

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 with distinctive traits, especially in regard to the thermohaline circulation. Recent investigations have basically confirmed the long-recognised oligotrophic nature of this sea, which increases along both the west-east and the north-south directions. Nutrient availability is low, especially for phosphorous (N:P up to 60), though this limitation may be buffered by inputs from highly populated coasts and from the atmosphere. Phytoplankton biomass, as chl *a*, generally displays low values (less than $0.2 \mu\text{g chl } a \text{ l}^{-1}$) over large areas, with a modest late winter increase. A large bloom (up to $3 \mu\text{g l}^{-1}$) is observed throughout the late winter and spring exclusively in the NW area. Relatively high biomass values are 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 is found at increasingly greater depths ranging from 30 m in the Alboran Sea to 120 m in the easternmost Levantine basin. Primary production reveals a west-east decreasing trend and ranges between 59 and $150 \text{ g C m}^{-2} \text{ y}^{-1}$ (in situ measurements). Overall, the basin is largely dominated by small autotrophs, microheterotrophs and egg-carrying copepod species. The microorganisms (phytoplankton, viruses, bacteria, flagellates and ciliates) and zooplankton components reveal a considerable diversity and

variability over spatial and temporal scales, although the latter is poorly studied. 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-rich copepod genera or families which dominate the basin. Major dissimilarities between western and eastern basins have been highlighted in species composition of phytoplankton and mesozooplankton, but also in the heterotrophic 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. In such areas, the intermittent nutrient enrichment promotes a switching between a small-sized microbial community and diatom-dominated populations. A classical food web readily substitutes the microbial food web in these cases. These switches, likely occurring within a continuum of trophic pathways, may greatly increase the flux towards higher trophic levels, in spite of the apparent heterotrophy. Basically, the microbial system seems to be both bottom-up and top-down controlled. A “multivorous web” is shown by the great variety of feeding modes and preferences and by the significant and simultaneous grazing impact on phytoplankton and ciliates by mesozooplankton.



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1 Introduction

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.)

The Mediterranean Sea (MS) is the largest quasi-enclosed sea on the Earth, its surface 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) distinctive 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 be 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; Thingstad et al., 2005). 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; Barale et al., 2008) as well as by in situ data (Turley et al., 2000; Christaki et al., 2001), ii) a high diversity compared to its surface and volume (Bianchi and Morri, 2000), and iii) a relatively high number of bioprovinces (*sensu* Longhurst, 2006), with boundary definition mostly based on the distribution of the benthos and the neuston (Bianchi, 2007). The MS is also a site of intense anthropic activity dating back to at least 5000 years BP, the impact of which on the marine environment has 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), followed a few years later by a collection of scientific papers edited by Minas and Nival (1988). Most of those contributions focused on bulk parameters (e.g., *chl a*, primary productivity, mesozooplankton biomass) and organism 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 perspectives 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 study carbon and nutrient fluxes and to provide insight into the key players of the

MS pelagic food web (e.g., Lipiatou et al., 1999; Thingstad and Rassoulzadegan, 1999; Tselepidis 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 physiological rates (e.g., Calbet et al., 1996; Estrada, 1996; Saiz et al., 1999; Moutin and Raimbault, 2002), while the phosphorus limitation hypothesis has inspired studies on the effects of phosphorus enrichment on the pelagic food web (Thingstad et al., 2005). Physical-biological coupling in general (Crise et al., 1999; Pinardi et al., 2004), as well as in relation to mesoscale dynamics, has also been addressed more frequently during the last decades (e.g., Champalbert, 1996; Alcaraz et al., 2007). Clearly these studies have provided valuable insights on the components of the MS plankton in different areas of the basin. Overall, significant knowledge was provided by international and European projects at basin (MATER) or sub-basin scale (POEM-BC).

The present review aims at providing an updated and integrated picture of the Mediterranean plankton in the offshore epipelagic waters (0–200 m depth) based on studies conducted during the last 25 years. The key issues addressed in the review are: i) the plankton components, from the viruses, 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 existing descriptions of planktonic food web structure (Thingstad, 1998; Sommer et al., 2002) and highlighting the principal carbon producers. A review could be helpful, among other things, as a baseline for the assessment of global change impact on MS ecosystems. In addition, as detailed in the following sections, the peculiar features of the main forcings in the basin and of their scales of variability might trigger non-trivial responses in plankton communities, which could be of general ecological interest beyond the Mediterranean boundaries.

2 Physical and chemical framework

Physical dynamics is a crucial driver for 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, to include both marine and atmospheric processes. The latter are particularly important in the MS because, besides determining the general circulation, they contribute to the fluxes of elements entering the basin. As compared to the open ocean or other internal seas, the inputs from land play a greater role in the MS, because the perimeter to surface ratio of the basin is particularly high and the catchment area of the inflowing waters is one of the largest for marginal seas (Meybeck et al., 2007). As it will be discussed later, this enhances the role of external inputs in regulating nutrient fluxes to the photic zone.

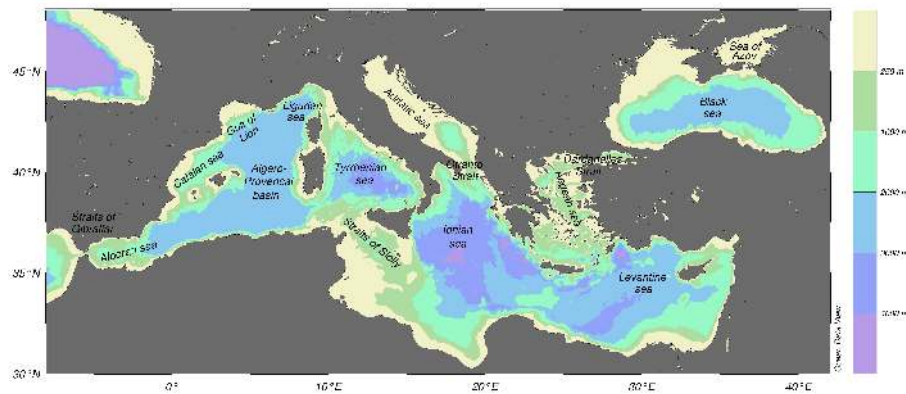


Fig. 1. Major seas, connecting straits and bottom topography of Mediterranean Sea.

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 any 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 the 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 an east-to-west intermediate transport (e.g., Zavatarelli and Mellor, 1995; Pinardi and Masetti, 2000). North-westerly wind stress prevails over the whole basin in winter, with a rotation towards north-east in summer, with no significant decrease in the W-to-E wind driven transport. The wind stress pattern, the morphology of the basin and the bottom topography produce 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) (Fig. 2).

The Atlantic Water (AW) 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 term to thermal stratification in large areas of the South West (SW) MS, decreasing the winter mixed layer depth (D'Ortenzio et al., 2005). From a dynamic view point, the inflow of MAW into the MS basin favours a system of high energy anticyclonic structures in both the Alboran Sea and the Algerian basin, resulting in anticyclonic eddies along the Algerian current path (Fig. 2), with a du-

ration between several months and 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 North West (NW) MS, which separates two drastically different sub-regions. The MAW flows across the Straits of Sicily creating a jet, 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 East Aegean Front) is formed in the area where colder less saline water (~ 30) meets warmer saltier water (~ 38.5) 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 controlled by the topography (Robinson and Golnaraghi, 1994). The most important 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), coupled with 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), and a more variable multipole anticyclonic structure S and SE of Cyprus, which has recently been analyzed in great detail (Zodiatis et al., 2005). This structure is often looked at as composed by the Shikmona gyre (south-east of Cyprus) and the warm Cyprus Eddy (south or 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 (Theocharis and Georgopoulos, 1993; Theocharis et al., 1999). In the Gulf of Lion (NW MS), a large scale cyclonic circulation and the extreme atmospheric

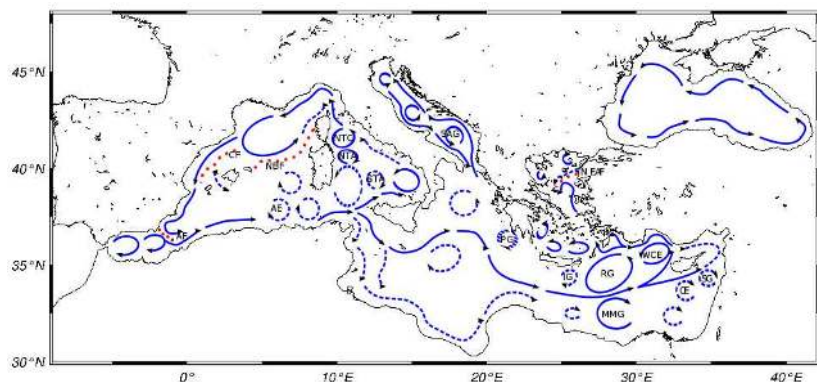


Fig. 2. Key traits of surface circulation of Mediterranean Sea. Acronyms: AE: Algerian Eddies; AF: Almerian Front; CE: Cyprus Eddy; WCE: West Cyprus Eddy; CF: Catalan Front; IG: Ierapetra Gyre; MMG: Mersa Matruh Gyre; NBF: North Balearic Front; NEAF: North East Aegean Front; NTA: North Tyrrhenian Anticyclon;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

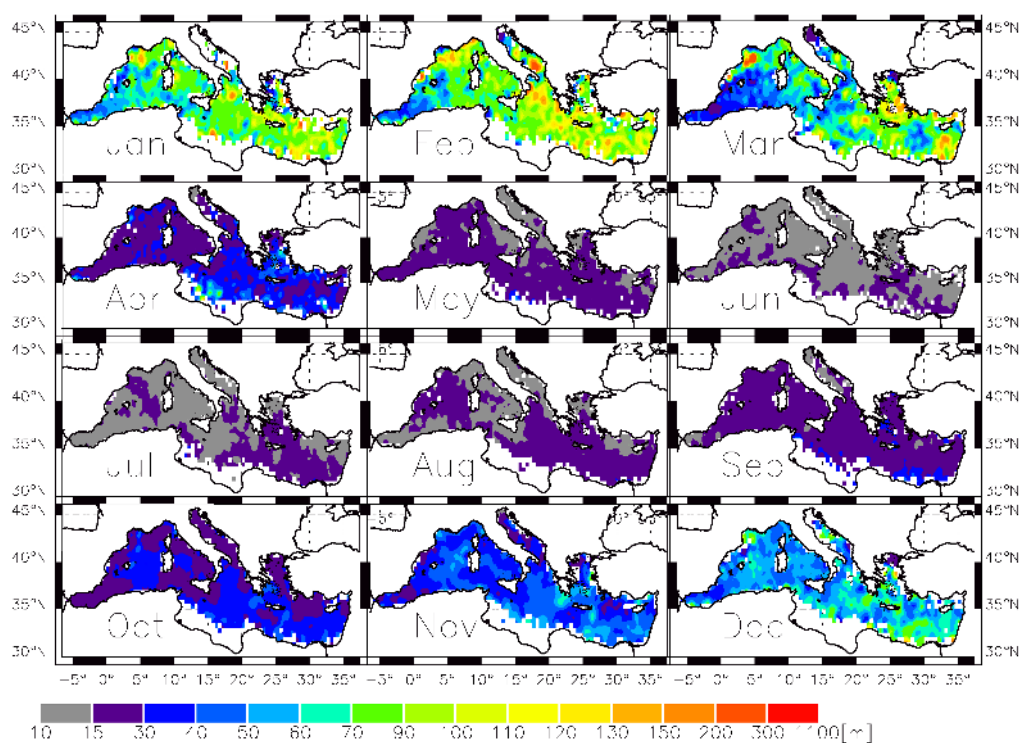


Fig. 3. Climatology of Mixed Layer Depth. Reproduced from D'Ortenzio et al. (2003) by permission of American Geophysical Union.

forcing, especially in winter, force intense convective events, which eventually reach the bottom. Based on an analysis of Ekman wind-driven surface transport, intermittent coastal upwelling events are also likely to take place in selected regions of the MS, namely the Alboran Sea, Balearic Sea, Straits of Sicily, East Adriatic Sea and North-East Aegean Sea (Agostini and Bakun, 2002). It is worth mentioning that, between the end of the eighties and the first half of the nineties, a sequence of events in atmospheric and marine dy-

namics caused the formation of a large volume of very dense water in the Southern Aegean Sea that spread into the deep layers of the Levantine and Ionian basins, strongly modifying their vertical thermohaline structure (Roether et al., 1996). This event, normally referred to as the Eastern Mediterranean Transient (EMT), caused traceable changes in biogeochemical processes in the Eastern Mediterranean Sea (EMS) (e.g., Civitarese and Gacic, 2001; La Ferla et al., 2003).

The two factors affecting the vertical flux of nutrients to the photic zone allowing new primary 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. The 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 increase vertical transport of nutrients at the time of the winter convective events; ii) clear differences among regions in the time when the mixed layer reaches the maximum depth; iii) a difference in the duration of the stratification season among different areas, with layer thickness variability, i.e., difference in the location of the pycnocline. As for the available nutrient pool, an inventory of average winter nitrate concentrations in surface (10 m) and subsurface (125 m) waters is represented in Fig. 4, based on the MEDAR-MEDATLAS data base (<http://www.ifremer.fr/medar/>). Although not fully processed for quality control, these data provide a comprehensive spatial overview for the basin. The two maps demonstrate 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 subsurface nutrient concentration.

Nutrient concentrations in coastal upwelling areas are lower than those found in other upwelling systems (Fig. 4), probably because the duration of upwelling events is very short, but also because of the lower concentrations of nutrients in the subsurface nutrient pool. These in turn depend on the anti-estuarine circulation discussed above, which prevents an accumulation of remineralized nutrients in the deeper layers of the basin. Therefore, upwelling areas do not display a striking difference in biological production as compared to 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, namely in: i) active frontal regions (North Balearic-Catalan, Almeria-Oran, North-East Aegean Sea Fronts) (e.g., Estrada and Salat, 1989; Estrada, 1991; Zervoudaki et al., 2007), ii) deep convection areas (Gulf of Lion, South Adriatic Gyre, Rhodes Gyre) (e.g., Lévy et al., 1998a,b; Siokou-Frangou et al., 1999; Gacic et al., 2002), and iii) sites where coastal morphology and intense wind stress generate a strong input of potential vorticity that leads to the formation of energetic filaments (Wang et al., 1988; Bignami et al., 2008). The latter process may significantly contribute to the dispersal of coastal inputs toward the open sea, along with plankton. Energetic filaments, previously detected only through Sea Surface Temperature anomalies, are also frequently observed in high resolution colour remote sensing chl *a* maps (Iermano et al., 2009).

External inputs from the coasts play a significant role in the MS. There are only three major rivers, the Po in the North Adriatic Sea, the Rhone in the Gulf of Lions and the Nile in

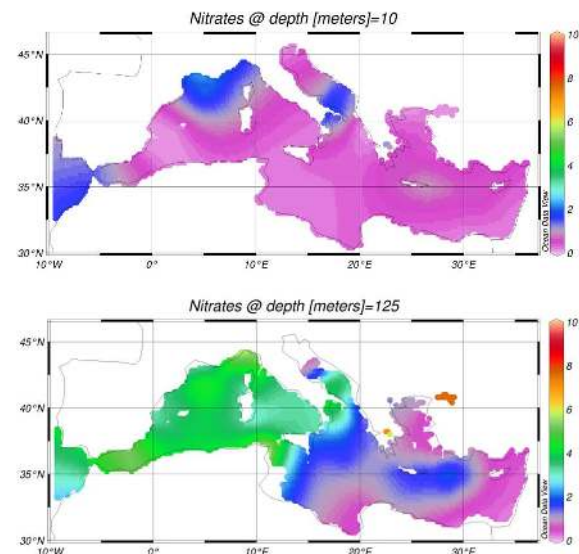


Fig. 4. Average nitrate concentration ($\mu\text{mol l}^{-1}$) at 10 m (upper panel) and 125 m (lower panel) in winter.

the South East Levantine Sea. The Nile, however, has suffered a dramatic decrease in water transport over the last decades, possibly suggesting a concurrent, though not proportional decrease in nutrient inputs. In fact, the relevance of riverine runoff to overall nutrient fluxes is still uncertain, despite several general (e.g., Ludwig et al., 2009) and regional studies (e.g., Degobbi and Gilmartin, 1990; Skoulidakis and Gritzalis, 1998; Cruzado et al., 2002; Moutin et al., 1998).

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 calculations (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 EMS. In particular, phosphorus from atmosphere may account for up to 40% of primary production, while nitrogen input may be sufficient for all of the export production, at least in the EMS (Bergametti, 1987; Migon et al., 1989; Guerzoni et al., 1999; Kouvarakis et al., 2001; Markaki et al., 2003). Atmospheric inputs are clearly a crucial factor in the functioning of the basin. A noteworthy biogeochemical feature in the MS is the very high N/P ratio in its deep layers. Processes leading to this anomalous feature are still controversial, but the high N/P ratio of atmospheric inputs indicates that they are among the factors that contribute to the unbalanced ratio recorded in Mediterranean waters (e.g., Markaki et al., 2008; Mara et al., 2009).

Markaki et al. (2008) also reported that between 30 and 40% of the atmospheric N and P input to the basin is in organic form, which highlights the role of these inputs as

a source of organic matter. Based on the estimates provided by these authors, about $0.35 \times 10^{12} \text{ mol y}^{-1}$ of organic carbon (OC) might be contributed by atmospheric inputs, assuming a conservative OC/ON ratio of 10. These inputs combine with riverine inputs that result from the erosion process on land, which were estimated to be approximately $0.8 \times 10^{12} \text{ mol C y}^{-1}$ (Ludwig et al., 1996). Clearly, inputs from the atmosphere and land contribute not only nutrients to support primary production but also reduced, potentially respirable carbon. To complete the picture, we should also consider the net DOC input through Gibraltar, which is in the order of $0.3 \times 10^{12} \text{ mol C y}^{-1}$ (Dafner et al., 2001). Inputs from the Black Sea would amount to 10% of those entering through Gibraltar (Sempéré et al., 2002), but a significant part of them are likely processed within the Aegean Sea, thus not affecting the overall picture. Hence the total allochthonous organic carbon entering the upper layer of the water column is estimated at $\sim 1.5 \times 10^{12} \text{ mol C y}^{-1}$. This very rough figure is likely to be in the lower range of the real value because of the underestimation of the impact of anthropic activities. This significant load of allochthonous OC, which eventually reaches deep layers as DOC via dense water sinking, may contribute to the high oxygen utilization rates recorded in intermediate and deep layers of the MS which have been attributed to the oxidation of DOC (Christensen et al., 1989; Ribera d'Alcalá and Mazzocchi, 1999; Roether and Well, 2001; La Ferla et al., 2003). Data show that oxygen utilization rates were further enhanced during the years of the EMT (Klein et al., 2003; La Ferla et al., 2003, and references therein). This is consistent with the picture above if one considers that the proportion of waters of surface origin in the mixture that constituted the newly formed dense waters in those years was significantly higher than in the pre-EMT deep water (Klein et al., 2003).

In synthesis, the 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. The scarcity of the internal pool increases 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 most obvious impact of the previously described physical and chemical features is on the distribution of phytoplankton biomass as satellite-derived chl *a* (Fig. 5). This corresponds to the average chl *a* concentration down to the first optical depth, which is the depth at which the downwelling irradiance reduces by $\sim 63\%$. Low values (less than

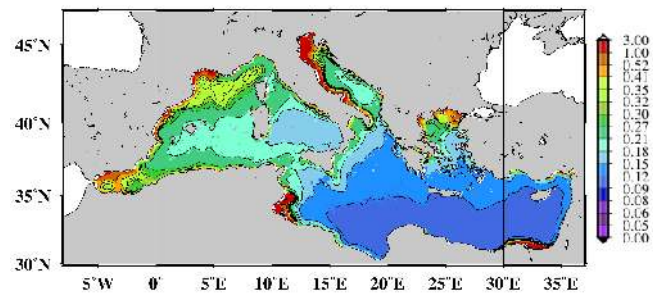


Fig. 5. Spatial distribution of satellite derived chl *a* as reported by D'Ortenzio and Ribera d'Alcalá (2009).

$0.2 \mu\text{g chl } a \text{ l}^{-1}$) are displayed over large areas, with the exception of a large bloom observed throughout the late winter and early spring in the Liguro-Provençal Region. Pronounced phytoplankton blooms, though spatially limited, are also recorded in the Alboran Sea and in the area of the Catalan-North Balearic front. Winds 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 waters plays a major role. More confined high biomass spots are located near the coastlines, especially in proximity to large river mouths or extended continental shelves (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 an increasing west-east 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 mg C m^{-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). The eastward latitudinal decrease is generally rather gradual and continuous across the Western Mediterranean Sea (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 western basins (e.g., Morel and André, 1991; Barlow et al., 1997), with the exclusion of higher values along the Algerian coast.

An intriguing picture was issued by grouping sites with similar seasonal cycles and dynamics of satellite-derived 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 had markedly different seasonal cycle

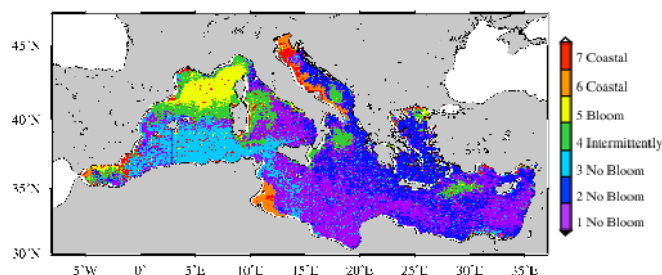


Fig. 6. Spatial distribution of the seven bioprovinces derived from the analysis of the SeaWiFS chl *a* dataset (D’Ortenzio and Ribera d’Alcalá, 2009).

patterns. The first province, mostly concentrated north of the North Balearic front (no. 5 in the figure), presents a pattern that is typical for temperate areas, but unique for the MS. This consists of a late winter-spring bloom lasting more than three months, with a biomass increase up to 6 times the background values (e.g., Cruzado and Velásquez, 1990; Lévy et al., 1998a,b). Other provinces show a typical subtropical cycle, with biomass maxima centred in January but extending from December to early March. The annual range of phytoplankton biomass in these provinces is much smaller, with maxima 2.5 times the background values. 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 south-eastern part of the basin. 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 described for the temperate and subtropical mode: the autumn bloom, typical of temperate regions, is followed by a progressive sinking 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 DYFAMED station in the Ligurian Sea, the only offshore Mediterranean site investigated regularly over more than a decade, the highest values (up to $3 \mu\text{g l}^{-1}$) 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. $2 \mu\text{g l}^{-1}$, Estrada, 1991; Estrada et al., 1993, 1999), whereas those in the Alboran Sea are still higher ($4.3 \mu\text{g l}^{-1}$, Mercado et al., 2005 and $7.9 \mu\text{g l}^{-1}$, Arin et al., 2002). Notably, the spring peak values were in many cases detected in deep waters in response to local doming of nutrient-rich waters, which in the Alboran Sea was forced by the Atlantic cur-

rent (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 $0.5 \mu\text{g l}^{-1}$ (Yacobi et al., 1995; Gotsis-Skretas et al., 1999), and the minima are as low as $0.003 \mu\text{g l}^{-1}$ (e.g., Herut et al., 2000). Exceptions are the peak values of $1.34 \mu\text{g l}^{-1}$ in the frontal zone of the North East Aegean Sea in April (Zervoudaki et al., 2007) and $3.07 \mu\text{g l}^{-1}$ in a small-scale cyclonic area of the North 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 not generally detected (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 DYFAMED station, showed a two to 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 inter-annual variability, often of the same magnitude as the seasonal variability, shown for the Cretan Sea (Psarra et al., 2000) and for the Alboran Sea (Claustre et al., 1994; Mercado et al., 2005). However, effects of climate variations have been hypothesized in some areas of the basin which have been monitored more regularly over the years. For example, higher winter temperature and low wind intensity were related to a decrease in biomass in oligotrophic coastal waters off Corse (Goffart et al., 2002). By contrast, an increase in biomass and production has been reported for the long-term Ligurian Sea DYFAMED station in recent years, probably due to more intense winter mixing driven by circulation and winds (Marty, personal communication). At the basin scale, chl *a* variability in the MS appears to be related to the 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 time, peak chl *a* values ($>2 \mu\text{g l}^{-1}$) were found 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 ($23 \mu\text{g chl } a \text{ l}^{-1}$) 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 $1.5 \mu\text{g chl } a \text{ l}^{-1}$, is a permanent feature for the whole basin over the entire annual cycle, with

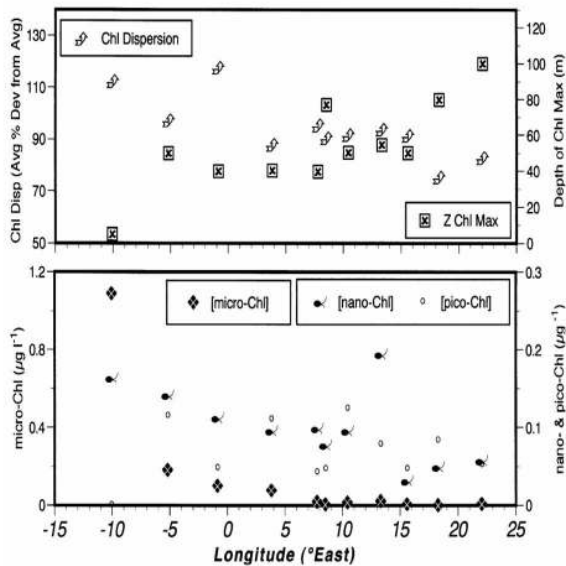


Fig. 7. The top panel shows the deepening of the DCM (Z Chl Max) and the chl a dispersion (Chl Dispersion) as an average of the discrete depth difference from water column average of chl a concentration, in percentage. Dispersion values in the WMS are closer to 100% than in the EMS, demonstrating a higher 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).

the exception of the short period of late winter mixing. The DCM progressively sinks across a west to east gradient from 30 m in the westernmost area (Dolan et al., 2002, Fig. 7), to 70 m in the South Adriatic Sea (Boldrin et al., 2002), down to 120 m in the Levantine basin (Christaki et al., 2001; Dolan et al., 2002). The eastward increase in DCM depth is probably related to lower productivity and hence higher seawater transparency in the Levantine Sea, but the level of DCM may vary considerably between cyclonic and anticyclonic areas (Ediger and Yilmaz, 1996). In the western MS, the depth of the DCM is strongly affected by the Atlantic water inflow and 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-based estimates range from 130 to 198 $\text{g C m}^{-2} \text{y}^{-1}$ over the years 1997–2001 (Bricaud et al., 2002; Bosc et al., 2004), with values for the EMS generally in the lower portion of the range. Estimates from in situ incubations in previous decades were as low as 80–90 $\text{g C m}^{-2} \text{y}^{-1}$ (Sournia, 1973). More recent measurements get closer to satellite-based estimates, e.g., in the Gulf of Lion (140–150 $\text{g C m}^{-2} \text{y}^{-1}$, Conan et al., 1998), but remain consistently lower in other areas such as the Cretan Sea (59 $\text{g C m}^{-2} \text{y}^{-1}$, Psarra et al., 2000). A clear eastward reduction in primary production was reported in the

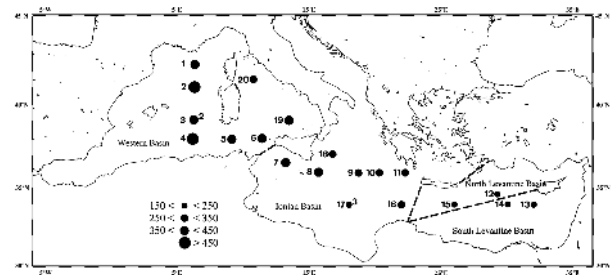


Fig. 8. Integrated primary production ($\text{mg C m}^{-2} \text{day}^{-1}$) during the MINOS cruise (May–June 1996). Reproduced with permission from Moutin and Raimbault (2002).

results from a late-spring (May–June) trans-Mediterranean cruise (Moutin and Raimbault, 2002), when maxima were close to $1 \text{ g C m}^{-2} \text{d}^{-1}$ in the south-western basin and minima ranged between 150 and 250 $\text{mg C m}^{-2} \text{d}^{-1}$ at several stations of the Levantine Sea (Fig. 8). Interestingly, estimates obtained in spring in other studies reflect the same spatial pattern and are within the same ranges as those shown by Moutin and Raimbault (2002) (Table 1). Comparably high values (up to $1.7 \text{ g C m}^{-2} \text{d}^{-1}$) were reported in the Catalan front area in March (Moran and Estrada, 2005), 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 mg C m^{-2} (over a 14 h incubation) (Vidussi et al., 2001) but reached values as high as $1.8 \text{ g C m}^{-2} \text{d}^{-1}$ 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) and the Catalan Sea (Granata et al., 2004). Inter-annual 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 deep chlorophyll maxima can be significant, in some cases reaching 30% of the total production of the water column (Estrada et al., 1985).

While satellite-based estimates represent gross primary production, values from in situ incubations are generally closer to net production. In neither case, however, is an estimate of the new versus recycled production provided, and it is hence impossible to appreciate the actual amount of biomass added to the system through phytoplankton activity. Indeed, values for new production, which can be equated to the export production assuming a quasi-steady state, are much lower, i.e. in the order of $4.5 \text{ mol C m}^{-2} \text{y}^{-1}$ ($1 \text{ mol C} \equiv 12 \text{ g C}$) and $1.5 \text{ mol C m}^{-2} \text{y}^{-1}$ for the WMS and EMS, respectively (e.g. Bethoux, 1989, but see also Minas et al., 1988 for a discussion). These estimates correspond

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

Area	Period	mg C m ⁻² d ⁻¹	g C m ⁻² y ⁻¹	mg C m ⁻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
MS	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)	186±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
Straits of Sicily	May–June 1996	419			Moutin and Raimbault (2002)	in situ ¹⁴ C
North Aegean	March 1997/98,	81.36		43.80–149.55	Ignatiades et al. (2002)	in situ ¹⁴ C
	September 1997				Ignatiades et al. (2002)	in situ ¹⁴ C
North Aegean	September 1999	232±45 (non-front) 326±97 (front)			Zervoudaki et al. (2007)	in situ ¹⁴ C
North Aegean	April 2000	256±62 (non-front) 245±27 (front)			Zervoudaki et al. (2007)	in situ ¹⁴ C
South Aegean	March 1997/98,	38.88		21.67–56.21	Ignatiades et al. (2002)	in situ ¹⁴ C
	September 1997				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 seasons)		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 nmol C l ⁻¹ h ⁻¹	Tanaka et al. (2007)	in situ ¹⁴ C
Cyprus eddy	May 2001–2002 (0–20 m)			8.5–11.5 nmol C l ⁻¹ h ⁻¹	Tanaka et al. (2007)	in situ ¹⁴ C
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	353–996	145		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±71 (max 1700)			Moran and Estrada (2005)	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		Lefèvre 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 mg C m ⁻² (14 h) ⁻¹			Vidussi et al. (2000)	in situ ¹⁴ C

^a corrected following Morel et al. (1996).

to 3.6×10^{12} and $2.1 \times 10^{12} \text{ mol y}^{-1}$ of new carbon produced in the two basins, which is not much higher than the rate of allochthonous carbon inputs for the whole basin ($1.5 \times 10^{12} \text{ mol y}^{-1}$, see Sect. 2). The conclusion is that external inputs not only sustain new production through nutrient supply, but also provide organic carbon at rates comparable to new production rates, with important implications that will be discussed in Sect. 6.

3.2 Phytoplankton community structure and composition

At first sight, the picture emerging from many studies shows the dominance of the picophytoplankton as the fingerprint of the MS and of its overriding oligotrophy. However, the peculiar and notably diversified physical structure of the MS is reflected in 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 Sects. 2 and 3.1). In these areas, 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. This highly dynamic patchwork of populations that vary over the temporal and spatial scales contrasts the situation of other oligotrophic seas, generally reported to host rather stable phytoplankton populations (e.g., Goericke, 1998; Venrick, 2002).

Studies on phytoplankton species distribution across the offshore MS are scattered in space and time and provide rather heterogeneous information in terms of methodology, sampling scales and organisms addressed. Therefore, it is impossible to trace large scale patterns or seasonal cycles that can parallel those depicted in the previous section for biomass and production. From the few studies conducted at the basin scale, it is clear that both quantitative and qualitative differences exist in phytoplankton populations across the MS. For example, in early summer 1999 the diversity of dinoflagellates and mainly of coccolithophores increased eastward, whereas an opposite trend was evident for diatoms (Ignatiades et al., 2009). Chemotaxonomic studies showed that in late spring 1999 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 appeared to be mainly caused by a decrease in microplankton and nanoplankton rather than by picoplankton (Dolan et al., 2002) (Fig. 7). In addition to west-east variations, significant latitudinal differences

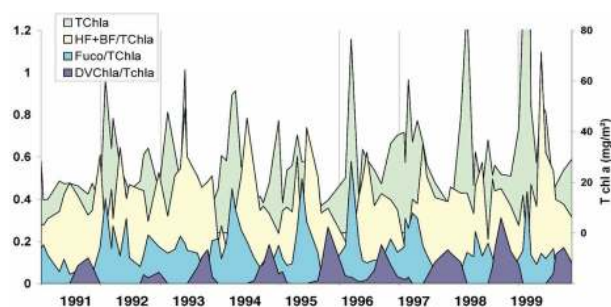


Fig. 9. Seasonal cycle of phytoplankton at the long-term station DYFAMED for the 1991–1999 period. Nanoflagellates (HF+BF), diatoms (Fuco) and *Prochlorococcus* (DVchl *a*) are represented as ratio of their distinctive pigments to total chl *a*. The total chl *a* integrated concentration (mg m^{-2}) is also represented in green. Reproduced with permission from Marty et al. (2002).

across the WMS were reported for chemotaxonomic markers of different phytoplankton groups in summer 1993, when nanoflagellates were more important in the northern than in the southern stations (Barlow et al., 1997). As for the seasonal cycle, some information is only available for the long term DYFAMED station in the Ligurian Sea (Fig. 9, Marty et al., 2002), where diatoms, nanoflagellates and prochlorophytes, identified from their pigment signatures, rather regularly occur over the year becoming more important in late winter, spring-summer and autumn, respectively.

In the following section, we present a brief account of the main microalgal groups in the MS under 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 involved 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), low biomass values in the MS 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). This smallest fraction of the phytoplankton can only be quantified using special techniques (flow-cytometry, chemotaxonomy, epifluorescence microscopy, size-fractionation), and has largely been ignored in classical light microscopy-based studies. As an average on the whole basin, picoplankton accounts for 59% of the total chl *a* and 65% of the primary

Table 2. Selected examples of phytoplankton size fractions and/or taxonomic composition in different areas of the MS. Values have been rounded to the first decimal digit. Abbreviations: SL for Surface Layer, DCM for Deep Chlorophyll Maximum, DI for Depth Integrated, C for Carbon, HPLC for pigment-based group discrimination, Dino. for dinoflagellates, Prymn. for prymnesiophytes, Pelago. for pelagophytes, Crypto. for cryptophytes, Chromo. for nanoflagellates containing 19′–HF and/or 19′–BF, Nano. for nanoplankton, Cocco. for coccolithophores, *Synecho.* for *Synechococcus*, *Prochloro.* for *Prochlorococcus*. The values reported in Refs. 1, 3, 7 and 9 are derived from figures in the respective papers.

Area	Date and Site	Depth	Method	Picoplankton	Nanoplankton	Microplankton	Cyanobacteria	Picoeukaryotes	Flagellates	Diatoms	Ref.
Alboran Sea	Apr–May 1991 Site 1 (jet front)	DCM (%size); DI (0–150 m) (%groups)	chl <i>a</i> HPLC	<1 µm: 11% 1–3 µm: 6%	3–10 µm: 8%	>10 µm: 75%	2% 2%		22%	76% (<i>Chaetoceros</i> , <i>Proboscia alata</i> <i>Pseudo-nitzschia</i> , <i>Thalassiosira</i> , <i>Leptocylindrus</i>) 19%	1 2
	Apr–May 1991 Site 2 (oligotrophic)			<1 µm: 40% 1–3 µm: 32%	3–10 µm: 8%	>10 µm: 8.5%	16%		65%		
	May 1998 upwelling	DI (photic zone)	chl <i>a</i>	<2 µm: 15.9%	2–20 µm: 26.6%	>20 µm: 57.5%				>20 µm at DCM (<i>Chaetoceros</i> , <i>Pseudo-nitzschia</i>)	3
	May 1998 non-upwelling			<2 µm: 46.1%	2–20 µm: 35.9%	>20 µm: 18.0%					
Catalan Sea	May 1989 front, St. 4	DI (0–100 m)	C (counts)	1–2 µm: 2.4% 2–5 µm: 44.7% 1–2 µm: 2.1% 2–5 µm: 20.7%	5–10 µm: 17.5% 10–20 µm: 9.4% 5–10 µm: 10.1% 10–20 µm: 8.0%	>20 µm: 5.6% >20 µm: 54.8%	20.3% 4.2%		Dino. (<i>Gyrodinium</i> , <i>Gymnodinium</i>)	(<i>Pseudo-nitzschia</i>)	4
	Feb 1990 front, St. 8									(<i>Chaetoceros</i> , <i>Pseudo-nitzschia</i> , <i>Guinardia striata</i> , <i>Asterionellopsis</i>)	
Gulf of Lion	Jun 2000	SL (4–8 m)	HPLC				6%		Prymn.: 51% Green algae: 21% Pelago.: 4% Dino.: 4%	13% (<i>Thalassionema nitzschoides</i> , small <i>Chaetoceros</i> , <i>Pseudo-nitzschia</i> , <i>Rhizosolenia</i>)	5
Ligurian Sea	May–Jun 1985	DI (water column)	chl <i>a</i>	<3 µm: 65.7%	3–10 µm: 22.0%	>10 µm: 12.2%					6
Ligurian Sea	May 1995 DYFAMED 1st leg	DI (0–200 m)	HPLC				8.41%		Crypto.: 11.6% Chromo.: 38.3% Green flag.: 5.3% Crypto.: 5.2% Chromo.: 31.8% Green flag.: 5.3%	29.0%	7
	DYFAMED 4th leg						18.3%			19.9%	
S Tyrrhenian Sea	Jul 2005	DI (water column)	chl <i>a</i> C (counts) (% groups)	0.2–2 µm: 64%	2–10 µm: 17%	>10 µm: 19%	48%		Dino.: 28% (<i>Ceratium</i> , <i>Heterocapsa niei</i> , <i>Prorocentrum minimum</i>)	23% (<i>Chaetoceros</i> spp., <i>Guinardia flaccida</i> , <i>Leptocylindrus mediterraneus</i> , <i>Proboscia alata</i>) 3.4% (<i>Chaetoceros</i> spp., <i>Thalassiosira</i> spp.)	8
	Dec 2005			0.2–2 µm: 76%	2–10 µm: 17%	>10 µm: 7%	52.9%		Dino.: 43.8% (<i>Prorocentrum minimum</i> , <i>Heterocapsa niei</i>)		
Straits of Sicily	Jul 1997	SL (0–50 m) DCM (50–80 m)	HPLC	<3 µm: 80%	>3 µm: 20% ♦		75.7% 40.9%	Pelago.: 13.5% Pelago.: 33.8%			9
	EMS (average)	DI (photic zone)	HPLC	27%	60%	13%					10
Adriatic Sea	Jan 1995			17%	57%	26%					
Ionian Basin				30%	58%	11%					
Aegean Sea				22%	61%	17%					
Levantine Basin				27%	62%	12%					
S Adriatic Sea	Aug 1997	SL (0 m) DCM (50–70 m)	chl <i>a</i>		<10 µm: 98% ★ <10 µm: 58% ★	>10 µm: 2% >10 µm: 42%				(<i>Chaetoceros</i> spp., <i>Leptocylindrus danicus</i> <i>Pseudo-nitzschia</i> , <i>Thalassionema nitzschoides</i>)	11
Ionian Sea	Apr–May 1999		HPLC								12
	W Ionian	SL (0 m) DCM					18% 16%	Pelago.: 11% Pelago.: 11%	57% (4% Dino.) 63% (3% Dino.)	13% 9%	
	E Ionian	SL (0 m) DCM					41% 13%	Pelago.: 5% Pelago.: 10%	34% (2% Dino.) 69% (4% Dino.)	19% 7%	
	Atlantic waters	SL (0 m) DCM					39% 10%	Pelago.: 8% Pelago.: 10%	47% (17% Dino.) 65% (15% Dino.)	6% 14%	
Aegean Sea	May 1997	DI (0–100 m)	C (chl <i>a</i>)	0.2–3 µm: 80% 0.2–3 µm: 81% 0.2–3 µm: 57%	>3 µm: 20% ♦ >3 µm: 19% ♦ >3 µm: 43% ♦						13
	Sep 1997			0.2–3 µm: 80% 0.2–3 µm: 81% 0.2–3 µm: 72%	>3 µm: 20% ♦ >3 µm: 19% ♦ >3 µm: 28% ♦						
	Sep 1999	DI (0–100 m)	C (chl <i>a</i>)	<3 µm: 88% <3 µm: 89.5%	>3 µm: 12% ♦ >3 µm: 10.5% ♦						14
	Apr 2000			<3 µm: 73.8% <3 µm: 71%	>3 µm: 27% ♦ >3 µm: 29% ♦						
Levantine Basin	Mar 1992 Cyprus eddy core	DI (0–500 m)	chl <i>a</i> HPLC	<2 µm: 64.2%	2–10 µm: 34%	>10 µm: 1.8%	<i>Synecho.</i> : 32% <i>Prochloro.</i> : 10%	58%			15
	Cyprus eddy boundary			<2 µm: 54.3%	2–10 µm: 38.7%	>10 µm: 7%		51%			
Levantine Basin	May 2002 Cyprus eddy	SL (0–12 m)	HPLC (pre-P fertilization)	<2 µm: 27%	2–20 µm: 65%	>20 µm: 8%					16

¹Videau et al., 1994, ²Claustre et al., 1994, ³Arin et al., 2002, ⁴Delgado et al., 1992, ⁵Latasa et al., 2005, ⁶Raimbault et al., 1988, ⁷Vidussi et al., 2000, ⁸Decembrini et al., 2009, ⁹Brunet et al., 2006 ♦ includes microplankton ¹⁰Vidussi et al., 2001, ¹¹Boldrin et al., 2002, ¹²Casotti et al., 2003, ¹³Siokou-Frangou et al., 2002, ¹⁴Zervoudaki et al., 2007, ¹⁵Zohary et al., 1998, ¹⁶Psarra et al., 2005 ♦ includes microplankton; ★ includes picoplankton

production (Magazzù and Decembrini, 1995). However the values widely vary depending on the locations, depths, seasons as well as on the method used and size fractions considered (Table 2). Values up to 80% of total biomass were reported for waters off Israeli coast (Berman et al., 1984), in the EMS, and in the Straits of Sicily during summer (Brunet et al., 2006). With the exception of the highly dynamic mesoscale structures, picoplankton dominates the upper water layers of the EMS through most of the year, e.g., in the southern part of the Levantine 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 in March and September (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) and in the Aegean Sea (Ignatiades et al., 2002).

The prokaryotic fraction of the picoplankton, namely *Synechococcus* and *Prochlorococcus*, can reach abundance values of up to 10^4 cells ml^{-1} (Zohary et al., 1998; Christaki et al., 2001). At the Ligurian Sea DYFAMED station, *Synechococcus* is dominant in the upper layers during stratification periods when, despite the pronounced oligotrophy, it is apparently responsible for maximum photosynthetic efficiency values, probably due to its capacity to cope with low nutrient conditions (Marty and Chiaverini, 2002). By contrast, as in other oceans, prochlorophytes are most often found in deeper layers in stratified conditions (Yacobi et al., 1995; Li et al., 1993), with a sharp peak near the bottom of the euphotic zone (Zohary et al., 1998; Partensky et al., 1999; Christaki et al., 2001), while they become abundant at surface over the autumn/winter (Fig. 9, Marty et al., 2002). However, prochlorophytes have been found to be abundant in surface waters even in summer (Vaulot et al., 1990). In fact, two distinct ecotypes of *Prochlorococcus* exist (Moore et al., 1998), which show preferences for high- and low-light conditions, respectively. Both types, substituting one another along the water column, have been identified for example in the Straits of Sicily (Brunet et al., 2007).

In addition to prokaryotes, quite a high diversity of eukaryotes may be found within the picoplanktonic fraction (Table 2), including prasinophytes, pelagophytes, prymnesiophytes and chrysophytes. Based on epifluorescence counts, tiny ($<3\mu\text{m}$) autotrophic and heterotrophic organisms were dominant (in the order of 10^3 – 10^4 cells ml^{-1} , ca 75% of the $<10\mu\text{m}$ size fraction) across the MS in June 1999 (Christaki et al., 2001). Several non-colonial picodiatoms (e.g., some *Chaetoceros*, *Thalassiosira*, *Minidiscus*, *Skeletonema* and some cymatosiracean species) have also been found to be abundant in some cases (Delgado et al., 1992; Sarno and Zingone, unpublished data), although their small size may prevent their identification even at the class level.

In general, it is difficult to interpret the apparent differences in the distribution and relative contribution of eukaryotes to picoplankton biomass, mainly because of the few and

scattered data and of the rather low and different taxonomic resolution provided by the various identification methods mentioned above. Specific distribution patterns have been gleaned in some cases from pigment signatures of different groups of picoeukaryotes. For example, pelagophytes have been found to be important in deep waters at several sites, 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). 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 spatial distribution (Fig. 10; 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 one of the least known component of the MS phytoplankton.

3.2.2 The nanoplankton

The size component smaller than $20\mu\text{m}$, commonly defined as nanoplankton, is mainly constituted of small flagellates (generally $<5\mu\text{m}$) and dinoflagellates, mostly naked species, in addition to coccolithophores and to a limited number of small solitary diatom species. In many cases, single cells of colonial diatoms are also smaller than $20\mu\text{m}$, but they are treated in a separate section 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 (Revelante and Gilmartin, 1976; Malej et al., 1995; Totti et al., 1999; Decembrini et al., 2009). Similarly to the $<3\mu\text{m}$ eukaryotic fraction, a long-standing lack of taxonomic resolution for these heterogeneous species has led to the view that they do not vary significantly in quality and quantity over time and space, probably because they are controlled 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 contribute significantly to blooms, e.g., in the Catalan Sea (Margalef and Castellví, 1967) and at DYFAMED (Marty et al., 2002).

Based on pigment signatures, prymnesiophytes represent a large part of nanoflagellates most of the year (Fig. 9, Marty et al., 2002) and at several localities (Latasá et al., 1992; Claustre et al., 1994; Bustillos-Guzmán et al., 1995; Barlow et al., 1997; Zohary et al., 1998). Among them, 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 most frequent and dominant within this group, 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

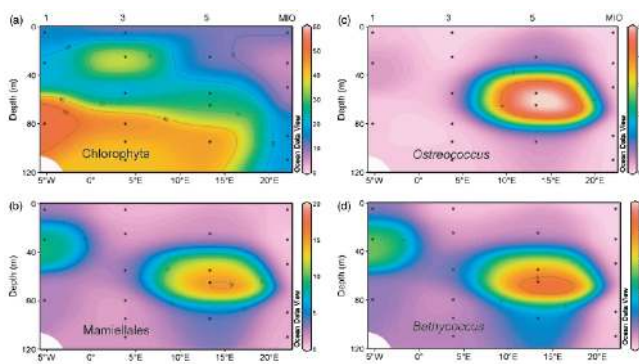


Fig. 10. Longitudinal differences in the distribution of selected autotrophic picoeukaryotes during the cruise PROSOPE from Gibraltar to the Southern Cretan Sea in September 1999. The distribution of the different taxa is represented as their percentage to the total eukaryotes estimated with quantitative PCR. Chlorophytes were abundant in deep and intermediate layers in the WMS, whereas *Ostreococcus*, *Bathycoccus* and other Mamiellales were only abundant at intermediate depths in the Sicily Channel. Reproduced with permission from Marie et al. (2006).

Aegean Sea (Ignatiades et al., 1995), South Adriatic and Ionian Seas (Rabitti et al., 1994). A consistent proportion of coccolithophores was also reported in winter offshore of the Catalan Front (Estrada et al., 1999) and in spring in the Aegean Sea (Ignatiades et al., 2002), while maximum fluxes were recorded in winter-spring in the central EMS (Ziveri et al., 2000). In a trans-Mediterranean study conducted in June 1999, coccolithophores were more abundant and diversified at eastern stations than at western ones (Ignatiades et al., 2009). Much less known is the diversity and distribution of non-calcifying prymnesiophytes (e.g., *Imantonia* and *Chrysochromulina* species), which can only be identified with special techniques (electron microscopy or molecular tools). Among the few species mentioned in this group are those 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.

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 DYFAMED station (Vidussi et al., 2001; Marty et al., 2002) or in the Cretan Sea (Gotsis-Skretas et al., 1999). *Plagioselmis prolonga* is one of the most frequently mentioned species in this group. However, reports of cryptophyte species from light microscopy investigations should all be reconsidered, since 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 de-

rives 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 $<5\mu\text{m}$ were not counted in these studies. Some small thecate species such as *Prorocentrum* (*P. minimus*, *P. balticum*, *P. nux*), *Heterocapsa* or *Scrippsiella*-like species are also part of the nanoplankton, 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. Where this occurs, colonial and microplanktonic diatoms (larger than $20\mu\text{m}$) belonging to several genera (*Asterionellopsis*, *Chaetoceros*, *Pseudo-nitzschia*, *Thalassionema*, *Thalassiosira*) become more important. In the following section, specific examples are provided of the distribution of microplanktonic diatoms in association with relatively dense biomass accumulation, namely in 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 (Claustre et al., 1994; Marty et al., 2002) and EMS (Wassmann et al., 2000; Gacic et al., 2002) 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 and hence not always detected 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 $>5\mu\text{m}$ 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 MS in winter (Miquel et al., 1994; Stemmann et al., 2002), suggesting that diatom blooms in this season are scarcely exploited by zooplankton populations (Duarte et al., 1999; Ribera d’Alcalá et al., 2004). In fact, they constitute 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 during the winter bloom, diatoms also dominate, and for longer periods, in deep convection areas. Here,

mixing largely exceeds the critical depth but blooms might be favoured by brief periods of quiescence. Colonial species belonging to the genera *Pseudo-nitzschia* and *Chaetoceros* were most dominant 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). Prymnesiophytes and prokaryotes instead of diatoms dominated in March in the Cyprus eddy, which is not a site of deep convection, 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). Apparently, also in highly dynamic areas, very high biomass only accumulates when diatoms are the species involved.

Colonial, bloom forming diatoms belonging to the genera *Chaetoceros*, *Thalassiosira*, *Proboscia*, *Rhizosolenia*, *Leptocylindrus* are generally the main contributors also to high chl *a* patches in 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 “oases” of the Mediterranean desert (Claustre et al., 1994). The biological phenomena that they drive strictly depend on water mass dynamics and hence are spatially heterogeneous, and show a very high temporal dynamic, as well as a marked inter-annual variability (Mercado et al., 2005).

Diatom-dominated chl *a* peaks are often found in sub-surface waters (Arin et al., 2002), as in the exceptional case of a monospecific bloom of a *Thalassiosira* (probably *Th. partheneia*) forming gelatinous colonies ($\sim 10^7 \text{ cells l}^{-1}$ and $23 \mu\text{g chl } a \text{ l}^{-1}$), 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 a DCM in the stratification period in oligotrophic waters. A significant contribution of diatoms to the latter seasonal DCMs 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). Frequently, the species involved are those that are also typical of the high production events described above, supporting the hypothesis that the DCMs are sites of active growth, rather than of passive accumulation. Overall, the intermittent and most probably undersampled pulses of diatom growth in deep waters might contribute in 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).

In the DCM, diatoms are found in association with picoplankton and at times they dominate the subsurface populations (e.g., Decembrini et al., 2009; Boldrin et al., 2002). Their relative importance may vary greatly over the time and across sites (Estrada and Salat, 1989; Estrada et al., 1993).

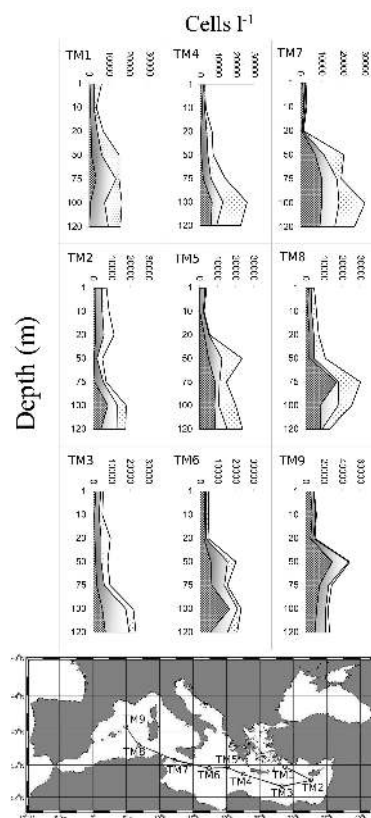


Fig. 11. Vertical profiles of diatoms (dotted), dinoflagellates (light gray) and coccolithophores (dark hatched gray) over an east-west longitudinal transect of the Mediterranean Sea in June 1999. Modified with permission from Ignatiades et al. (2009).

In one of the few cases of across-basin studies at the species level (Ignatiades et al., 2009), diatoms seemed to be 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 DYFAMED station, diatoms are associated with the highest chl *a* concentrations and sit under a layer occupied by prochlorophytes and nanoflagellates, whereas *Synechococcus* dominates in the oligotrophic surface waters (Marty and Chiaverini, 2002). This vertical zonation, similar to that reported in the Atlantic waters (Claustre and Marty, 1995), points at a tightly structured system, within which the distinct phytoplankton components may have different ecological roles.

Colonial *Chaetoceros* species are a rather constant feature of diatom-dominated DCMs, but 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* and *Thalassionema* were found south of Crete in July (Berland et al., 1987), whereas *P. delicatissima*, *Dactyliosolen fragilissimus*, and *Thalassionema*

frauenfeldii were found north of Crete in June (Gotsis-Skretas et al., 1999). Finally, in the Southern Tyrrhenian Sea, the DCM was dominated exclusively by *Leptocylindrus danicus* in June 2007 (Percopo and Zingone, unpublished data). These differences in species composition are remarkable, but more observations are needed to assess their actual consistency and ecological significance.

While the above-mentioned colonial species often appear in relatively high concentrations, other large-sized diatoms are found at much lower concentrations in the offshore MS waters. In fact, these large diatoms have been reported as responsible for a substantial but underestimated fraction of primary production in oligotrophic waters characterized by a strong seasonal thermocline and nutricline 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, along 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). Diatom-diazotroph associations have been rarely been investigated in the MS, but off the Israeli coast their role in nitrogen fixation seems to be very limited, 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 abundance 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 nanoplanktonic dinoflagellates. With the exception of the high productivity events mentioned above, dinoflagellates are generally more abundant than diatoms in the size fraction higher than 20 µm (Marty et al., 2009). The species most commonly reported are those of the genera *Gymnodinium*, *Gyrodinium*, *Neoceratium* (formerly *Ceratium*), *Protoperidinium*, *Oxytoxum*, which are generally associated with warm and stratified waters (Estrada, 1991). Very rarely the percentage contribution of microplanktonic dinoflagellates 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, but their role can be significant despite their low abundances. Some of them, e.g., in the genera *Ornithocercus*, *Histioneis* and *Citharistes*, can host endosymbiotic cyanobacteria that allow them to survive even under conditions of severe nitrogen limitation (Gordon et al., 1994). Species of the widespread genus *Neoceratium* may be mixotrophic (Smalley and Coats, 2002). They occupy selected depths (Tunin-Ley et al., 2007), and their distribu-

tion could change as a consequence 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 MS has rarely been assessed (see Margalef, 1985).

Among other algal groups, the silicoflagellates *Dictyocha* and *Distephanus* are also a constant although scarce component of offshore MS microplankton, 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, a few other 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 MS 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 recent years (Margalef, 1995). Another interesting species is the prasinophyte *Halosphaera viridis*, which is found up to depths of 1000 m in autumn-winter (Wiebe et al., 1974; 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 on primary production, first 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.

Table 3. Site, sampling data depths and variables measured and source of the studies considered in this review. S: surface, INT: integrated 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)	<i>n</i>	Variables	References
WMS					
NW MS	June 1995	5–200 (S, INT)	42	chl <i>a</i> , BA, VA, VBM, VBR	Guixa-Boixereu et al. (1999b)
NW MS	June 1999	5–200 (S, INT)	10	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 MS	October and November 2004	1–200 (S, INT)	16	BA, VA, BP, VBR	Magagnini et al. (2007)
Tyrrhenian 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)
EMS					
Adriatic Sea	May 91–November 1992	0,5 (S)		chl <i>a</i> , BA, VA, VBR	Weinbauer et al. (2003)
	January–February 2001	1–1200 (S)	6	BA, VA, BP, VBR	Corinaldesi et al. (2003)
	April–May 2003	(S)		BA, VA, BP, VBR	Bongiorni et al. (2005)
Ionian Sea	October and November 2004	1–200 (S, INT)	19	BA, VA, BP, VBR	Magagnini et al. (2007)

4.1 Viruses

The net effect of viruses with regard 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 scarce, even less than in other marine regions. To date, most Mediterranean work has addressed viral control on bacterial biomass rather than the characterization of the viral community. The studies have revealed viral abundance in the surface waters which vary between $0.08 \pm 0.01 \times 10^7$ and $1.6 \pm 4.8 \times 10^7$ viruses ml^{-1} , while lower values occur in deeper waters (Fig. 12, Table 3). In the MS as in other marine areas, viral abundance increases from oligotrophic to more eutrophic waters. Existing data (Table 3) also suggest 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 abundance ($n=46$, $r=0.549$, $p<0.01$) implying that bacteria are more probable virus hosts than phytoplankton cells. Considering the data set for bacterial abundances and bacterial production (BP), we found that viral abundance were related to both variables ($n=24$, $r=0.520$, $p<0.05$ and $n=24$, $r=0.421$, $p<0.05$, respectively). The low correlation between viral and bacterial abundance partly reflects 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 be associated to different types of host organisms, and/or that viral concentrations vary over short times, causing different sampling events to reflect different phases of infection and release from host cells.

Comparing the WMS and EMS, viral and bacterial abundance appears to be more tightly coupled in the west than in the east (Fig. 13 and Table 4). However, these trends

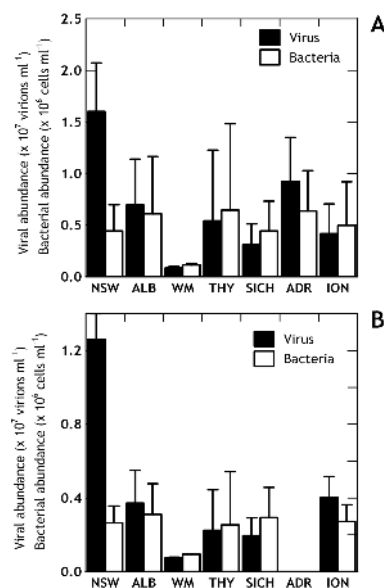


Fig. 12. Average surface viral and bacterial abundance from the different Mediterranean sites (A), average integrated values (1–200 m), that were normalized in each case dividing them by the maximal considered depth (B). Bars are SD of the mean. NWM: NW-MS, ALB: Alboran, WM: WMS, THY: Tyrrhenian, SICH: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

have to be taken cautiously, because the number of samples from the EMS is relatively limited, and differences between slopes are not statistically significant (*t*-student, $t_{\text{value}} = 2.3$; $p=0.17$). 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

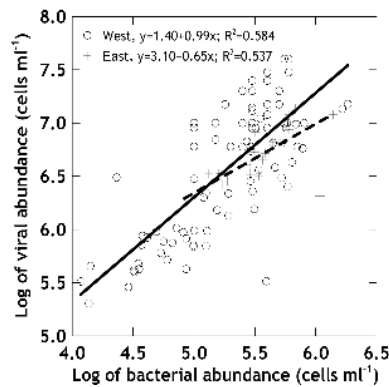


Fig. 13. Relationship between bacterial and viral abundance (log transformed), taken at depths between 5 and 200 m, for WMS and EMS waters.

nanoflagellates, for example at higher bacterial abundance in coastal waters (Weinbauer and Peduzzi, 1994; Boras et al., 2009). In a gradient from eutrophic to oligotrophic waters in 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 their size ranged between 30 nm and >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 MS examined the ultra-oligotrophic waters of the Levantine Sea (Zohary and Robarts, 1992) revealing that bacterial abundance, at 3×10^8 cells l^{-1} , was clustered around the lower threshold of the world ocean value (Cho and Azam, 1990). In the MS, while bacterial concentrations are quite stable and bacterial production is low (Table 5) there are important variability aspects to consider: (i) the west-east gradient of decreasing 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 (Fernández 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 the WMS and EMS (Fig. 14a) are not significantly different ($t_{\text{value}} = -0.22$; $p=0.85$) with both slopes being smaller than 0.4, thus suggesting top-down control on bacteria (Billen et al., 1990; Ducklow, 1992).

Table 4. Number (n) of data used to find out the relationships between different variables in the Western Mediterranean (WMS) and the Eastern Mediterranean (EMS). BA: bacterial abundance; BP: Bacterial production; VA: viral abundance; PP: primary production; HNF: heterotrophic nanoflagellates abundance; Cil: ciliate abundances; Chl: chl a concentration.

Variables	WMS (n)	EMS (n)	Source
BA-VA	42	0	Guixa-Boixereu et al. (1999a)
	38	19	Magagnini et al. (2007)
	0	6	Weinbauer et al. (2003), Corinaldesi et al. (2003)
	10	0	Bongiorni et al. (2005) Weinbauer et al. (2003)
BA-BP	0	174	Christaki et al. (2003)
	8	0	Vaqu�� et al. (2001)
	0	13	Robarts et al. (1996)
	13	18	Van Wambeke et al. (2002)
	26	50	Christaki et al. (2001)
BP-PP	0	91	Van Wambeke et al. (2000)
	48	29	Turley et al. (2000)
	22	24	Christaki et al. (2002)
	26	0	Pedr��s-Ali�� et al. (1999)
HNF-BA	12	0	Christaki et al. (1996), Christaki et al. (1998)
	36	45	Christaki et al. (2001)
	8	0	Vaqu�� et al. (2001)
	0	48	Siokou-Frangou et al. (2002)
Cil-Chl	20	42	Pitta et al. (2001)
	8	0	Vaqu�� et al. (2001)
	79	0	Dolan and Marras�� (1995)

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. Expanding on the data set from Turley et al. (2000) (Table 4), plots of log BP and log primary production (PP) for the WMS and the EMS display similar positive slopes ($t_{\text{value}} = -0.22$; $p=0.87$) (Fig. 14b). This 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. Nutrient control on bacterial production, as well as on bacterial adaptations to cope with the oligotrophy of the open MS, has 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

Table 5. Bacterial abundance (BA), Heterotrophic Nanoflagellate abundance (HNF) and Bacterial Production (BP) in different Mediterranean Sea areas. Note that BP is expressed in different units depending on the data given by the authors and depth (m) indicates the maximum depth considered in the study. (TdR: 3H-thymidine incorporation, other BP are measured by 3H-leucine incorporation)

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

chl *a* concentration and an increase in bacterial production. It was suggested 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 MS lives 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 just 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 Rasoulzadegan, 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 an indicator of bacterial P-limitation (Van Wambeke et al., 2002). Alkaline phosphatase turnover times of less than 100 h were documented and corresponded to situations of P limitation on 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 ($50 \pm 18\%$) (Christaki et al., 2003). The authors hypothesized

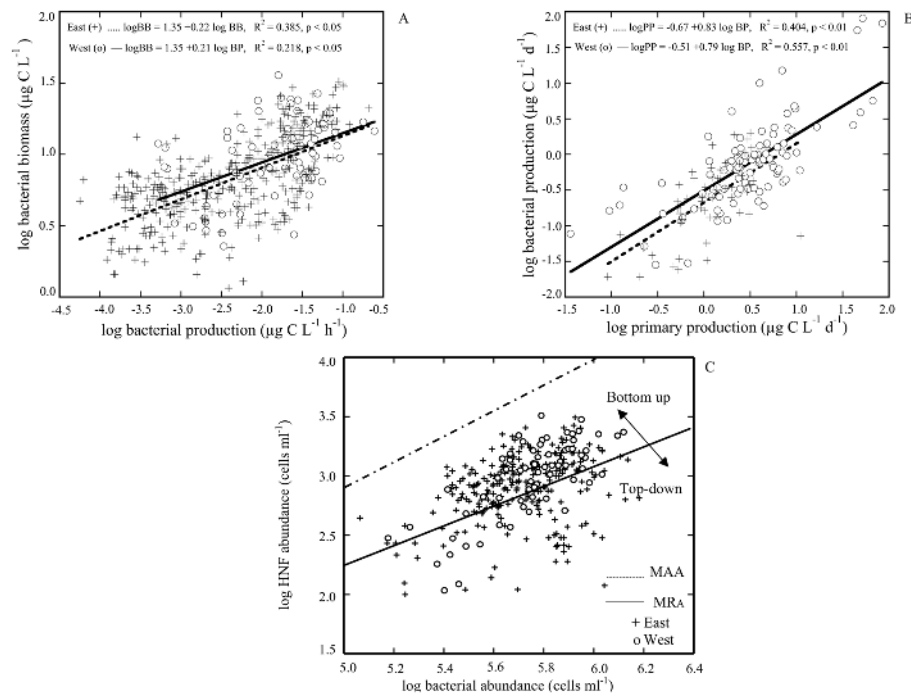


Fig. 14. (A) Log-log linear regression between bacterial biomass ($\mu\text{g C l}^{-1}$) and bacterial production ($\mu\text{g C l}^{-1} \text{ h}^{-1}$) and (B) between bacterial production and primary production ($\mu\text{g C l}^{-1} \text{ d}^{-1}$) for the WMS and EMS waters; (C) Relationship between log heterotrophic nanoflagellates abundance (HNF, cells ml^{-1}) and log bacterial prey (cells ml^{-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 Realized Abundance for marine environment (MRA) in the EMS and WMS, respectively, generally suggesting bottom-up control prevailing on HNF (cf. open sea studies on Table 4).

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 ($\text{BGE} = \text{BP}/[\text{BP} + \text{BR}]$) 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 $3.64 \mu\text{mol O}_2 \text{ l}^{-1} \text{ d}^{-1}$ (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 suggested to result from nutrient limitation of bacterial activity (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) and lower values ($2.6 \pm 0.1\%$) were obtained in the NW-Mediterranean through a coastal-

offshore gradient (Moran et al., 2002). 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 emphasize that they could not identify any regulatory mechanisms of BGE and respiration over this period.

Preliminary heterotrophic 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 the diversity index followed 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 (Schauer et al., 2003).

4.3 Heterotrophic nanoflagellates

In open MS, some heterotrophic nanoflagellates (HNF) are usually dominated by small cells ($\geq 80\%$ less than $5\ \mu\text{m}$) with total abundances between 10^5 and $10^6\ \text{cells l}^{-1}$ (Zohary and Roberts, 1992; Christaki et al., 1999, 2001, Tables 4 and 5). 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 (Vaque 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 5), they provide a quite good spatial coverage of the open MS, and overall suggest that bacterivory is the dominant cause of bacterial mortality. According to the model by 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 MS; four genetic libraries for surface waters from Blanes Bay (NW Mediterranean) showed that some heterotrophic picoeukaryotes belong to the marine stramenopiles (MAST) (Massana et al., 2004). In the Alboran Sea, MAST were found in the upper ocean, including the photic zone and the upper aphotic zone, and appeared to be more abundant at subsurface (near the DCM) than at surface (5 m, Rodríguez-Martínez et al., 2009).

4.4 Ciliates

Ciliate abundance in the MS 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 $850\ \text{cells l}^{-1}$ were found at the DCM, whereas in the Ligurian Sea in May average surface layer values (5–50 m) were $\sim 3.3 \times 10^3\ \text{cells l}^{-1}$ with a maximum of $\sim 10^4\ \text{cells l}^{-1}$ (Pérez et al., 1997). These high values contrast with those for the Aegean Sea, where ciliate abundance was always lower than $5 \times 10^2\ \text{cells l}^{-1}$ (Pitta and Giannakourou, 2000). 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 the ciliate 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

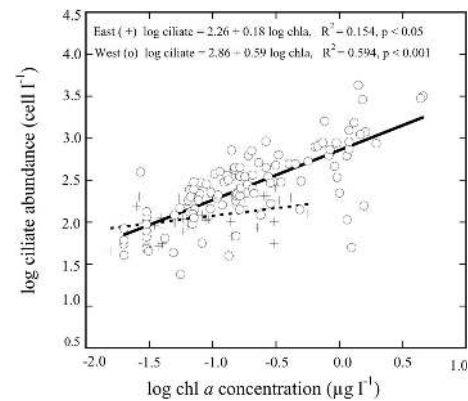


Fig. 15. Log–log linear regression between chl *a* concentration ($\mu\text{g l}^{-1}$) and ciliate abundance (cell l^{-1}), taken at depths between 5 and 200 m, for Western and Eastern Mediterranean waters.

between slopes are not statistically significant ($t_{\text{value}} = 1.7$; $p = 0.23$) probably, due to the restricted data set for the EMS (Table 4).

Since most of the primary production in the MS 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, where ciliate maximum abundance was found near the DCM (Dolan and Marrasé, 1995). In the Ligurian Sea, Pérez et al. (1997) estimated that ciliates could graze from 8 to 40% of primary production. The importance of ciliates as primary production consumers seems 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) found that large mixotrophic ciliates were more abundant in the EMS than in the WMS both in absolute and relative terms. In a later study across the MS, 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 WMS. 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 (Pérez et al., 1997). In

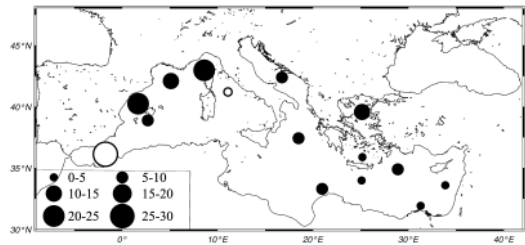


Fig. 16. Spatial distribution of total mesozooplankton abundance (black circles) or total copepod abundance (open circles) ($10^4 \times \text{ind. m}^{-2}$) in spring time in the 0–200 layer of MS. Sources: Benović et al., 2005 (Adriatic Sea); Christou et al., 1998 (South of Crete, Rhodos gyre); Fernández de Puellés et al., 2004 (0–100 m layer, Balearic Islands); Gaudy and Champalbert, 1998 (Gulf of Lion); Mazzocchi et al., 2003 (Ionian Sea); Mazzocchi, unpublished data (North Balearic Sea); Pasternak et al., 2005 (0–150 m layer, Cyprus Eddy); Pinca and Dallot, 1995 (Ligurian Sea); Porumb and Onciu, 2006 (offshore Lybia); Saiz et al., 1999 (Catalan Sea); Scotto di Carlo et al., 1984 (Tyrrhenian Sea); Seguin et al., 1994 (Alboran Sea); Siokou-Frangou, unpublished data (Aegean Sea); Zakaria, 2006 (0–100 m layer, offshore Egypt).

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 $18 \mu\text{m}$ dominated in South Aegean Sea, whereas North Aegean Sea, receiving the outflow of the Black Sea, presented a mixotrophic fauna characterized by a relative abundance of cells of 18 to $50 \mu\text{m}$ size.

Patterns of taxonomic diversity have been investigated with regard to tintinnid ciliates. Along a west-east MS longitudinal transect sampled in June, the concentration of tintinnids varied little, but the 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} , Pérez et al., 1997).

5 Mesozooplankton

5.1 Standing stock

An overview of the distribution of the mesozooplankton standing stock in epipelagic Mediterranean waters highlights a generalized scarcity and higher values in a few regions (Fig. 16, Table 6). Total abundance and biomass values are comparable to those measured at the same latitudes in the North-East Atlantic (Barquero et al., 1998; Head et al., 2002). A west-to-east decrease of standing stock emerged from the surveys across the basin conducted in June and September 1999 (Dolan et al., 2002; Siokou-Frangou, 2004, Fig. 17), and in June 2007, when mean zooplankton abundance at midday in the 0–200 m layer was higher in the western (64 ind. m^{-3}) than in the eastern sector (32 ind. m^{-3}) (Minutoli and Guglielmo, 2009). Zooplankton distribution patterns may show high local variability, with notable spatial changes even during the same season (Nival et al., 1975). Sampling with finer mesh nets than the standard $200 \mu\text{m}$, or with large bottles, which has been rarely conducted in the open MS, has revealed that biomass and abundance can increase by 2 to 20 fold when the smaller metazooplankters (~ 50 – $200 \mu\text{m}$) are considered (Böttger-Schnack, 1997; Kršinić, 1998; Youssara and Gaudy, 2001; Andersen et al., 2001a; Zervoudaki et al., 2006; Alcaraz et al., 2007). These latter studies also highlight west-east differences in zooplankton standing stock.

In the open MS, the bulk of epipelagic mesozooplankton is concentrated in the upper 100 m layer and sharply decreases below this depth (Scotto di Carlo et al., 1984; Weikert and Trinkaus, 1990; Mazzocchi et al., 1997). It is in this upper layer that mesozooplankton plays a major role in biological processes, based on its linkage with phyto- and microzooplankton in the euphotic zone (Longhurst and Harrison, 1989). During daytime in the stratification period, the decreasing vertical pattern of mesozooplankton abundance is interrupted by a small-scale increase at the level of the DCM (Alcaraz, 1985, 1988), where the highest abundance of nauplii and copepodites is reported (Sabatés et al., 2007). At the DCM depth, the deep zooplankton maximum (DZM) is associated with high diatom and phaeophorbide concentrations (Latasa et al., 1992), and copepod feeding is enhanced (Saiz and Alcaraz, 1990).

Similarly to the world ocean, the MS epipelagic layer is enriched during the night by the diel migrants that ascend from the mesopelagic layer (Weikert and Trinkaus, 1990; Andersen et al., 2001b; Raybaud et al., 2008). Nevertheless, the epipelagic mesozooplankton standing stocks do not differ significantly between day and night (Mazzocchi et al., 1997; Ramfos et al., 2006; Raybaud et al., 2008), due to the paucity of long-range migrant copepod species in the MS compared to the neighboring Atlantic Ocean (Scotto di Carlo et al., 1984). Diel changes in zooplankton abundance are reported at a smaller scale within the epipelagic layer, as in the case

Table 6. Mean values (range) of mesozooplankton biomass (as dry mass or organic C) in different areas of the Mediterranean Sea.

Area	Sampling period	Net mesh size	Layer	Biomass (mg m ⁻³)	Reference
Alboran Sea	Winter 1997	200 µm	0–200 m	14.4 (5.5–25)	Youssara and Gaudy (2001)
Alboran Sea	April–May 1991	200 µm	0–200 m	10.1 (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	8.0 ^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	8.7 (3–13.5)	Gaudy et al. (2003)
E Ligurian Sea	December 1990	200 µm	0–200 m	(0.8–4.2)	Licandro and Icardi (2009)
C Ligurian Sea	September–October 2004	200 µm	0–200 m	(0.8–19.0)	Raybaud et al. (2008)
Tyrrhenian Sea	Autumn 1986	200 µm	0–50 m	(3.6–32) (AFDW)	Fonda Umani and de Olazábal (1988)
N Ionian Sea	Spring 1999	200 µm	0–100 m	7.9 (4.4–13.4)	Mazzocchi et al. (2003)
				2.1 (1.1–3.8) ^b	
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.

of the nocturnal increase in copepod abundance observed in June in the upper 50 m of the Tyrrhenian Sea (Scotto di Carlo et al., 1984). In the Catalan Sea, almost half of the zooplankton standing stock residing at the DCM in the 50–90 m layer during the day moved to the 0–50 m layer during the night in summer (Alcaraz, 1988).

Over the annual cycle, mesozooplankton abundance in off-shore waters oscillates within a narrow range and reveals lower seasonal variability than in coastal waters (Scotto di Carlo et al., 1984; Fernández de Puelles et al., 2003). Peaks occur in February–March and in May off Mallorca in the Balearic Sea (Fernández de Puelles et al., 2003), and in April in the Tyrrhenian Sea (Scotto di Carlo et al., 1984). Notwithstanding differences in amplitude, the timing of the zooplankton annual cycle along coastal-offshore gradients is synchronous (Fernández de Puelles et al., 2003). A time-series conducted on a monthly basis between 1994 and 1999 off Mallorca constitutes up to now the only interannual scale study of mesozooplankton in the open MS. This effort highlighted the influence of large scale climatic factors (e.g., the North Atlantic Oscillation) on the temporal variability of local copepods (Fernández de Puelles et al., 2007).

5.2 Composition

5.2.1 Copepods

Epipelagic mesozooplankton communities in the open MS are highly diversified in terms of taxonomic composition, but copepods represent 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 abundance in the open EMS (Koppelman and Weikert, 2007). The importance of the small-sized copepods has also been highlighted in Mediterranean coastal waters (Calbet et al., 2001).

A few small-sized and species-rich 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., 2001a; 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. 18). The contribution of *Oithona* and oncaeids to species abundance and diversity becomes extremely significant in samples collected by fine mesh nets, where the harpacticoids *Microsetella norvegica* and *M. rosea* are also very common (Böttger-Schnack, 1997; Kršinic, 1998; Zervoudaki et al., 2006).

Several species of the above genera display distinct distribution patterns along the water column and/or over the seasons, suggesting differences in their ecological traits (Böttger-Schnack, 1997; Fragopoulou et al., 2001; Kršinic and Grbec, 2002; Peralba and Mazzocchi, 2004; Zervoudaki et al., 2007; Peralba, 2008), as observed in the tropical Atlantic (e.g., Paffenhöfer and Mazzocchi, 2003). Although

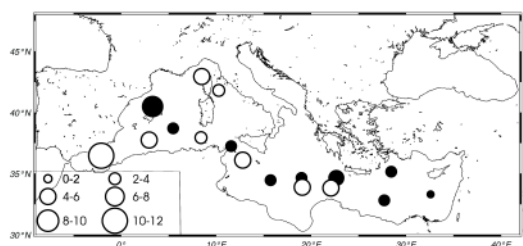


Fig. 17. Distribution of total mesozooplankton abundance ($10^4 \times \text{ind. m}^{-2}$) in the 0–100 m layer during June 1999 (black circles) (Source: Siokou-Frangou, 2004) and of total copepod abundance ($10^4 \times \text{ind. m}^{-2}$) in the 0–200 m layer during September 1999 (white circles) (reproduced with permission from Dolan et al., 2002).

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). Similar peak succession was 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 EMS 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).

West-to-east differences in the percentage contribution of some important species to the whole copepod assemblage might reflect differences in species biogeography, but might also be indicative of different structural and functional features of these systems. For example, *Centropages typicus* and *Temora stylifera*, also very common in neritic and coastal waters, are mentioned among the dominant species only in the WMS (Vives, 1967; Boucher and Thiriot, 1972; Pinca and Dallot, 1995; Saiz et al., 1999; Fernández de Puellas 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. 18). By contrast, *Calocalanus* spp. (e.g., *C. pavo*, *C. pavoninus*), *Haloptilus longicornis*, oncaeids (e.g., *Oncaea* “media” group, *O. mediterranea*), and corycaeids (e.g., *Farranula rostrata*) contribute more to total copepod abundance in the EMS than in the WMS (Weikert and Trinka, 1990; Siokou-Frangou et al., 1997; Mazzocchi et al., 2003; Ramfos et al., 2006).

The occurrence of large calanoids such as *Calanus helgolandicus* is much less important in the open MS than in the North Atlantic (reviewed by Bonnet et al., 2005). This species mainly inhabits intermediate and deep layers of the NW MS, Adriatic Sea, and North Aegean Sea, and ascends to epipelagic waters in late winter-spring (e.g., Bonnet et al., 2005; Siokou-Frangou, unpublished data). Its pres-

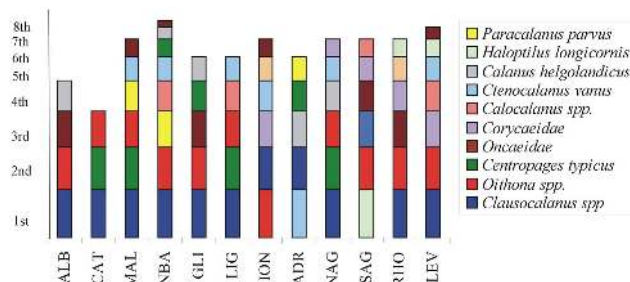


Fig. 18. Rank order of dominant copepod species or genera in the 0–200 m layer of several areas of the MS in spring. The rank order of each species or genus is given in the y axis and the height of the relevant column decreases with the rank order of the species. ALB: Almeria-Oran area (Seguin et al., 1994); MCH: Mallorca Channel (Fernández de Puellas et al., 2004, 0–100 m layer); NBA: North Balearic Sea (Mazzocchi, unpublished); GLI: Gulf of Lion (Gaudy et al., 2003); LIG: Ligurian Sea (Pinca and Dallot, 1995); ADR: Adriatic Sea (Hure et al., 1980); ION: Ionian Sea (Mazzocchi et al., 2003); NAG: North Aegean Sea, SAG: South Aegean Sea (Siokou-Frangou et al., 2004, and unpublished); RHO: Rhodos cyclonic gyre (Pancucci-Papadopolou et al., 1992); LEV: Central Levantine Sea (Pasternak et al., 2005, 0–150 m layer)

ence was considered extremely rare in the Levantine Sea until an outstanding abundance was recorded in June 1993 ($15.6 \times 10^3 \text{ ind. m}^{-2}$ in 4000 m water column), probably as a consequence of changes in the deep circulation induced by the EMT (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 (Andersen et al., 2004; Siokou-Frangou et al., 1999; Weikert and Trinka, 1990). *C. helgolandicus* was found in high density patches at the frontal zone in the open Ligurian Sea, in association with high phytoplankton concentration (Boucher, 1984). *S. monachus* was very abundant in the Rhodos Gyre during the spring of 1992 when the upwelling of waters rich in nutrients led to high phytoplankton biomass dominated by large diatoms (Siokou-Frangou et al., 1999). The distribution of these two large calanoids suggest that they are vicariant species that can co-occur but peak in different areas of the MS. The copepods reported as the strongest vertical migrants in the MS, i.e., *Pleuromamma gracilis*, *P. abdominalis*, *Euchaeta acuta*, enter the epipelagic layer only during their nocturnal ascent from deeper waters (Scotto di Carlo et al., 1984; Weikert and Trinka, 1990; Andersen et al., 2001b; Raybaud et al., 2008).

5.2.2 Other groups

The other mesozooplankton groups that contribute to community diversity in the open MS are much less abundant than copepods (Gaudy, 1985). Among crustaceans, cladocerans are very abundant in coastal waters and expand their distribution beyond the continental slope only in narrow neritic areas, generally in summer (Saiz et al., 1999; Riandey

et al., 2005; Isari et al., 2006). In the South Aegean Sea, *Evadne spinifera* contributed 6% to mesozooplankton abundance in September (Siokou-Frangou et al., 2004), while in the Straits of Sicily and the EMS, all cladocerans accounted for just 0.3% of total zooplankton during autumn (Mazzocchi et al., 1997).

Ostracods, which are not numerous in the mesozooplankton communities at temperate latitudes (Angel, 1993), present a remarkably consistent distribution in different Mediterranean regions (Scotto di Carlo et al., 1984; Mazzocchi et al., 1997; Isari et al., 2006). Their contribution to total zooplankton numbers increases gradually with depth and varies from ~2% in the upper 50 m to ~11% in the 200–300 m layer. The highest ostracod abundance is recorded in the winter period in neritic waters, probably in relation to temperature conditions and the scarcity of potential predators (Brautovic et al., 2006).

Gelatinous zooplankton represents an important group of various organisms that play different and significant roles in the pelagic communities as efficient filter-feeders or voracious predators. However, they are generally underestimated because standard sampling devices used for mesozooplankton damage or destroy their fragile bodies and are therefore inappropriate for their quantitative estimation. The pelagic filter-feeding tunicates, and especially the salps, are known to occur periodically in dense swarms, sometimes with outbreaks lasting for days or 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 the 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-water zooplankton, but, given their high population growth rate under favourable conditions (Gorsky and Palazzoli, 1989), their abundance seems to depend on the selected sampling area and time. They accounted for 8% of the total spring zooplankton abundance in the open Catalan Sea (Saiz et al., 1999) and between 1 and 8% in the Ionian Sea (Mazzocchi et al., 2003). The range of their relative abundance was very wide among several regions of the EMS 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). The contribution of appendicularians to zooplankton abundance was very high (38%) in the Ligurian Sea in winter, when the group was dominated by *Fritillaria* (Licandro and Icardi, 2009).

Among the carnivorous gelatinous zooplankton, chaetognaths are more abundant than siphonophores (Mazzocchi et al., 1997; Isari et al., 2006). However, the latter group can easily be underestimated because of the damage caused by nets during sampling (Lučić et al., 2005). In both WMS

and EMS during autumn, the most abundant chaetognaths are *Sagitta enflata*, *S. decipiens*, *S. bipunctata*, *S. minima* and *S. serratodentata* (Dallot et al., 1988; Kehayias, 2003). During the same season, the siphonophores *Muggiaea atlantica*, *Abylopsis tetragona*, *Lensia subtilis*, *Eudoxoides spiralis* and the medusae *Rhopalonema velatum*, *Liriope tetraphylla*, *Aglaura hemistoma* are common in the WMS (Dallot et al., 1988).

5.3 Influence of hydrology

Mesozooplankton abundance and biomass display patterns at sub-basin scale that broadly follow hydrological features, similarly to the distribution of primary producers discussed in the previous sections. In the Alboran Sea, the highly energetic dynamics contributes to higher plankton biomass and diversity on the Mediterranean than on the Atlantic side of the Strait of Gibraltar (Vives et al., 1975). In the same area, 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). This enrichment is also reflected in the demographic structure of the chaetognaths and siphonophores, which are found to have a high proportion of juveniles and eudoxids, respectively (Dallot et al., 1988). 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. 19). Increased mesozooplankton standing stock values are associated with the fronts in the Balearic, Catalan, and Ligurian Seas (Razouls and Thiriot, 1973; Sabatés et al., 1989; Alcaraz et al., 1994; Pinca and Dallot, 1995; Mc Gehee et al., 2004; Licandro and Icardi, 2009). The hydrographic features of the frontal system in the Catalan Sea also affect the metabolic activities (e.g., respiration, excretion) of zooplankton in the area, as well as their variability in different seasons (Alcaraz et al., 2007). The zooplankton abundance in the Straits of Sicily seems to be enhanced by intermittent upwelling (Mazzocchi et al., 1997). The strong thermohaline front between the inflowing modified Black Sea water and the Aegean Sea water harbors the highest mesozooplankton standing stock recorded in the epipelagos (0–100 m) of the very oligotrophic EMS (up to 3875 ind. m^{-3} and 26.73 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 cyclonic 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).

Mesoscale circulation and hydrodynamic features affect not only standing stock but also composition and structure of mesozooplankton communities. 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 Black Sea Water and by the Aegean Sea 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 cyclonic and anticyclonic eddies synoptically. In the Algerian basin, the eastern edge of an anticyclonic eddy seems to be favorable for *Paracalanus/Clausocalanus*, *Calocalanus*, and *Calanus*, due to the downward entrainment of chl *a* down to a depth of 200 m. Chaetognaths were more abundant in the center of the above structure. 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 sub-surface 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 showed distinct patterns at small spatial scale due to both physical environment and animal behavior (Pinca and Dallot, 1995). 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).

5.4 Production

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, copepod production ranges from 19 to 58 mg C m⁻² d⁻¹ over the seasons (Table 7). The values are much lower in the North and South Aegean Sea, in accordance with the remarkable oligotrophy of these areas.

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 waters, dominated by copepod species whose reproductive biology is very poorly known (e.g., *Clausocalanus*, *Calocalanus*, *Ctenocalanus*, *Oithona* and *Oncaeidae*). A few studies were conducted in the open MS for the egg-carrying *Oithona* and *Oncaeidae*, and the egg-carrying

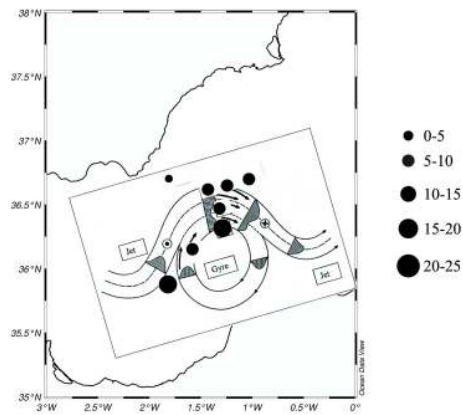


Fig. 19. Distribution of mesozooplankton biomass (dry mass in mg m⁻³) in the 0–200 m layer of the Almeria-Oran area, as affected by the hydrological features. Modified with permission from Youssara and Gaudy, 2001).

species belonging to the genus *Clausocalanus* (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 (Kjørboe and Sabatini, 1995), these species can maintain quantitatively limited but persistent populations in a wide range of trophic conditions. In fact, the cosmopolitan and abundant *Oithona similis* has very low and similar egg production rates (~ 2 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 either sea. By contrast, for the broadcast-spawners *C. typicus*, *T. 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 by Saiz et al., 2007). Unfortunately, no information is available so far on the reproduction of *Calocalanus* species, and a few data have been provided only recently for *Ctenocalanus vanus* in the Red Sea (Cornils et al., 2007).

5.5 Respiration and excretion

The metabolic rates of bulk mesozooplankton communities of the epipelagic MS have been examined only in a very limited number of studies conducted in the WMS (Alcaraz, 1988; Calbet et al., 1996; Gaudy and Youssara, 2003; Gaudy et al., 2003), except for one trans-Mediterranean cruise in the spring of 2007 (Minutoli and Guglielmo, 2009). Zooplankton respiration rates in the MS appear to vary across space and seasons, according to community composition and water mass characteristics. In the Catalan Sea, the specific respiratory carbon demand of zooplankton is slightly but not significantly lower in winter-spring (0.180 d⁻¹) than in summer-autumn (0.219 d⁻¹) (reviewed by Alcaraz et al., 2007). By contrast, in the Gulf of Lion respiration increases during spring, in correspondence with the increase of the general

Table 7. 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 (mg C m ⁻² d ⁻¹)	Reference
Gulf of Lion	Winter 1999			19 (MZP)	Gaudy (1985)
	Spring 1998			54 (MZP)	
Catalan sea	March 1999	<i>C. typicus</i>	105		Calbet et al. (2002)
		<i>A. clausi</i>	15		
		<i>C. lividus</i>	14		
Catalan Sea	June 1995	<i>C. typicus</i>	5		Saiz et al. (1999)
		<i>T. stylifera</i>	7		
		<i>C. lividus</i>	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)
	September 1997			15 (CP)	
NE Aegean Sea	March 1997			41 (CP)	Siokou-Frangou et al. (2002)
	September 1997			58 (CP)	
S Aegean Sea	March 1997			5 (CP)	Siokou-Frangou et al. (2002)
	September 1997			6 (CP)	
NE Aegean Sea	April 2000	<i>C. typicus</i>	(7–49)	36 (CP)	Zervoudaki et al. (2007)
		<i>C. helgolandicus</i>	(3–24)		
		<i>A. clausi</i>	(1–25)		
		<i>P. parvus</i>	(9–25)		
		<i>O. similis</i>	(0.3–9)		
		<i>A. clausi</i>	(1–25)		
	September 1999	<i>T. stylifera</i>	(1–128)	15 (CP)	
		<i>C. furcatus</i>	(2–15)		
		<i>P. parvus</i>	(3–8)		
		<i>O. media</i>	(3–7)		

physiological activity of zooplankton and particularly of the growth and reproduction rates of most copepods (Gaudy et al., 2003). In the Alboran Sea during winter, zooplankton respiration rates are significantly lower in the Mediterranean water mass than in the Almeria-Oran front or in the water of Atlantic origin (Gaudy and Youssara, 2003). The patterns of carbon demand from zooplankton estimated from measurements of electron transport system (ETS) activity indicate spatial and day/night variations in the MS. Demand is significantly lower in the western (mean 290 $\mu\text{g C g wet wt}^{-1} \text{d}^{-1}$) than in the eastern (mean 387 $\mu\text{g C g wet wt}^{-1} \text{d}^{-1}$) sector (Minutoli and Guglielmo, 2009). The increasing west-east gradient observed for both day and night is not due to structural properties of zooplankton communities but likely related to zooplankton ETS activity and seawater temperature. In the Catalan Sea during the summer and autumn months, routine zooplankton metabolism requires between 20% and 63% of the carbon fixed by primary producers (Alcaraz, 1988; Calbet et al., 1996).

Reviewing zooplankton metabolic rates in the Catalan Sea, Alcaraz et al. (2007) show that the specific excretion rates $\text{NH}_4\text{-N}$ in summer-autumn (average 0.111d^{-1}) are slightly higher but not statistically different from those in winter-spring (0.082d^{-1}). Similarly, $\text{PO}_4\text{-P}$ excretion rates do not differ statisti-

cally between summer ($0.0069 \mu\text{g P } \mu\text{g C}_{\text{zoo}}^{-1} \text{d}^{-1}$) and winter ($0.0022 \mu\text{g P } \mu\text{g C}_{\text{zoo}}^{-1} \text{d}^{-1}$) periods. Nevertheless, the higher C:N metabolic ratios in winter (average 20.85) suggest either that zooplankton metabolism in this season is based on lipids or carbohydrates, or that the community is composed of a higher proportion of herbivores than in summer, when the C:N metabolic ratios are lower (average 12.01). The increase of ammonium excretion indicates a more intense catabolism of proteins by zooplankton, as it is observed in spring in the Gulf of Lion (Gaudy et al., 2003). Although no clear trends appear when comparing the average metabolic activities of zooplankton for the different hydrographic structures in the Catalan Sea, the variability is higher at the front (Alcaraz et al., 2007). Six times more nitrogen is excreted in coastal and frontal waters than offshore (Alcaraz et al., 1994). During the stratification period, zooplankton excretion could provide up to 16.8% of the N (as ammonia) and 76.6% of the P requirements for primary production, values that seem to be low in comparison with data from other oligotrophic areas (Alcaraz, 1988). In the Gulf of Lion, the excretion of nitrogen and phosphorus by zooplankton was estimated to account, respectively, for 31% and 16% of the primary production requirements in spring and for 10% and 27% in winter (Gaudy et al., 2003). Furthermore, excretion by copepods migrating to the surface during the night may fuel the

regenerated production in the layer above the DCM (Saiz and Alcaraz, 1990) and enhance bacterial production (Christaki et al., 1998).

5.6 Feeding

The dominant copepod species in the MS are extremely diverse not only in terms of taxonomy and morphology but also in life history traits and behaviour, greatly affecting their modes of interacting with prey and predators (Mazzocchi and 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. By contrast, *Clausocalanus* moves continuously without creating feeding currents and it captures cells that enter a restricted volume just in front of its head (Mazzocchi and Paffenhöfer, 1998; Paffenhöfer, 1998; Uttieri et al., 2008). Oithonids stand motionless for most of the time perceiving hydromechanical signals from moving prey 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 allow them to scrape food items from particle aggregates, such as discharged appendicularian houses and marine snow (Alldredge, 1976; Ohtsuka et al., 1993). The comparison of individual activity and motion behavior between the autumnal *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). All these distinct behaviours point to a different functional roles in the epipelagos, with the occupation of distinct niches even in apparently homogeneous waters. The overall picture emerging from the diversified characters of the small copepods prevailing in the open MS indicates that they may efficiently exploit the whole spectrum of resources available in the open oligotrophic waters.

Though their natural diet and feeding performances have been measured only rarely in the open MS, copepods are likely to prefer ciliates over autotrophic food, as reported for various regions of the world oceans (reviewed by Calbet and Saiz, 2005) and in the coastal MS (Wiadnyana and Rasoulzadegan, 1989). Indeed in the North-East Aegean Sea 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, probably suggesting that not all autotrophs provided adequate food supply in terms of quality and/or size (Zervoudaki et al., 2007).

Rare measurements of feeding rates in the open MS 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 $5.8 \times 10^6 \mu\text{m}^3$ particles mg^{-1} zooplankton dry weight h^{-1} and the highest value was recorded in the layer with chl *a* maximum concentration (Gaudy and Youssara, 2003). Most of the in situ studies have provided evidence that mesozooplankton feeding can change in relation to the prevailing type of food and that copepod feeding can be selective even when a homogeneous food assemblage is available. For example, at the DYFAMED site, copepod filtration rates rose from 0.54 to 1.89 ml copepod $^{-1}$ h^{-1} when the diet switched from mixotrophic to heterotrophic nanociliates (Pérez et al., 1997). In offshore waters of the NW MS, communities dominated by the same four copepod genera (*Clausocalanus*, *Paracalanus*, *Oithona*, and *Centropages*) fed on phytoplankton in June, when cells $>10 \mu\text{m}$ occurred, whilst relying on microzooplankton or detritus in October, when small cells ($<10 \mu\text{m}$) were most abundant, or under strong 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 proteins sustained the enhanced secondary production in spring, as indicated also by the increased ammonium excretion (Gaudy et al., 2003). A seasonal shift was also observed in the Catalan Sea, where copepods were strongly coupled with the autotrophic biomass during phytoplankton blooms (dominated by cells $>5 \mu\text{m}$) in March, and on heterotrophs in late spring and early summer, when autotroph abundance was lower (Calbet et al., 2002).

Switches in feeding preferences and performances might result from a real group/genus plasticity in response to different food environment. However, it is also possible that this apparent flexibility masks neglected differences among congeneric species that are very similar morphologically but have different food quantity and quality needs. This second case can be hypothesized for *Clausocalanus pargens* and *C. paululus* by observing their distribution in different regions of the MS and the Atlantic Ocean (Peralba, 2008; Peralba et al., 2010). Both species are widespread in the 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; Peralba et al., 2010). Unfortunately, data on the natural diet of the dominant *Clausocalanus*, *Oithona*, *Oncaea* species are almost lacking. Differences in the trophic regimes 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 areas, while in open waters it contributes significantly to copepod assemblages only during

spring blooms, i.e., in the Gulf of Lion, Ligurian Sea, and North Aegean Sea (Andersen et al., 2001a; Siokou-Frangou et al., 2004; Calbet et al., 2007). This distribution indicates a rather 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 can affect mesozooplankton. Food limitation is suggested to occur in the Catalan Sea, since mesozooplankton ingestion rates correlate with food availability but are lower than in experimental studies (Saiz et al., 2007). Food limitation may lead to competition among mesozooplankters in the open MS. However, the ability to exploit different food sources may overcome this problem and allow the co-occurrence of various and numerous taxa. This is suggested by grazing experiments conducted in the coastal Catalan Sea, where doliolids, small copepods and cladocerans show clear food niche separation (Katechakis et al., 2004).

5.7 Grazing impact

The prey preference of copepods could significantly affect ciliate abundance, exerting a strong top down control on their populations. This control has been hypothesized as the major factor for the low standing stock of ciliates across the entire MS (Dolan et al., 1999; Pitta et al., 2001). Additionally, in situ measurements indicate that mesozooplankton grazing impact on phytoplankton can be significant. Namely, in the Gulf of Lion, the percentage of primary production removed by zooplankton grazing was estimated to be important in both winter (47%) and spring (50%) (Gaudy et al., 2003). Previous estimations in the area suggested that half of the phytoplankton loss from March to April should be due to zooplankton grazing (Nival et al., 1975). In the very oligotrophic South Aegean Sea, copepods grazed 14% (in March) to 35% (in September) of the primary production from cells $>3\ \mu\text{m}$ (Siokou-Frangou et al., 2002). The grazing impact would be even higher had these estimates included copepod nauplii and 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 et al. (2001) that zooplankton should exert a tighter control on autotrophs in oligotrophic environments than in productive systems. However, data available for the open MS are still too few to provide conclusive evidence.

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 appeared overall negligible in the Catalan Sea (Duró and Saiz, 2000, $<1\%$), whereas it varied between 0.3 and 7.8% in several areas of the EMS (Kehayias, 2003).

A good coupling between mesozooplankters and their prey is suggested by the horizontal patterns of mesozooplankton in the open MS, which match those of autotrophic biomass and production (e.g., the west-to-east decrease) and, to a lesser extent, those of microheterotrophs. This coupling also occurs at a 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, occasionally the areas of the maximum zooplankton abundance do not coincide with those of the highest phytoplankton concentration (Calbet et al., 1996, e.g., in the Catalan Sea), and this contrast might be attributed to factors other than nutrition, such as zooplankton mortality due to predation.

5.8 Predation by fish

Mesozooplankton is the major prey of small pelagic fish (both larvae and adults) in the MS. Diet and diel feeding of anchovy larvae in the WMS suggest that their distribution is trophically-driven and closely connected to the occurrence of DZM in summer (Sabatés et al., 2007). Indeed, in the Algerian basin, the Catalan Sea and the Gulf of Lion, larvae of *Engraulis encrasicolus* feed mostly on copepods (*C. typicus*, *T. stylifera*, *M. rosea*, *Clausocalanidae-Paracalanidae*) and, to a lesser extent, on molluscs, cladocerans, other crustaceans and appendicularians (Tudela and Palomera, 1995, 1997; Plounevez and Champalbert, 2000; Bacha and Amara, 2009). In particular, copepod nauplii and copepodites are the major prey items of anchovy and sardine larvae in the Adriatic Sea and in the WMS (Tudela and Palomera, 1995; Stergiou et al., 1997; Tudela and Palomera, 1997; Plounevez and Champalbert, 2000; Coombs et al., 2003; Bacha and Amara, 2009; Morote et al., 2010). In the Adriatic Sea, sardine adults and larvae seem to feed on phytoplankton too (Rasoanarivo et al., 1991), while sprats feed on copepods, decapod larvae, cladocerans and chaetognaths (Ticina et al., 2000). Borme et al. (2009) report that the principal prey of all size classes of *E. encrasicolus* in the NW Adriatic Sea are small-sized copepods (0.2–0.6 mm in prosome length), such as *Euterpina acutifrons* and *Oncaea* spp. These authors comment that the observed preference of anchovy for these few copepod species might be related to their abundance, but also to species-specific behavioural (e.g., swimming patterns, patchy distribution) and/or physical characteristics (e.g., colour, bioluminescence) of the prey.

The constant and important presence of copepods in the diet of anchovies and clupeids reported above, and the relevant portion (20%) of total zooplankton production estimated to be consumed by adult anchovies in the Catalan Sea

(Tudela and Palomera, 1997) definitely indicate that mesozooplankton play a crucial role as the major links between plankton and the small pelagic fish production in the MS.

6 Planktonic food webs in the Mediterranean epipelagos

After the first reports 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 (Thingstad and Rassoulzadegan, 1995; Christaki et al., 1996; 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 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 had been exploited only by bacteria, which could utilize DON, 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 (by-pass hypothesis). ii) The relaxation of P limitation had produced a “luxurious” accumulation of P in both bacteria and picophytoplankton (presumably less in the latter) forming a P enriched diet for grazers, which stimulated the observed increase in egg production (tunneling hypothesis). In either scenario, a community emerges that would not always respond to nutrient inputs with an accumulation of autotrophic biomass, 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 the Levantine Sea is tightly controlled by the heterotrophic component.

The leading role of heterotrophs in the MS, as it emerges from a mainly heterotrophic plankton standing stock dominated by the pico size group, is the recurrent 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). Accordingly, the distribution of biomass between 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 common scenario in oligotrophic oceanic waters (Gasol et al., 1997). In other words, the prevalent pattern is that of a high ratio between primary production and total biomass (P/B), which is typical of oligotrophic ecosystems and is a sign of high efficiency in keeping the resources within the system (e.g., Margalef, 1986, chap. 22 and chap. 26, Frontier et al., 2004, chap. 3).

The above outlook suggests two different scenarios for the Mediterranean epipelagic food web: i) the system is net heterotrophic, with a dominance of heterotrophic bacteria and protists not only as biomass but also as rates. In this scenario, bacteria outcompete autotrophs in P uptake and bypass the autotrophic link, relying on allochthonous C (Sects. 2 and 3.1), which would be used more or less efficiently according, e.g., to the season or the area; 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 of microheterotrophs in the central Ionian Sea in spring), or higher turnover rates in autotrophs than in heterotrophs, or both. The latter scenario 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 heterotrophic microbes and picocautotrophs in offshore MS waters, prevalence of nano- and micro-autotrophs has been observed after intermittent nutrient pulses. These shifts are typically associated with highly dynamic mesoscale physical structures that favour deep vertical mixing and nutrient upwelling in frontal areas, as well as in areas close to extended and highly productive coastal systems enriched by large river outflow (Gulf of Lion, Adriatic and North Aegean Seas) (Sect. 2). Such pulses are spatially limited and concentrated, in contrast to the nutrient inputs from the atmosphere, which are spread over large areas and diluted. They determine a considerable variability of the food web structure along trophic gradients, which changes 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 to the following stratification period in early June 1995 (Andersen et al., 2001a). The central divergence of the NW 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).

The areas characterized by a high level of primary and secondary productivity favoured by upwelling are often associated with physical processes that retain food and fish larvae, thus providing favourable reproductive habitats to fish

(Agostini and Bakun, 2002). Indeed, the Alboran Sea, the Gulf of Lion and the nearby Catalan Sea, the Adriatic Sea and the North Aegean Sea are known as successful spawning grounds and areas of high yield of small pelagic fish, mainly anchovy and sardine (Stergiou et al., 1997; Agostini and Bakun, 2002; Palomera et al., 2007). In these areas, the larvae of small pelagic fish feed mainly on copepods and other mesozooplankters, as mentioned in the previous chapter, but ciliates and flagellates have also been found to contribute to their diet (Rossi et al., 2006). New production also occurs at the DCM (with frequent presence of diatoms) close to the nutricline over a broad time interval, but its overall weight on the production of the basin is poorly quantified. Whether the DCM hosts a significantly different planktonic web is still an open question (e.g., Estrada et al., 1999).

A first approximation may then be that the microbial food web is the prevailing structure in the offshore waters of the MS, with few exceptions where larger, bloom forming phytoplankton might initiate the “classical” food web. However this simplification is becoming less and less robust in the light of new findings on the 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 from the global ocean in this respect. Part of 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 of feeding on pico- and small nanoplankton (Deibel and Lee, 1992), constitute a bypass from the lower trophic levels to fishes (Deibel and Lee, 1992), contributing to a more efficient food web like the one 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 in their diet, during both mixing and stratified seasons (Sect. 5), indicates a flexible and possibly efficient connection between autotrophs and microheterotrophs and the higher trophic levels. All this suggests that 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 the 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, a common fea-

ture among oligotrophic systems (Margalef, 1986, chap. 23 and chap. 26).

Most of the studies describing phytoplankton biomass dynamics in the MS (Sect. 3) have stressed the bottom up constraints on 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-down control, which was revealed for both ciliates and bacteria (Sects. 4 and 5). We are then confronted with two possible views: i) the low standing stock of autotrophs results from low availability of dissolved nutrients which, as typical for oligotrophic regime, also determine a low standing stock of intermediate and top predators (bottom-up control); ii) the low standing stock of autotrophs would rather result from a very effective top-down control that propagates along the food web, ultimately affecting the top predators (see Sects. 4 and 5). The two views are not in contrast, although the former points at geochemical constraints while the latter emphasizes the ecosystem dynamics as a whole. Indeed, a bottom-up control does exist, and determines the carrying capacity of the system. This is relatively low because of the moderate nutrient fluxes and the continuous loss of the internal nutrient pool into the Atlantic Ocean. On the other hand, the view of a top-down control is supported by the structure of the planktonic food web discussed above as well as by the evidence that fisheries in the MS are richer than expected on the basis of measured chl *a* and nutrient concentrations (Fiorentini et al., 1997). It is the latter aspect that is at the origin of the so called “Mediterranean paradox” (Sournia, 1973; Estrada, 1996), which however is less paradoxical in the light of the effective food web discussed above, and is coherent with general ecological theories (e.g., Margalef, 1986). We can thus hypothesize that the intricate and very flexible food web (e.g., Paffenhöfer et al., 2007) contributes in minimizing carbon loss to deeper layers (POC export is very low in the MS, e.g., Wassmann et al., 2000; Boldrin et al., 2002) and predators can optimally profit from carbon produced and transformed within the system, thus being the ultimate controllers of plankton abundance in the MS. The paradox becomes even less paradoxical if one takes into account the significant role of external organic matter inputs, which corroborates 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 satisfying, both at the spatial and at the temporal scales. Apart from 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 established 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 that are the major component of the MS epipelagos are still largely understudied. The few molecular studies conducted 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 intriguing 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. These might affect the biological structure of the basin more rapidly compared to the large oceans, thus strongly supporting 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, the first signals might regard the spatial re-organization of communities. Indeed, as a consequence of scales much smaller than in comparable oceanic regions, the MS is highly flexible and can shift from one regime to another, since all the players are already present. 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. Such models could be used to approach a broad

range of marine environmental issues such as fisheries, climate change impact, harmful blooms, emerging diseases and pollution. All of these could more easily be tested due to the scale and accessibility of the MS, and inferences later extended to other less tractable marine systems.

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