological structure of the basin at a more rapid scale as compared to the large oceans, and strongly support the role of Mediterranean as a sensitive sentinel for future changes. The question is: which signals the sentinel will send? From our survey we speculate that in such a flexible biome, signals will first manifest as spatial reorganization of communities.

In fact the scales are much smaller than oceanic regions at similar latitudes, which makes the regions of MS highly flexible in shifting from one regime to another, since all the "actors" are already there. The MS offers then an attractive marine environment to study general ubiquitous processes across multiscale and multidirectional physical, biological and trophic gradients. In some areas, many pieces of this multidimensional puzzle are already in place, meaning that new research efforts can grow on some already existing ground and that the relevance of new results can be amplified in the frame of old data.

In general, basic exploratory research is still needed, while gaps in knowledge should be filled taking advantage of modern technologies and new approaches. Among these, a great opportunity is represented by a clever merge of modern oceanographic tools such as Autonomous Systems and the sophisticated methods of the “omics”, whose results may feed tentative integrated conceptual models of the system dynamics to approach a broad range of marine environmental issues such as fisheries, climate change impact, harmful blooms, emerging diseases and pollution. All those could be more easily verified due to the scales and accessibility, and their inferences later extended to other less tractable marine systems.

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Table 1. Values of primary production reported for the MS.

Area	Period	mgCm^{-2}d^{-1}	g C m^{-2}y^{-1}	mgCm^{-2}h^{-1}	Reference	comments
MS	1979–1983		156		Antoine et al. (1995)[a]	Satellite data
MS	1997–1998		154–198		Bricaud et al. (2002)	Satellite data
MS	1998–2001		130–140		Bosc et al. (2004)	Satellite data
MS			80–90		Sournia (1973)	in situ ^{14}C
Whole basin	May–June 1996	168–221			Moutin and Raimbault (2002)	in situ ^{14}C
EMS	1979–1983		137		Antoine et al. (1995)[a]	Satellite data
EMS	1997–1998		143-183		Bricaud et al. (2002)	Satellite data
EMS	1998–2001		121±5		Bosc et al. (2004)	Satellite data
EMS			137–150		Bethoux et al. (1998)	Budget analysis
EMS			20.3		Dugdale and Wilkerson (1988)	in situ ^{14}C
EMS	May–June 1996		99		Moutin and Raimbault (2002)	in situ ^{14}C
South Adriatic	1997–1999		97.3		Boldrin et al. (2002)	in situ ^{14}C
South Adriatic	March (avg 1997/99)	297±56			Bianchi et al. (1999) in Boldrin et al. (2002)	in situ ^{14}C
Ionian Sea	August (avg 1997/98)	18±65			Bianchi et al. (1999) in Boldrin et al. (2002)	in situ ^{14}C
Ionian Sea	1997–1999		61.8		Boldrin et al. (2002)	in situ ^{14}C
Ionian Sea	May–June 1996	119–419 (315±71)			Moutin and Raimbault (2002)	in situ ^{14}C
Ionian Sea	April–May 1999	208–324.5			Casotti et al. (2003)	in situ ^{14}C
Strait of Sicily	May–June 1996	419			Moutin and Raimbault (2002)	in situ ^{14}C
North Aegean	March 1997/98, September1997	3.4		56.49–149.55	Ignatiades et al. (2002)	in situ ^{14}C
North Aegean	September 1998			43.8	Ignatiades et al. (2002)	in situ ^{14}C
North Aegean	September 1999	232±45 (no-front) 326±97 (front)			Zervoudaki et al. (2007)	in situ ^{14}C
North Aegean	April 2000	256±62 (no-front) 245±27 (front)			Zervoudaki et al. (2007)	in situ ^{14}C
South Aegean	March 1997/98, September 1997	38.88		33–56.21	Ignatiades et al. (2002)	in situ ^{14}C
Cretan Sea	1994–1995		59		Psarra et al. (2000)	in situ ^{14}C
Cretan Sea	1994 (four easons)		24.79	5.66	Ignatiades (1998)	in situ ^{14}C (0–50 m)
Cretan sea	March 1994			6.56 (5.73-7.98)	Gotsis-Skretas et al. (1999)	in situ ^{14}C (0–50 m)
Cyprus eddy	May 2002			0.091±0.014 mgC m^{-3} h^{-1}	Psarra et al. (2005)	in situ ^{14}C
Cyprus eddy	May 2001–2002 (all depths)			1.8–12.5 nmolCl^{-1}h^{-1}	Tanaka et al. (2007)	in situ ^{14}C
Cyprus eddy	May 2001–2002 (0–20 m)			8.5–11.5 nmolCl^{-1}h^{-1}	Tanaka et al. (2007)	in situ ^{14}C
MS	May–June 1996	168–221			Moutin and Raimbault (2002)	in situ ^{14}C

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Table 1. Continued.

Area	Period	$\text{mgCm}^{-2}\text{d}^{-1}$	$\text{g C m}^{-2}\text{y}^{-1}$	$\text{mgCm}^{-2}\text{h}^{-1}$	Reference	comments
WMS	1979–1983		197		Morel and André (1991), Antoine et al. (1995)[a]	Satellite data
WMS	1997–1998		173–198		Bricaud et al. (2002)	Satellite data
WMS			105.8–119.6		Bethoux et al. (1998)	Oxygen consumption
WMS	May–June 1996		145		Moutin and Raimbault (2002)	in situ ^{14}C
WMS	May–June 1996	353–996			Moutin and Raimbault (2002)	in situ ^{14}C
Alboran Sea	May 1986 (non front)	330–600 (avg. 480)			Lohrenz et al. (1988)	in situ ^{14}C
Alboran Sea	May 1986 (front)	500–1300 (avg. 880)			Lohrenz et al. (1988)	in situ ^{14}C
Alboran Sea	May 1988	632, 388 and 330			Moran and Estrada (2001)	in situ ^{14}C
Alboran Sea	November 2003	6.15–643.88 (avg.142.38)			Macías et al. (2009)	in situ ^{14}C
Catalan-Balearic	May–July 1982–1987	160–760			Estrada et al. (1993)	in situ ^{14}C
Catalan-Balearic	April 1991	150–900			Granata et al. (2004)	in situ ^{14}C
Catalan-Balearic	June 1993	450,700			Granata et al. (2004)	in situ ^{14}C
Catalan-Balearic	October 1992	210,250			Granata et al. (2004)	in situ ^{14}C
Catalan Balearic	March 1999	1000±471 (max 1700)			Moran and Estrada (2001)	in situ ^{14}C
Catalan Balearic	January–February 2000	404±248 (max 1000)			Moran and Estrada (2005)	in situ ^{14}C
Algerian Basin	October 1996	186–636 (avg. 440)			Moran et al. (2001)	in situ ^{14}C
Gulf of Lion	March–April 1998	401			Gaudy et al. (2003)	in situ ^{14}C
Gulf of Lion	January–February 1999	166			Gaudy et al. (2003)	in situ ^{14}C
South Gulf of Lion			78–106		Lefevre et al. (1997)	Review
South Gulf of Lion			140–150		Conan et al. (1998)	in situ ^{14}C
Tyrrhenian Sea	May–June 1996	398			Moutin and Raimbault (2002)	in situ ^{14}C
Tyrrhenian Sea	July 2005	273			Decembrini et al. (2009)	in situ ^{14}C
Tyrrhenian Sea	December 2005	429			Decembrini et al. (2009)	in situ ^{14}C
Ligurian Sea (DYFAMED)	1993–1999		86–232 (avg. 156)		Marty and Chiaverini (2002)	in situ ^{14}C
Ligurian Sea (DYFAMED)	May 1995	240–716 $\text{mgCm}^{-2}(14\text{h})^{-1}$			Vidussi et al. (2000)	in situ ^{14}C

[a] corrected following Morel et al. (1996).

Table 2. Site, sampling data depths and variables measured and source of the studies considered in this review. S: surface, INT: integrate data, chl-*a*: chl-*a* concentration, BA: bacterial abundance, VA: Viral abundance, BP: bacterial production, VBR: ratio of viral abundance respect to bacterial abundance, VBM: viral mortality on bacteria, *n*: number of data.

Location	Date	Depth (m)	*n*	Variables	References
West					
NW Mediterranean	June 1995	5–200 (S, INT)	42	chl-*a*, BA, VA, VBM, VBR	Guixa-Boixereu et al. (1999b)
NW Mediterranean	June 1999	5–200 (S, INT)	6	BA, VA, VBM, VBR	Weinbauer et al. (2003)
Alboran Sea	October and November 2004	1–200 (S, INT)	6	BA, VA, BP, VBR	Magagnini et al. (2007)
W Mediterranean	October and November 2004	1–200 (S, INT)	16	BA, VA, BP, VBR	Magagnini et al. (2007)
Thyrrenean Sea	October and November 2004	1–200 (S, INT)	11	BA, VA, BP, VBR	Magagnini et al. (2007)
Straits of Sicily	October and November 2004	1–200 (S, INT)	15	BA, VA, BP, VBR	Magagnini et al. (2007)
East					
Adriatic Sea	May 91–November 1992 January–February 2001 April–May 2003	0,5 (S) 1–1200 (S) (S)	6	chl-*a*, BA, VA, VBR BA, VA, BP, VBR BA, VA, BP, VBR	Weinbauer et al. (1993) Corinaldesi et al. (2003) Bongiorni et al. (2005)
Ionian Sea	October and November 2004	1–200 (S, INT)	19	BA, VA, BP, VBR	Magagnini et al. (2007)

Table 3. Number (*n*) of data used to find out the relationships between different variables in the Western Mediterranean (W-Med) and the Eastern Mediterranean (E-Med). BA: bacterial abundance; BP: Bacterial production; VA: viral abundance; PP: primary production; HNF: heterotrophic nanoflagellates abundance; Cil: ciliate abundances; Chl: chl-*a* concentration.

Variables	W-Med (*n*)	E-Med (*n*)	Source
BA-VA	42	0	Guixa-Boixereu et al. (1999a)
	38	19	Magagnini et al. (2007)
	0	6	Weinbauer et al. (1993), Corinaldesi et al. (2003) Bongiorni et al. (2005)
	10	0	Weinbauer et al. (1993)
BA-BP	0	174	Christaki et al. (2003)
	8	0	Vaqué et al. (2001)
	0	13	Robarts et al. (1996)
	13	18	Van Wambeke et al. (2002)
	26	50	Christaki et al. (2001)
	0	91	Van Wambeke et al. (2000)
BP-PP	48	29	Turley et al. (2000)
	22	24	Christaki et al. (2002)
	26	0	Pedrós-Alió et al. (1999)
HNF-BA	12	0	Christaki et al. (1996), Christaki et al. (1998)
	36	45	Christaki et al. (2001)
	8	0	Vaqué et al. (2001)
	0	48	Siokou-Frangou et al. (2002)
Cil-Chl	20	42	Pitta et al. (2001)
	8	0	Vaqué et al. (2001)
	79	0	Dolan and Marrasé (1995)

Table 4. Bacterial (BA), Heterotrophic Nanoflagellate (HNF) abundance and Bacterial Production (BP) in different areas of the basin *(BP units are those reported by the authors)*.

Period	Location	BA (cells 10^8 l^{-1})	BP*	HNF (cells 10^6 l^{-1}) % BP consumption	Reference
	West				
May	Almeria-Oran front front (Alboran Sea)	2.3–13.5	0.04–3.26 μgCl^{-1}d^{-1} 124–199 mgCm^{-2}d^{-1} (150 m)		Fernàndez et al. (1994)
May and June	NW Mediterranean current	3.6–9.6	1.2–7.2 μgCl^{-1}d^{-1} (5 and 40 m) 1.0–2.1 pmolTdRl^{-1}h^{-1}	0.8–2.2	Christaki et al. (1996, 1998)
June	Barcelona: In-Offshore transect	1.5–6.0	0.5–3.0 pmolTdRl^{-1}h^{-1} 20–360 mgCm^{-2}d^{-1} (60–80 m)		Gasol et al. (1998)
Stratification period (3 yr)	Barcelona Balearic islands	3.1–5.4	0.02–2.5 μgCl^{-1}d^{-1} 1–104 mgCm^{-2}d^{-1} (0–200 m)		Pedrós-Alió et al. (1999)
October	Algerian current	6.6–9.0	0.3–4.5 μgCl^{-1}d^{-1} 33–384 mgCm^{-2}d^{-1} (120 m)		Moran et al. (2001)
March	NW Mediterranean: transects off-shore	1.5–8.9 (HDNA 25-87%)	0.09–5.9 μgCl^{-1}d^{-1}	0.3–3.0	Vaqué et al. (2001)
Monthly (one year)	NW Mediterranean: station off-Nice	1.4–11.0	n.d.–4.8 μgCl^{-1}d^{-1} 60–468 mgCm^{-2}d^{-1} (130 m)		Lemée et al. (2002)
November, January	Almeria-Oran front (Alboran Sea)	5.0–15.0	0.1–5.5 μgCl^{-1}d^{-1} 68–215 mgCm^{-2}d^{-1} (200 m) Atl.jet 52–70 mgCm^{-2}d^{-1} (200 m) Med water		Van Wambeke et al. (2004)
	East				
September	Cyprus eddy core and boundary	2.8–4.9	0.2–0.4 pmolTdRl^{-1}h^{-1} 0.2–0.48 10^6 cellsl^{-1}h^{-1}	0.4–0.9	Zohary and Robarts (1992)
October–November	Levantine basin	0.4–3.9	0.04–0.2 μgCl^{-1}d^{-1} 0–3.9, avg: 0.3 pmolTdRl^{-1}h^{-1} 8–43, avg 24 mgCm^{-2}d^{-1} (200 m)		Robarts et al. (1996)
March	Cyprus eddy	2.5–3.5	0.0–0.2 average 0.1 pmolTdRl^{-1}h^{-1}		Zohary et al. (1998)
September, March	S.Aegean Sea (transect off-shore)	3.0–5.0	0.45–1.96 μgCl^{-1}d^{-1} 7–131, avg 45 mgCm^{-2}d^{-1} (100 m)		Van Wambeke et al. (2000)
September, March	North and South Aegean	2.3–15.2	0.22–0.94 μgCl^{-1}d^{-1} 48–110 mgCm^{-2}d^{-1} (10 m)	0.3–3.1 35–100%	Christaki et al. (2003), Siokou-Frangou et al. (2002)
June–July	east-west transect	2.9–5.0	0.0048–1.3 μgCl^{-1}d^{-1} 13–75 mgCm^{-2}d^{-1} (200 m)	0.5–1.2 45–85%	Christaki et al. (2001), Van Wambeke et al. (2002)

Table 5. Mean values (range) of mesozooplankton biomass (as dry weight or organic C) in different areas of the Mediterranean Sea.

Area	Sampling period	Net mesh size	Layer	Biomass (mgm^{-3})	Reference
Alboran Sea	Winter 1997	200 μm	0–200 m	14.44 (5.5–25)	Youssara and Gaudy (2001)
Alboran Sea	April–May 1991	200 μm	0–200 m	10.13 (3.6–18.3)	Thibault et al. (1994)
Algerian Basin	July–August 1997	200 μm	0–200 m	8.2 (2.1–34.5)	Riandey et al. (2005)
Catalan Sea	Autumn 1992	200 μm	0–200 m	2.9 (2.2–3.4)[b]	Calbet et al. (1996)
Catalan Sea	June 1993	200 μm	0–200 m	5.8 (4.8–8)[b]	Calbet et al. (1996)
Catalan Sea	Annual mean	200 μm[a]	0–200 m	7.95[b]	Alcaraz et al. (2007)
N Balearic Sea	March 2003	200 μm	0–200 m	8.4 (0.4–17.8)	Mazzocchi, unpublished data
	April 2003			5.9 (2.0–13.2)	
Gulf of Lion	Spring 1998	200 μm	0–200 m	8.73 (3–13.5)	Gaudy et al. (2003)
E Ligurian Sea	December 1990	200 μm			
Tyrrhenian Sea	Autumn 1986	200 μm	0–50 m	(3.6–32) (AFDW)	Licandro and Icardi (2009)
N Ionian Sea	Spring 1999	200 μm	0–100 m	7.9 (4.4–13.4)	Fonda Umani and de Olazàbal (1988)
				2.1 (1.1–3.8)	Mazzocchi et al. (2003)
S Adriatic Sea	April 1990	No info	0–50 m	(0.1–7.4) (AFDW)	Fonda Umani (1996)
N Aegean Sea	March 1997	200 μm	0–200 m	8 (5.5–13.3)	Siokou-Frangou, unpublished data
S Aegean Sea	March 1997	200 μm	0–200 m	4 (2.5–5.1)	Siokou-Frangou, unpublished data

[a] collection by bottles and filtering through 200 μm mesh size netting,
[b] organic C measured with CHN analyzer.

Table 6. Mean values (range) of egg production rates (EPR) and estimated copepod (CP) or mesozooplankton (MZP) production in areas of the Mediterranean Sea.

Area	Period	Species	EPR (eggs f^{-1} d^{-1})	Production (mgC m^{-2} d^{-1})	Reference
Gulf of Lion	Winter 1999			19 (MZP)	Gaudy (1985)
	Spring 1998			54 (MZP)	
Catalan sea	March 1999	*C. typicus*	105		Calbet et al. (2002)
		A. clausi	15		
		C. lividus	14		
Catalan Sea	June 1995	*C. typicus*	5		Saiz et al. (1999)
		T. stylifera	7		
		C. lividus	4		
Catalan Sea	Annual mean			(20–40) (MZP)	Saiz et al. (2007)
Adriatic Sea	Annually			(0.6–3) (MZP)	Fonda Umani (1996)
N Aegean Sea	March 1997			5 (CP)	Siokou-Frangou et al. (2002)
	Sept 1997			15 (CP)	
NE Aegean Sea	March 1997			41 (CP)	Siokou-Frangou et al. (2002)
	Sept 1997			58 (CP)	
S Aegean Sea	March 1997			5 (CP)	Siokou-Frangou et al. (2002)
	Sept 1997			6 (CP)	
NE Aegean Sea	April 2000	*C. typicus*	(7–49)	36 (CP)	Zervoudaki et al. (2007)
		C. helgolandicus	(3–24)		
		A. clausi	(1–25)		
		P. parvus	(9–25)		
		O. similis	(0.3–9)		
		A. clausi	(1–25)		
	Sept 1999	*T. stylifera*	(1–128)	15 (CP)	
		C. furcatus	(2–15)		
		P. parvus	(3–8)		
		O. media	(3–7)		

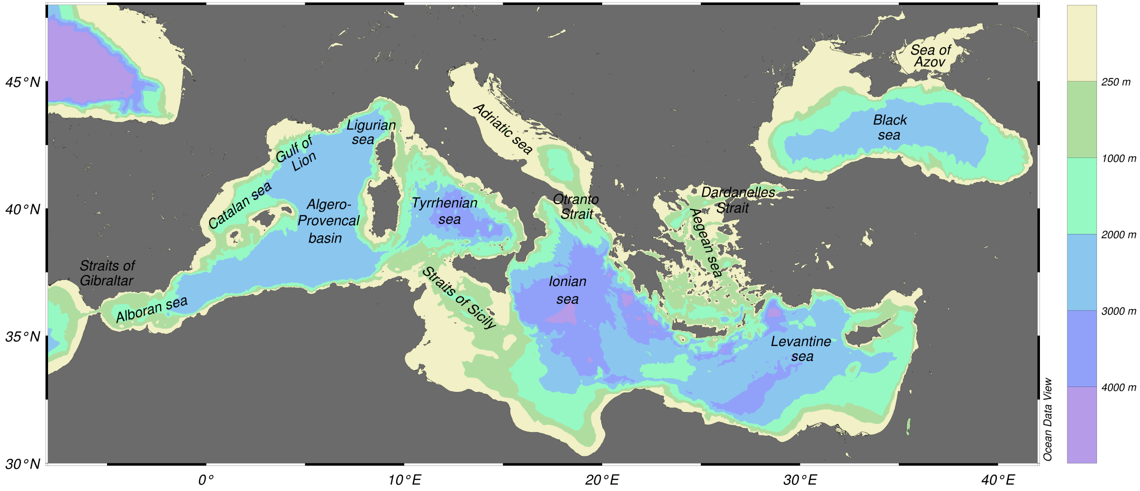

Fig. 1. Major seas, connecting straits and bottom topography of Mediterranean Sea.

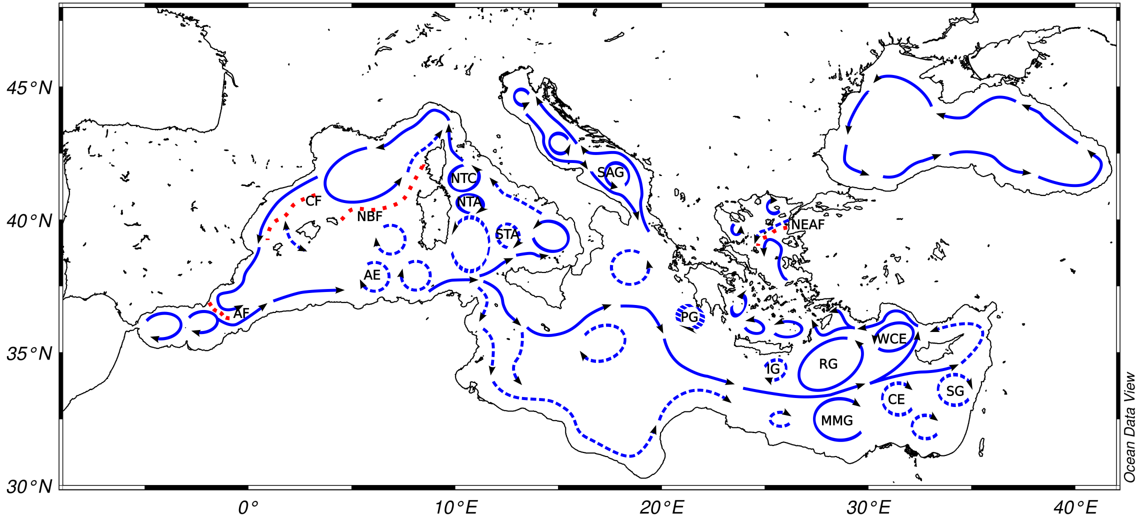

Fig. 2. Key traits of surface circulation of Mediterranean Sea. Acronyms: AE: Algerian Eddies; AF: Almerian Front; CE: Cyprus Eddy; WCE: West Cyprus Eddy; NCF: Catalan Front; IG: Ierapetra Gyre; MMG: Mersa Matruh Gyre; NBF: North Balearic Front; NEAF: North East Aegean Front; NTC: North Tyrrhenian Antiyclon; NTA: North Tyrrhenian Cyclon; PG: Pelops Gyre; RG: Rhodos Gyre; SAG: South Adriatic Gyre; SG: Shikmona Gyre (sources: Artegiani et al., 1997; Astraldi et al., 2002; Karageorgis et al., 2008; Malanotte-Rizzoli et al., 1997; Millot, 1999; Rinaldi et al., 2009).

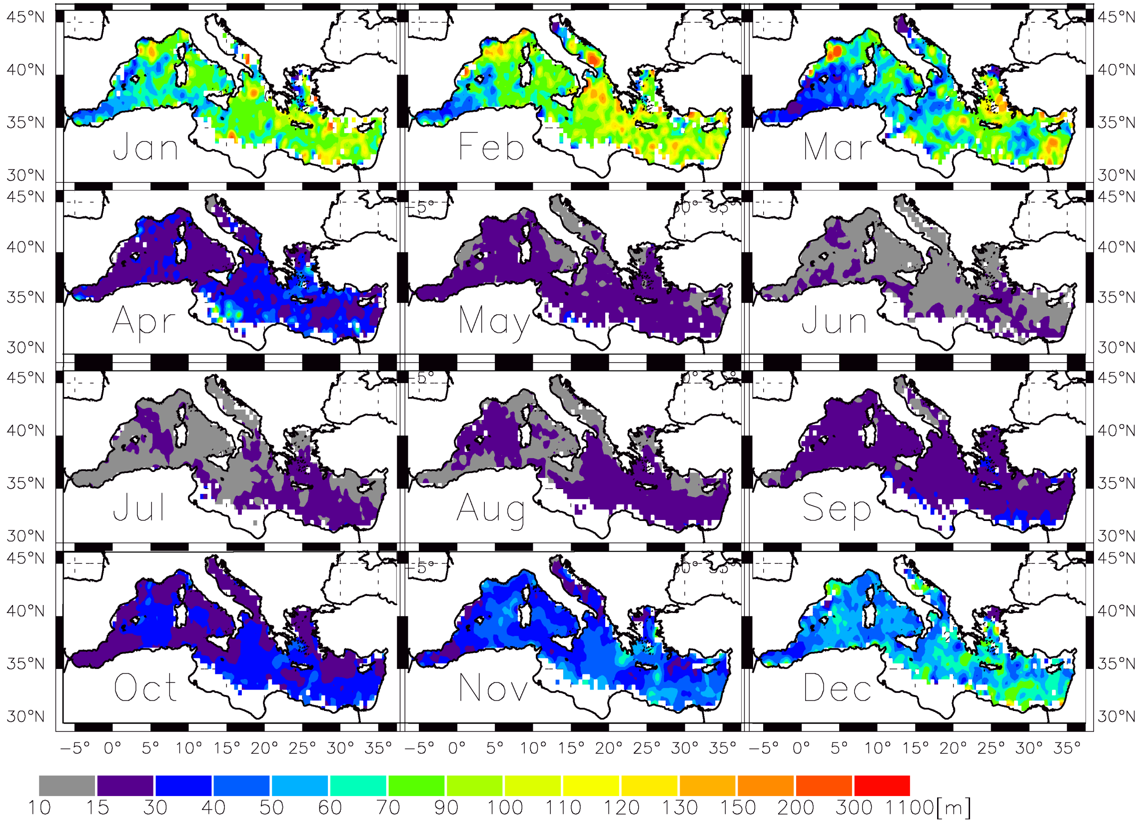

Fig. 3. Climatology of Mixed Layer Depth. Reproduced from D'Ortenzio et al. (2003) by permission of American Geophysical Union.

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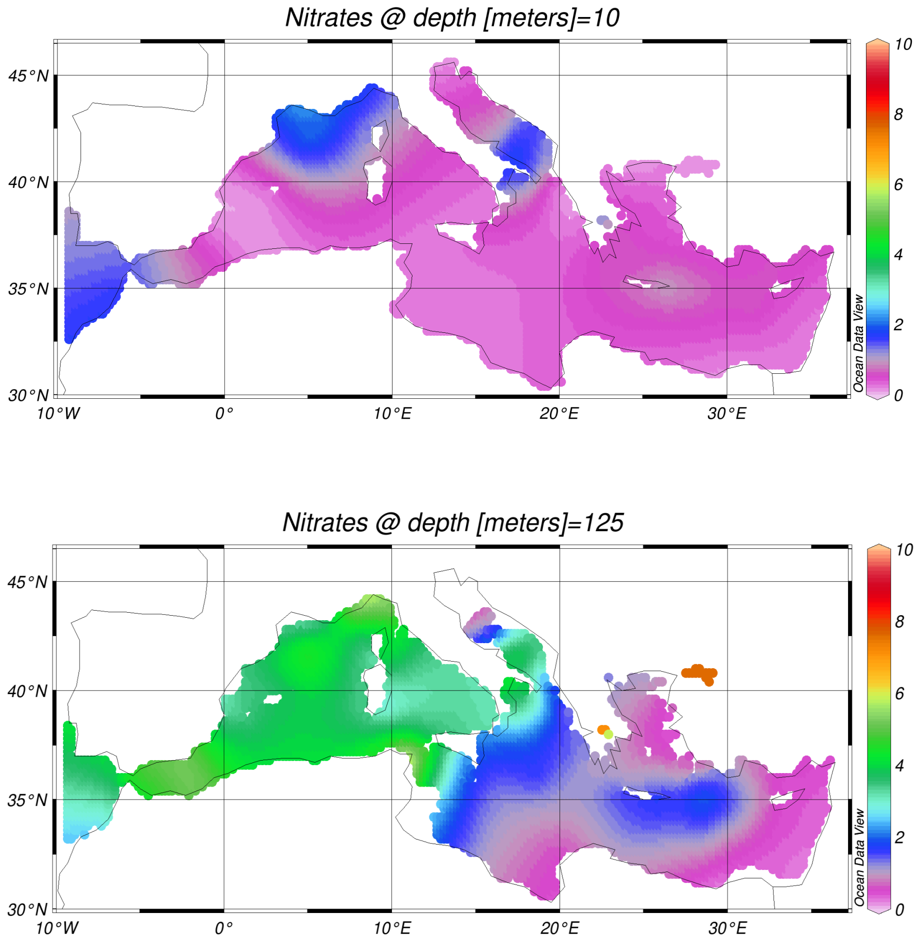

Fig. 4. Average nitrate concentration (μmol l^{-1}) at 10 m (upper panel) and 125 m (lower panel) in winter.

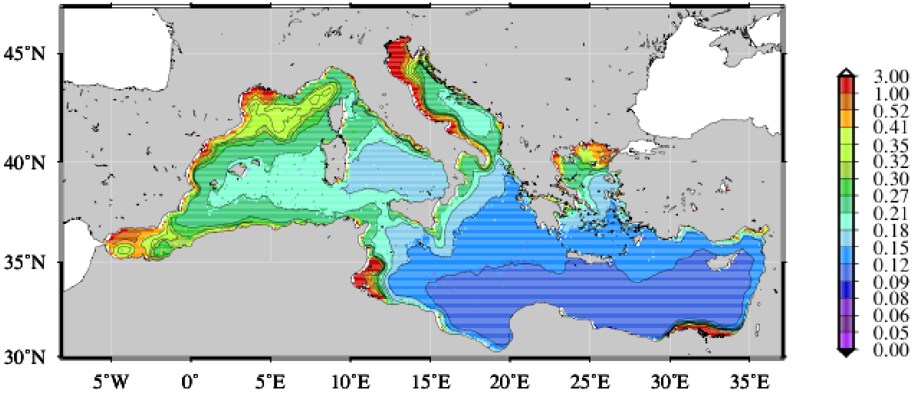

Fig. 5. Spatial distribution of satellite derived chl-*a* as reported by D'Ortenzio and Ribera d'Alcalá (2009).

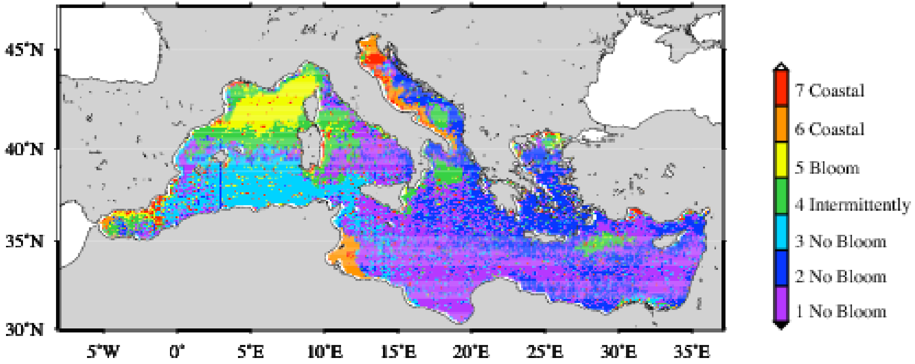

Fig. 6. Spatial distribution of the seven bioprovinces derived from the analysis of the SeaWiFS chl-*a* dataset (D'Ortenzio and Ribera d'Alcalá, 2009).

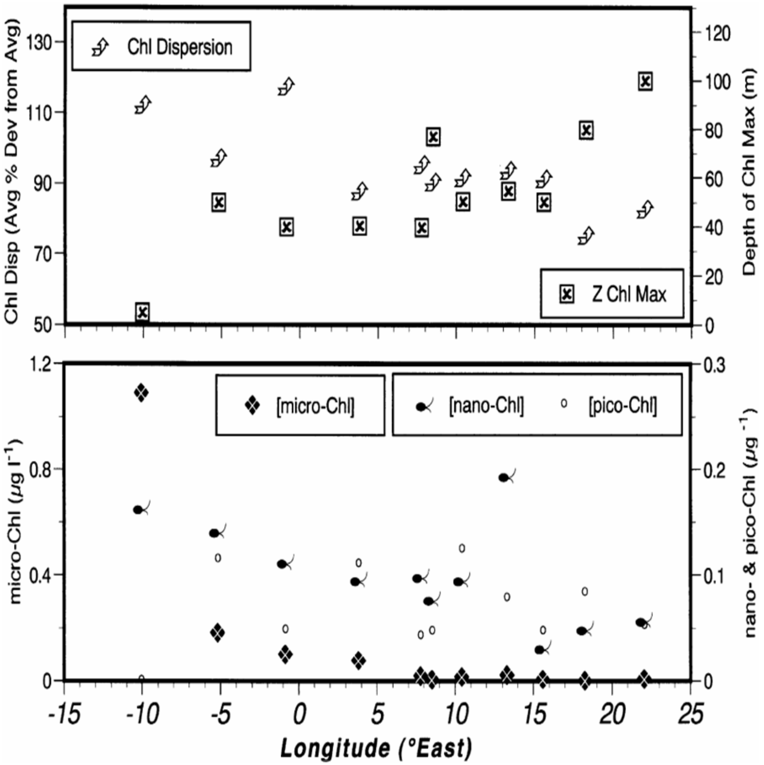

Fig. 7. The top panel shows the deepening of the DCM (Z Chl Max) and the chl-*a* dispersion (Chl Dispersion) as an average of the discrete depth difference from water column average of chl-*a* concentration, in percentage. Dispersion values in the western basin are closer to 100% than in the Eastern Basin, demonstrating a higher vertical patchiness in the latter. The bottom panel represents the west to east decrease for calculated chl-*a* in pico-, nano- and microplankton. Note the Longitude scale: the two data points to the left are outside the MS, while the Levantine basin was not sampled. Modified with permission from Dolan et al. (2002).

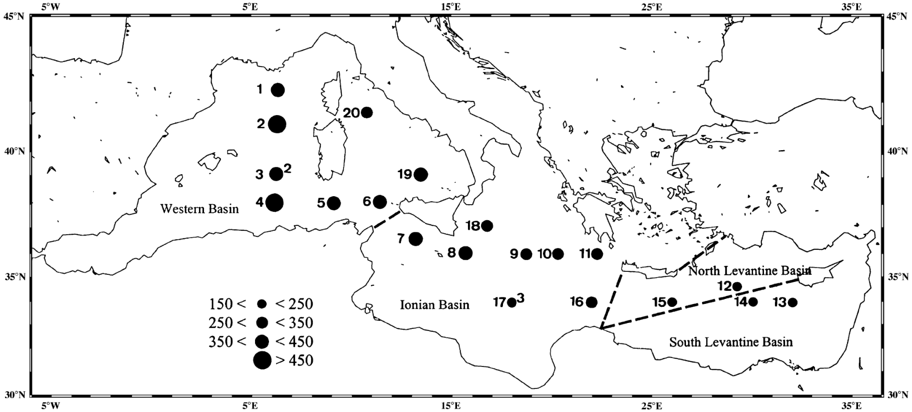

Fig. 8. Integrated primary production (mg C m^{-2} day^{-1}) during the MINOS cruise (May-June 1996), reproduced with permission from Moutin and Raimbault (2002).

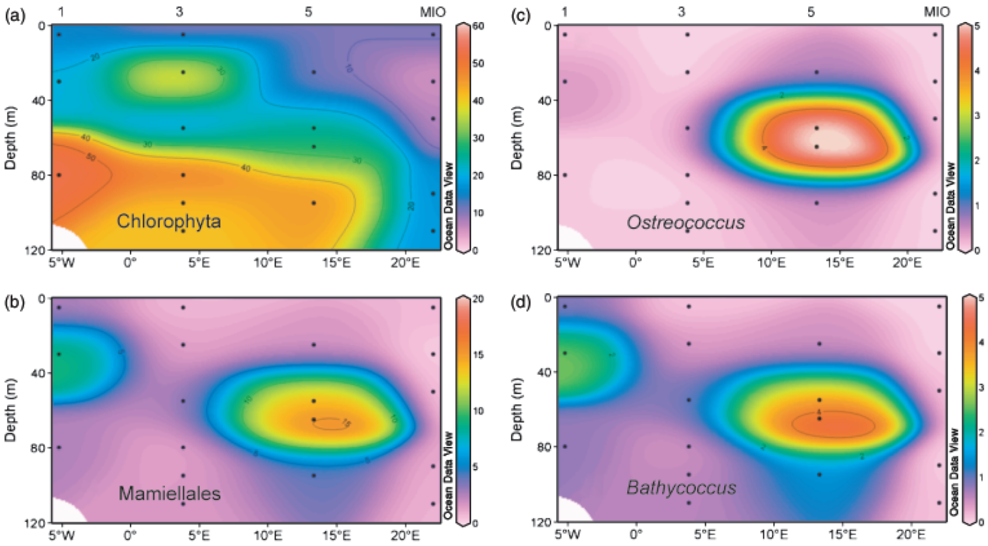

Fig. 9. Longitudinal differences in the distribution of selected autotrophic picoeukaryotes during the cruise PROSOPE from Gibraltar to the Southern Cretan Sea in September 1999. The distribution of the different taxa is represented as their percentage to the total eukaryotes estimated with quantitative PCR. Chlorophytes were abundant in deep and intermediate layers in the western basin, whereas *Ostreococcus*, *Bathycoccus* and other Mamiellales were only abundant at intermediate depths in the Sicily Channel, reproduced with permission from Marie et al. (2006).

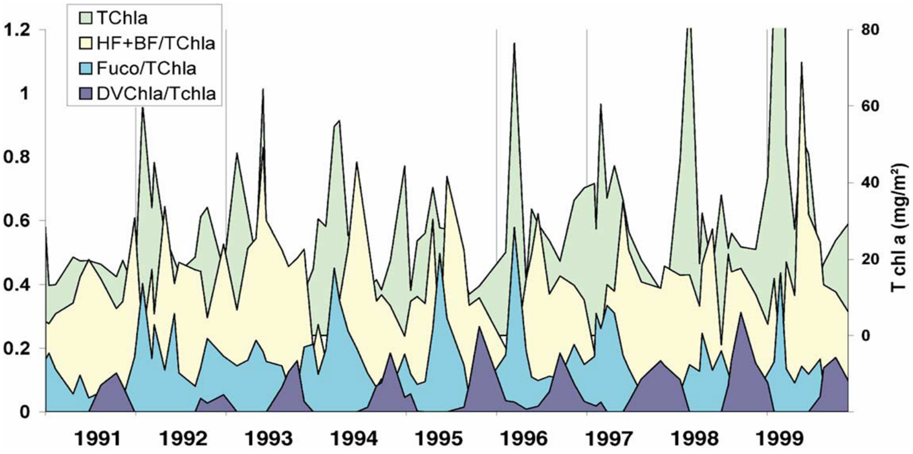

Fig. 10. Seasonal cycle of phytoplankton at the long-term station DYFAMED for the 1991–1999 period. Nanoflagellates (HF+BF), diatoms (Fuco) and *Prochlorococcus* (DVChl*a*) are represented as ratio of their distinctive pigments to total chl-*a*. The total chl-*a* integrated concentration (mg m^{-2}) is also represented in green, reproduced with permission from Marty et al. (2002).

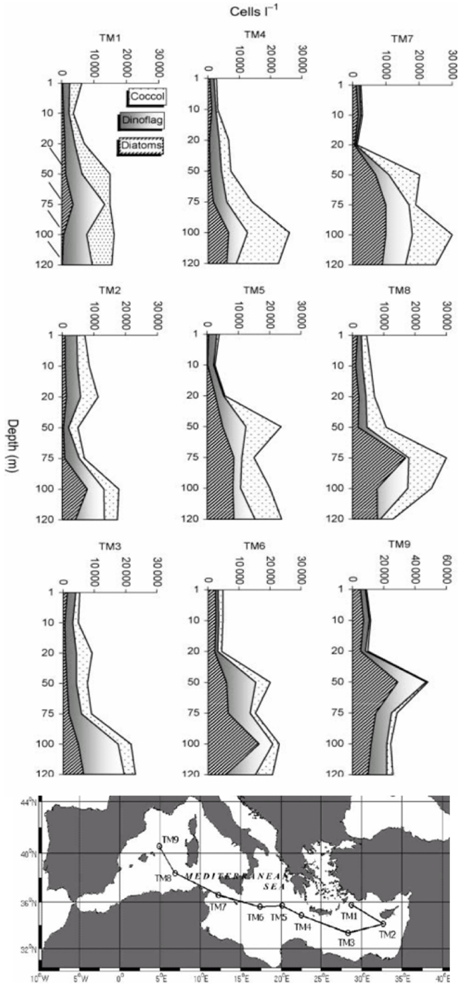

Fig. 11. Vertical profiles of diatoms, dinoflagellates and coccolitophores over an eastwest longitudinal transect of the Mediterranean Sea in June 1999, modified with permission from Ignatiades et al. (2009).

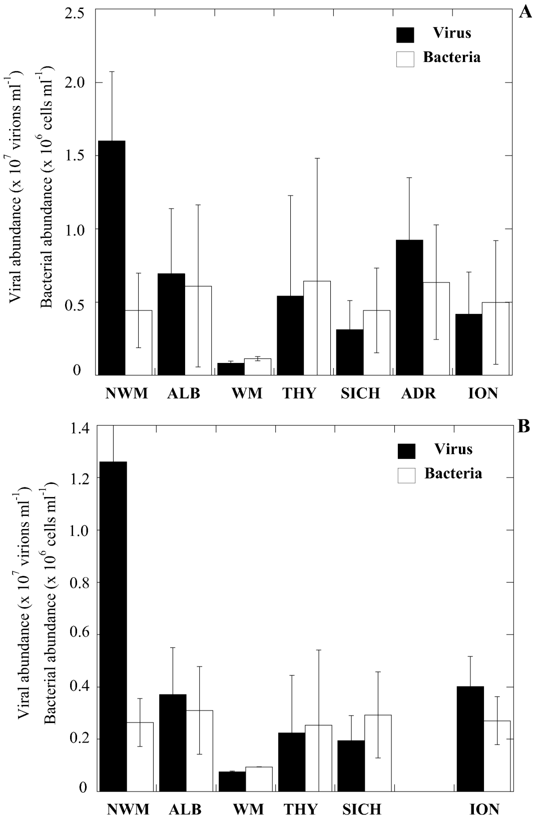

Fig. 12. Average surface viral and bacterial abundance from the different Mediterranean sites **(A)**, average integrated values (1–200 m), that were normalized in each case dividing them by the maximal considered depth **(B)**. Bars are SD of the mean. NWM: NW-Mediterranean, ALB: Alboran, WM: WMediterranean, THY: Tyrrhenian, SICH: Straits of Sicily, ADR: Adriatic, ION: Ionian (B).

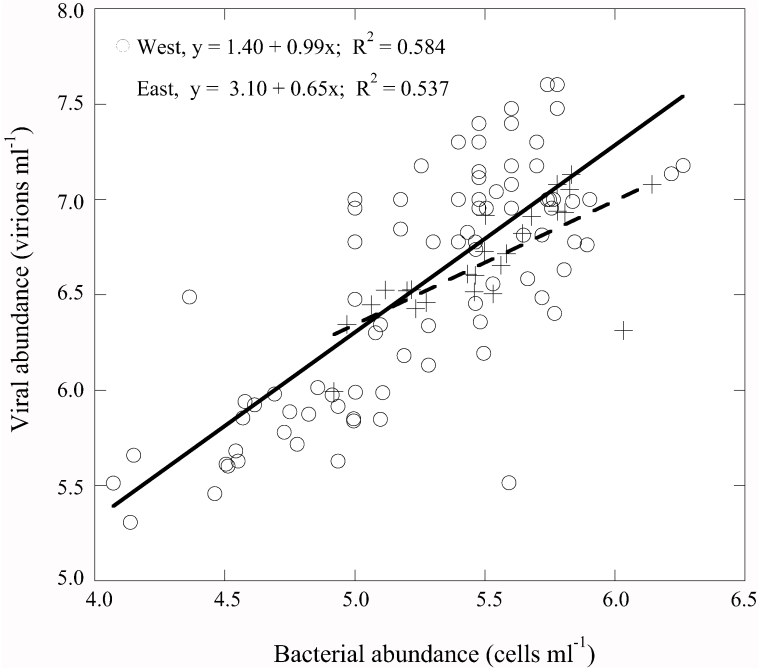

Fig. 13. Relationship between bacterial and viral abundance (log transformed), taken at depths between 5 and 200 m, for Western and Eastern Mediterranean waters.

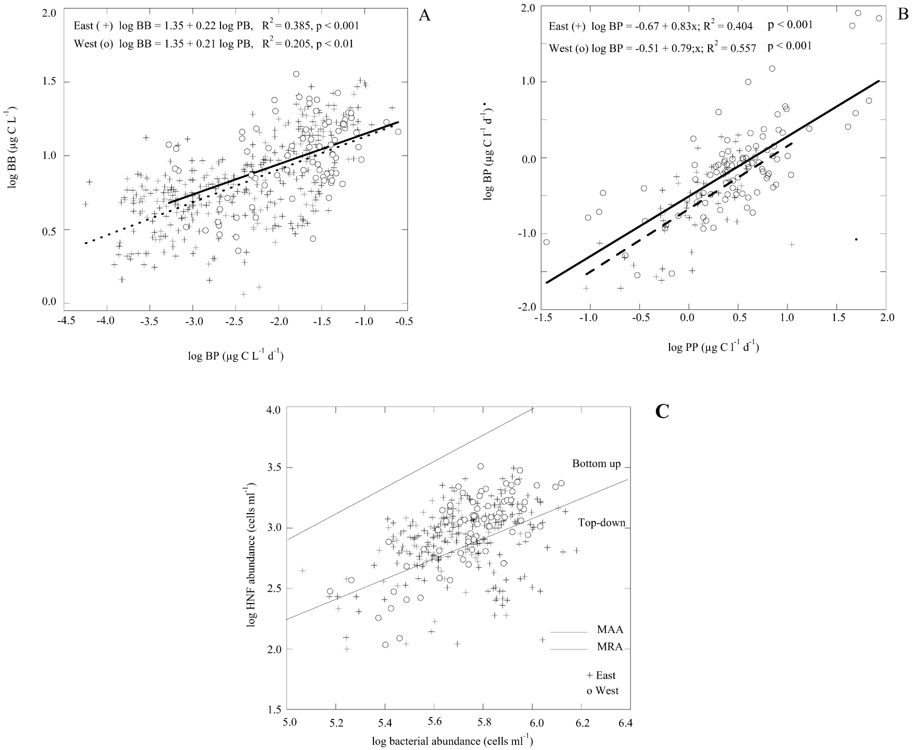

Fig. 14. **(A)** Log–log linear regression between bacterial biomass (μgCl^{-1}) and bacterial production (μgCl^{-1}h^{-1}) and **(B)** between bacterial production (μgCl^{-1}h^{-1}) and primary production for the West and East Mediterranean Sea waters; **(C)** Relationship between log heterotrophic nanoflagellates abundance (HNF, cellsml^{-1}) and log bacterial prey (cellsml^{-1}) from the model of (Gasol, 1994). All HNF abundances fall below the Maximum Attainable Abundance line (MAA) while 70 and 75% HNF fall above the Mean Realised Abundance for marine environment (MRA) in the East and the West Mediterranean, respectively, generally suggesting bottom-up control prevailing on HNF (cf. open sea studies on Table 3).

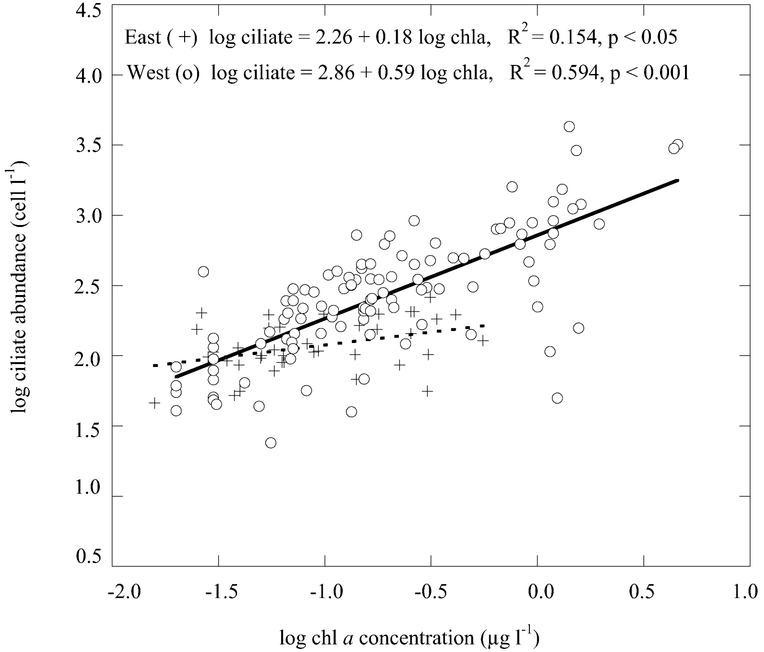

Fig. 15. Log–log linear regression between chl-*a* concentration ($\mu g l^{-1}$) and ciliate abundance ($cell l^{-1}$), taken at depths between 5 and 200 m, for Western and Eastern Mediterranean waters.

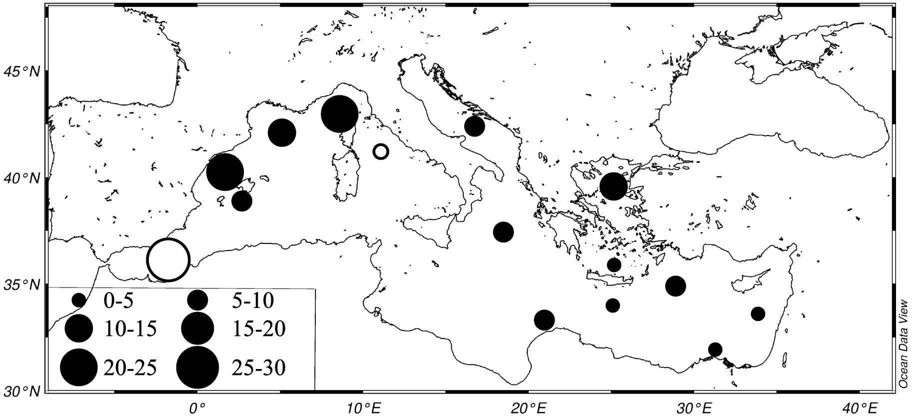

Fig. 16. Spatial distribution of total mesozooplankton abundance (black circles) or total copepod abundance (open circles) (1000×ind. m^{-2}) in spring time in the 0–200 layer of MS. (Sources: Benović et al., 2005; Christou et al., 1998; Fernàndez de Puelles et al., 2004 (0–100 m layer); Gaudy and Champalbert, 1998; Mazzocchi et al., 2003; Mazzocchi, unpublished data; Pasternak et al., 2005 (0–150 m layer); Pinca and Dallot, 1995; Porumb and Onciu, 2006; Saiz et al., 1999; Scotto di Carlo et al., 1984; Seguin et al., 1994; Siokou-Frangou, unpublished data; Zakaria, 2006) (0–100 m layer).

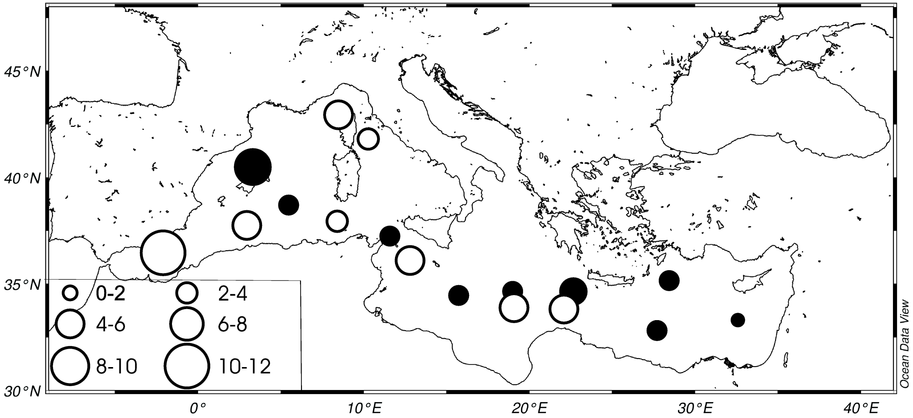

Fig. 17. Distribution of total mesozooplankton abundance (1000×ind.m^2) in the 0–100 m layer during June 1999 (black circles), (Source: Siokou-Frangou et al., 2004) and of total copepods abundance (1000×ind.m^2) in the 0–200 m layer during September 1999 (white circles), (Source: Dolan et al., 2002).

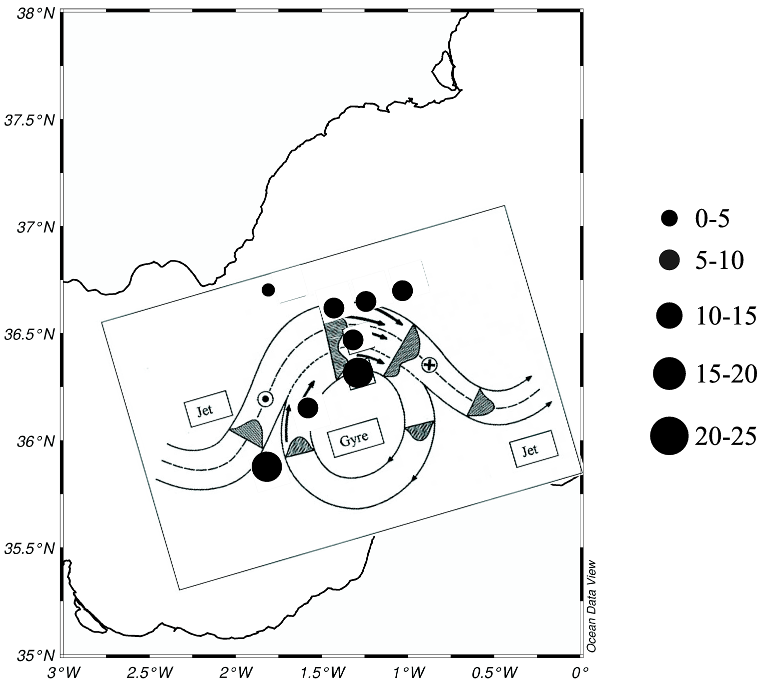

Fig. 18. Distribution of mesozooplankton biomass (dry weight in mgm^{-3}) in the 0–200 m layer of the Almeria-Oran area, as affected by the hydrological features. Modified with permission from Youssara and Gaudy, 2001).

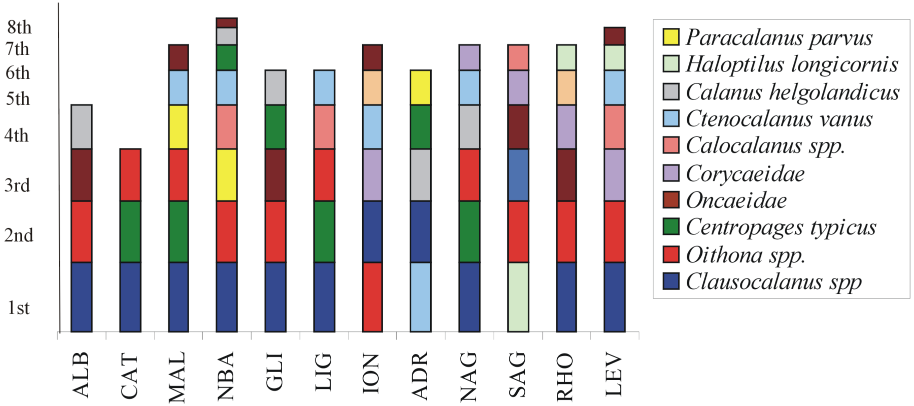

Fig. 19. Rank order of dominant copepod species or genera in the 0–200 m layer of several areas of the MS in spring. The rank order of each species or genus is given in the y axis and the height of the relevant pattern decreases with the rank order of the species. ALB: Almeria-Oran area, MCH: Mallorca Channel, NBA: North Balearic Sea, GLI: gulf of Lion; LIG: Ligurian Sea, ADR: Adriatic Sea, ION: Ionian Sea, NAG: North Aegean Sea, SAG: South Aegean Sea; RHO: Rhodos cyclonic gyre; LEV: Central Levantine Sea (Sources: Fernàndez de Puelles et al., 2004 (0–100 m layer); Gaudy et al., 2003; Hure et al., 1980; Mazzocchi et al., 2003 and unpublished; Pasternak et al., 2005 (0–150 m layer); Pancucci-Papadopoulou et al., 1992; Pinca and Dallot, 1995; Seguin et al., 1994; Siokou-Frangou et al., 2004 and unpublished).