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**Abstract**

This chapter presents an overview of the diversity, distribution and ecology of major groups of microbial plankton in the Mediterranean Sea, including phytoplankton, viruses, heterotrophic prokaryotes and flagellates, and ciliates. Some protists with hard structures like diatoms, thecate dinoflagellates, coccolithophorids and tintinnids have been relatively well studied from a morphological point of view, but in general microbial diversity is poorly known, in particular with respect to prokaryotes and the smallest eukaryotes. This situation is rapidly changing, in a large part due to the incorporation of molecular techniques. The general oligotrophy of the Mediterranean, which increases from west to east, is reflected in a strong contribution of the picoplankton and the microbial food web. However, a variety of nutrient-enrichment mechanisms, including winter mixing, meso-scale hydrographic structures and land runoff, which operate at various spatio-temporal scales, may enhance primary production and result in the intermittent dominance of diatoms and the herbivorous food web. During the stratification period, a deep chlorophyll maximum is a general feature throughout the basin and plays a substantial role in the fertility of the Mediterranean.

**Keywords**

“Phytoplankton mandala” • Bacteriophages • Blooming taxa • Chemotaxonomic and molecular techniques • Chlorophyll maximum, Colonial diatoms • Cryptophytes • Cyanobacterial genera • Dinophyceae • Eutrophication • Free-living pelagic bacterial cells • Global change • Heterotrophic bacteria • Large-scale phytoplankton community • Long-term trends • Mediterranean photic zone • Microbial diversity • Microbial DNA • Microbial eukaryotes • Microbial food web • Microbial plankton • Nano-and picoplanktonic flagellates • Pelagophyceae • Phytoplankton biomass • Phytoplankton blooms • Pigment chemotaxonomic approach • Plankton ecosystem dynamics • Plankton • Planktonic ciliates • Planktonic community • Prasinophyceae • Primary production • Prymnesiophytes • Seasonal succession of phytoplankton • Silicoflagellates • The mediterranean • Toxic benthic dinoflagellate • Viral community • Viral effects on bacterial biomass and production • Viral infection • Viruses • Winter phytoplankton bloom

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## Introduction

In the Mediterranean Sea, as in other marine ecosystems, microbial components of the plankton are major agents in biogeochemical cycles and account for most of the biodiversity. In spite of their importance, many groups of marine microbes are still poorly known, although the situation is rapidly changing thanks to the introduction of molecular techniques. The structure and dynamics of Mediterranean plankton has been considered in a number of collective volumes such as Margalef (1985), Moraitou-Apostolopoulou and Kiortsis (1985) and Minas and Nival (1988). Recently, Siokou-Frangou et al. (2010) published an updated review of studies conducted during the last 25 years in offshore epipelagic waters and Coll et al. (2010) presented a synthetic account of Mediterranean marine biodiversity. This chapter addresses the biodiversity and ecology of the major microbial groups in the Mediterranean, as part of the ecological background for a book on history and present challenges. In the following section (“Main groups and trophic roles of microbial plankton”), we present a brief account of the taxonomic affiliation and functional roles of microbial groups. The main fertilization mechanisms in the Mediterranean and the general patterns of temporal distribution and vertical organization of phytoplankton biomass are considered in sections “Fertilization mechanisms in the Mediterranean” and “Overview of diversity of the main microbial groups”. The next section (“Phytoplankton”), devoted to phytoplankton, presents an overview of the taxonomic diversity of the main groups, a brief review of harmful algal events in the Mediterranean and some insights obtained from the study of long-term series. Section “Viruses and heterotrophic microbes” deals with the distribution and diversity of viruses, heterotrophic prokaryotes and flagellates, and ciliates. Finally, section “Microbial and classical food webs. The example of the Catalan Sea” deals with the structure of the planktonic food webs and describes a case study in the NW Mediterranean.

## Main Groups and Trophic Roles of Microbial Plankton

Until about three decades ago, the classical view of the planktonic food web featured phytoplankton of sizes above a few micrometers as primary producers, microzooplankton such as ciliates, as herbivores, and zooplankton (mainly copepods), as a bridge between the former trophic levels and fishes. Phytoplankton, roughly defined as the autotrophic component of the planktonic food web, was considered as mostly composed of eukaryotic microalgae. However, many exceptions had long been recognized, as some groups classically

considered as phytoplankton, like the dinoflagellates, comprise heterotrophic taxa that prey on other organisms, and many autotrophic forms are also capable of phagotrophy and osmotrophy. Phototrophic organisms of sizes below a few micrometers had been described, but the available techniques did not allow their reliable enumeration. The occurrence of bacteria, considered mainly as decomposers, was known, but the methods used at the time, mostly based on culture techniques derived from medical microbiology, allowed only the detection of a small proportion of them. This general picture changed around the mid 1970s with the incorporation of DNA staining and epifluorescence microscopy, which allowed a reliable observation and counting of prokaryotic and eukaryotic cells <2–3  $\mu\text{m}$  in size, known collectively as “picoplankton”, an operational category that complements those of “nanoplankton” (>2  $\mu\text{m}$  and >20  $\mu\text{m}$ ) and “microplankton” (>20  $\mu\text{m}$  and <200  $\mu\text{m}$ ). These techniques and the later addition of automatic counting by means of flow cytometry demonstrated the abundance and ubiquity not only of heterotrophic bacteria, but also of autotrophic cyanobacteria of the genera *Synechococcus* and *Prochlorococcus*, and of auto- and heterotrophic picoeukaryotes. The use of radioactive markers helped to point out the magnitude of the bacterial assimilation of organic matter originated from phytoplankton or from allochthonous sources, and the role of picoplankton as food of small heterotrophic flagellates that could be in turn consumed by other microheterotrophs and by zooplankton (Ducklow et al. 1986). The pathway in which dissolved organic matter was assimilated by bacteria and reintroduced into the marine food web via heterotrophic pico- or nanoflagellates and microzooplankton received the name of “microbial loop” and has been shown to be particularly important in the functioning of oligotrophic aquatic systems such as the Mediterranean. More recently, the application of molecular techniques to the study of microbial DNA has led to the detection of an immense amount of previously unknown biodiversity. Among other surprises, came the realization that Archaea, a group of prokaryotes previously known from extreme environments, and now considered together with bacteria and eukaryotes as one of the three main branches of life, were widespread in the pelagic marine domain (Karner et al. 2001). Given the rapid changes in taxonomic knowledge, there is not yet a generally accepted classification system for the different taxa of planktonic microbes within the so-called tree of life of living organisms (Pennisi 2003), although there is increasing agreement on the basic features. Work carried out in the last decades has uncovered links between certain groups and particular metabolic activities. For example, 16S rDNA and nitrogenase genes have been targeted to show the presence of several lineages of unicellular diazotrophic cyanobacteria (Zehr et al. 2003) and other genetic procedures have allowed the detection of heterotrophic bacteria that can enhance their energy sources by means of aerobic anoxygenic photosynthesis (Jiao et al. 2007)

or light-driven proton pumps based on proteorhodopsin (DeLong and Béjà 2010). A new phycobilin-containing group (the picobiliphytes) was described by Not et al. (2007); they were initially described as algae, but could be heterotrophs (Massana 2011). Another recent development has been the proof that viruses are the most abundant and ubiquitous entities of aquatic communities (Bergh et al. 1989; Weinbauer 2004; Suttle 2007, and references therein). The net effect of viruses in the pelagic food web, described as ‘the viral shunt’ by Fuhrman (1999), consists of transforming the particulate organic matter of the host into more viruses, and returning biomass in the form of dissolved and colloidal organic matter.

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### Fertilization Mechanisms in the Mediterranean

The Mediterranean is the largest quasi-enclosed sea on Earth (Siokou-Frangou et al. 2010) and functions as a negative estuary because of the excess of evaporation over precipitation plus runoff. However, the Mediterranean has also been considered as one of the most complex marine environments of the planet (d’Ortenzio and Ribera d’Alcalà 2009) due to the variety of physical processes that operate in it, including deep water formation, thermohaline circulation, sub-basin gyres and mesoscale activity. The exchange of water at Gibraltar, where denser and relatively nutrient-rich Mediterranean water flows out at depth and fresher Atlantic water enters at surface has contributed to the low nutrient content of deep mediterranean waters as compared to other world oceans (McGill 1965). In turn, the eastern basin presents an anti-estuarine exchange with respect to the western basin. These relationships originate an eastward transport of surface waters and a westward transport of intermediate waters (Pinardi and Masetti 2000), and underlie the general Mediterranean gradient of increased oligotrophy towards the east. The wind distribution, and the morphology and characteristics of the basin contribute to a water circulation pattern with a dominance of cyclonic gyres in the north and anticyclonic gyres in the south of the basin. Deep convection can occur in winter in the Gulf of Lions and parts of the Eastern Mediterranean (EM), such as the Aegean Sea (MEDOC-Group 1970; Zervakis et al. 2004).

The main mechanisms of nutrient input in the Mediterranean photic zone include winter mixing, coastal upwelling and other mesoscale features, and land runoff. Eolic inputs are also significant for certain elements. However, the efficacy of some fertilization mechanisms such as mixing or upwelling is limited by the relatively low nutrient content of the deep Mediterranean waters. Winter mixing occurs throughout the Mediterranean, but the mixing depth varies and with it the degree of nutrient enrichment of the surface layers (Estrada et al. 1985). Wind-driven upwelling occurs in some areas

with favourable coastal profiles, such as the coast of the Gulf of Lions. In the Alboran sea, another important upwelling region is influenced by the system of anticyclonic eddies associated to the jet of Atlantic water entering the basin (Tintoré et al. 1991). In addition to upwelling, the Atlantic water inflow contributes to nutrient enrichment by causing turbulent mixing in the Straits of Gibraltar, which entrains nutrients from the deeper Mediterranean waters into the euphotic zone, and by producing fertilization spots associated with eddies of the Atlantic Current along the Algerian coast (Taupier-Letage and Millot 1988; Morán et al. 2001). Other important mesoscale and submesoscale features in the Mediterranean include gyres, frontal regions and filaments (Wang et al. 1988; Iermano et al. 2009). The cyclonic circulation in the northern part of the western basin is bound by a series of shelf-slope fronts and leaves a central divergence that may be a site of deep convection in winter and, because of the shallower depth of the pycnocline, of enhanced nutrient supply to the upper water layers in summer (Estrada 1996). The shelf-slope fronts, including the Ligurian, Catalan and Balearic Fronts, are affected by meanders, eddies and filaments, that together with the ageostrophic coastal circulation could originate enrichment events (Estrada and Margalef 1988; Font et al. 1988). Both the central divergence and these fronts appear to be important in the fertility of the NW Mediterranean (Marty et al. 2002; Estrada 1996). Other permanent or quasi-permanent sub-basin gyres with winter convective events are the Rhodos Gyre (NW Levantine sea) and the South Adriatic Gyre (Siokou-Frangou et al. 2010). Coastal fertilization due to land runoff from rivers is particularly important in the areas of influence of large rivers like the Rhône and the Ebre, in the NW Mediterranean, the Po in the North Adriatic Sea and the Nile, but input from land due to smaller rivers, storms and wastewater discharge may be locally significant (see Stambler, this volume, for primary production figures).

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### Overview of Diversity of the Main Microbial Groups

The earlier studies of microbial plankton in the Mediterranean and other marine regions of the world centered on taxa with cellular characteristics that could be described under optical microscopy, like diatoms, thecate dinoflagellates, coccolithophorids and silicoflagellates among the phytoplankton, and Tintinnids, Foraminifera or Radiolaria among the microheterotrophs. In fact, many early illustrated books and checklists were based on Mediterranean samples (e. g. Jörgensen 1920; Pavillard 1925; Schiller 1928). Later on, the introduction of electron microscopy allowed a better description of morphological species diversity and helped to establish the biogeography of some taxa. In the last decades, the

implementation of molecular genetics has brought a rapid change of ideas and concepts to the field of both prokaryotic (Bacteria and Archaea) and eukaryotic (Protists) microbial diversity. Techniques now in use may provide a measure of the diversity of organisms (for example, by determining 16S rRNA sequences) or of the number of taxonomic units in an environmental sample (by means of metagenomic approaches). The new findings highlight the problem posed by the inconsistencies in the morphological, biological or phylogenetic species concept when applied to marine microbial communities (Coll et al. 2010). The picture that has emerged is that of a high microdiversity, with accepted morphospecies encompassing a number of cryptic or pseudocryptic variants.

The rapidly changing state of taxonomical knowledge makes it difficult to assess the number of microbial taxa in the Mediterranean and to establish comparisons with other areas. Hofrichter et al. (2002) estimated that about 4,400 species of protists had been described in the region, although this figure must be taken with caution, given the problems with cryptic and pseudocryptic taxa mentioned above. The compilation of Velasquez (1997) for the Western Mediterranean (WM) recorded 96 genera and 736 diatom species and Gómez (2006) listed 104 genera and 673 dinoflagellate species, none of them endemic, in contrast with the situation for many macroscopic organisms. The biodiversity of coccolithophores in the WM was revised by Cros (2001), who compiled 166 taxa. The recent recognition that holococcolithophores, previously considered as a separate family, are part of a life cycle that includes holo- and heterococcolith-bearing stages was based, mainly, on combination coccospheres sampled in the WM (Cros et al. 2000) and has resulted in an overhaul of coccolithophore taxonomy. Much less known is the biodiversity of naked flagellates and small-sized picoplankton, although recent work combining optical and electron microscopy with pigment chemotaxonomy, molecular techniques and experimental cultures is clarifying phylogenetic relationships and uncovering much unknown diversity.

Assessing bacterial biodiversity is hindered not only by the lack of knowledge of the existing organisms, but also by the difficulties in reaching a consensus about bacterial “species”. Bacterial richness has been shown to peak in the tropics (Pommier et al. 2007; Fuhrman et al. 2008) and, for the latitude of the Mediterranean (30–45°N), a number of detectable “operational taxonomic units” between 100 and 150 would seem logical. In fact, Zaballos et al. (2006) reported a similar value that, once extrapolated using statistical techniques, suggested a number of ca. 360 for surface waters (Coll et al. 2010). A slightly smaller value was found for the coastal Blanes Bay Microbial Observatory (Alonso-Saez et al. 2007) based on a different approach. However these techniques usually refer only to the dominant

organisms. Recent application of new methodologies (such as metagenomics and 454- tag sequencing) will in the near future provide more accurate estimates (Coll et al. 2010).

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## Phytoplankton

### Temporal Distribution and Vertical Organization of Phytoplankton Biomass

Measurements of phytoplankton biomass covering at least a year cycle are numerous in coastal areas but rare in the open sea. However, satellite imagery has shown the main features of the distribution of phytoplankton biomass in open waters of the Mediterranean (Morel and André 1991; Antoine et al. 1995; Bosc et al. 2004). Using SeaWiFS data, D’Ortenzio and Ribera d’Alcalá (2009) defined seven open sea bioprovinces with distinct seasonal patterns and concluded that a temperate regime, with a marked late winter-early spring bloom was only observed in the northern part of the NW Mediterranean (their “blooming” province) and, intermittently, in a few other areas, while a subtropical mode, with seasonal biomass enhancement centered in January but lasting for 2–3 months, occurred in most of the basin. A recurrent autumn peak attributed to breakup of the thermocline has been detected in the “blooming” province (D’Ortenzio and Ribera d’Alcalá 2009) and in some coastal regions (Margalef 1969). In a study of monthly composites of SeaWiFS images (from 1997 to 2004) for squares of 0.25° (longitude) × 0.25° (latitude), representative of 11 subregions of the NW Mediterranean, Morales (2006) found a generally unimodal seasonal variability, with a chlorophyll *a* (chl *a*) concentration maximum occurring in January off the Iberian Coast (Valencia) around 40°N, in February in the Catalan Sea, near the sill between Majorca and Minorca, in March in two coastal subregions near Barcelona and Fréjus (Southern France), around 41° and 43°N, respectively, and in April in the center of the Gulf of Lions. Interannual variability can also be very high, depending on factors such as climate variations that affect the intensity of winter mixing or the amount of precipitation (Siokou-Frangou et al. 2010). Superimposed to these general patterns, there is a strong smaller-scale spatio-temporal variability, in particular in areas of intense mesoscale activity such as the Liguro-Provençal Catalan front and the Alboran Sea (Morán et al. 2001; Estrada 1996; Siokou-Frangou et al. 2010). In coastal waters and estuarine areas of the Mediterranean, the interactions among topography, wind patterns and highly variable continental water inputs originate a large interannual, seasonal and short-term diversity in the distribution patterns of phytoplankton biomass (see section “The seasonal succession of phytoplankton” and Stambler, this volume). During blooms, chl *a* concentrations in offshore surface waters of the NW

Mediterranean reach often around 2–3 mg m<sup>-3</sup> (Vidussi et al. 2001; Marty et al. 2002; Estrada et al. 1993, 1999), but there are point records of values up to 6 mg m<sup>-3</sup> in February 2009, during the FAMOSO cruise in the Gulf of Lions (M. Estrada, unpublished data). High chl *a* concentrations have also been measured in the Alboran Sea (e. g., 7.9 mg m<sup>-3</sup>, Arin et al. 2002).

After the relatively short period winter mixing, there is a progressive stabilization of the water column until the pycnocline starts to breakup in the fall. As the winter-spring phytoplankton bloom consumes the nutrients of the upper layers, the peak of phytoplankton biomass migrates downwards, following the nutricline. During most of the year, the vertical distribution of phytoplankton in the open Mediterranean is characterized by the presence of a deep chlorophyll maximum (DCM), consisting in general of a combination of higher cell numbers and enhanced chlorophyll content per cell, with the second factor becoming more important later in the stratification period. The DCM is closely associated with the nutricline and its depth, which ranges from around 50 m in the NW Mediterranean (Estrada 1985) to 120 m in the Levantine Basin (Dolan et al. 2002), is determined by the availability of both sufficient nutrients and light to carry out photosynthesis. As happens with deep chl *a* maxima of tropical and subtropical regions (Herbland and Voituriez 1979), the Mediterranean DCM is accompanied by a slightly shallower oxygen maximum, indicative of a relative primary production maximum, and by a nitrite maximum (Estrada et al. 1993). The chl *a* concentration within the Mediterranean DCM may reach values around 1.5 mg m<sup>-3</sup> and can be very patchy, indicating an important spatio-temporal dynamism (Estrada 1985) related to processes such as mesoscale variability or internal waves.

## Phytoplankton Composition

### Cyanobacteria

Well represented cyanobacterial genera in the Mediterranean include *Synechococcus* and *Prochlorococcus*, which are the main components of the prokaryotic picophytoplankton, and two filamentous nitrogen-fixers, the free-living *Trichodesmium* and *Richelia intracellularis*, which is an endosymbiont of diatom genera such as *Rhizosolenia* and *Hemiaulus*. Peaks of cyanobacterial picoplankton tend to occur from summer to autumn (Bernardi Aubry et al. 2006; Charles et al. 2005) but have been recorded also in spring (Cerino et al. 2011). Latasa et al. (2010), who compared the distribution of various phytoplankton taxonomic groups in bloom, postbloom and stratification conditions in the NW Mediterranean, classified *Synechococcus* as mesotrophic and *Prochlorococcus* as oligotrophic. *Synechococcus* may be an important component of offshore (Denis et al. 2010)

and coastal picophytoplankton (Agawin et al. 1998; Bernardi Aubry et al. 2006; Cerino et al. 2011), while *Prochlorococcus* was first reported offshore, but may be also important nearshore (Charles et al. 2005). In the survey that Denis et al. (2010), carried out in winter 1995 across the whole Mediterranean basin, *Synechococcus* represented a 65 % of the overall ultraphytoplanktonic carbon biomass while the contribution of *Prochlorococcus* did not exceed 6.5 %. The authors did not detect clear large-scale patterns, but found a significant relationship between *Synechococcus* abundance and mesoscale structures in the Adriatic and Ionian sub-basins. *Prochlorococcus* was represented by two ecotypes, one occupying the upper 75 m and the other adapted to low light and growing mainly below 75 m. Garczarek et al. (2007) used amplification and sequencing of the *pcb* gene (encoding the major light-harvesting proteins) of *Prochlorococcus* in a late summer-early autumn Mediterranean-wide survey, to find at least four different ecotypes in the photic zone, large microdiversity, and strong vertical but low horizontal heterogeneity. A vertical stratification with *Synechococcus* in the upper 40 m and prochlorophytes at the base of the chl *a* maximum was found by Ghigliione et al. (2008) during early autumn 2004 in the DYFAMED site of the Gulf of Lions. The depth relationships of *Synechococcus* and *Prochlorococcus* are in a large part related to the presence of ecotypes adapted to factors such as different light levels and nutrient availability, although temperature can also be a factor. For example, Mella-Flores et al. (2011) compared the ecotype diversity of *Synechococcus* and *Prochlorococcus* during cruises carried out 9 years apart and reported that the dominant clades of the two genera in both cruises were typical of temperate waters, while groups typical of (sub)tropical and warm waters were only present in low concentrations. Based on these results, the authors concluded that there had not yet been a substitution of clades related to climate change.

The occurrence of the nitrogen-fixing *Trichodesmium* and diatom – *Richelia intracellularis* consortia is frequent during the stratification season, albeit in low concentrations (Béthoux and Copin-Montégut 1986). Krom et al. (2010) concluded that their impact on the global nitrogen budget in the Mediterranean is insignificant, in part due to strong P limitation, but the sporadic finding of *Trichodesmium* sp. filaments and the consistent presence of *Hemiaulus hauckii* and *Rhizosolenia styliformis* hosting *Richelia intracellularis* in the DCM of the whole Mediterranean basin during the stratification period led Crombet et al. (2011) to suggest that their role could be more important than previously accepted. Recent studies have pointed out the presence of diazotrophic unicellular cyanobacteria in coastal areas of the Eastern (Man-Aharonovich et al. 2007) and NW Mediterranean Sea (Le Moal and Biegala 2009) and in open waters across the entire basin, where the dominant unicellular diazotrophs

were  $\alpha$ -proteobacteria (Le Moal et al. 2011). However, the role of these organisms in the nitrogen budget of the Mediterranean Sea is still unclear.

### Diatoms (Bacillariophyceae)

Large colonial diatoms are the principal phytoplankters in most seasonal blooms and represent the typical primary producers of the so-called classical food web, leading from phytoplankton to zooplankton and fish. However, diatoms can be also important in oligotrophic situations (Scharek et al. 1999) and some taxa have sizes close to the picoplankton range. In the Mediterranean, diatoms dominate the winter-spring bloom in many areas, although their proliferation may be of short duration and easily missed by field measurements. Chemotaxonomic determinations in the DYFAMED area have shown that the contribution of diatoms to phytoplankton biomass is maximal in January or February (Marty et al. 2002). In March 1995, the phytoplankton of a station occupied by Latasa et al. (2010) in the open NW Mediterranean (41.45°N, 05.10°W) was dominated by *Pseudo-nitzschia* spp., *Chaetoceros* subgenus *Hyalochaete* spp., *Thalassiosira* spp., *Guinardia delicatula*, *Bacteriastrum delicatulum* and *Dytilum brightwellii*. In the Catalan Sea, the main nano- and microplankton taxa inshore of the Catalan Front in winter and early spring were the diatoms *Chaetoceros* spp, *Thalassiosira* spp. and *Pseudo-nitzschia* spp. (Estrada 1991; Estrada et al. 1999). The genera *Chaetoceros* and *Pseudo-nitzschia*, which dominate winter–spring proliferations, accompanied by others like *Thalassiosira*, *Bacteriastrum*, *Rhizosolenia* and *Leptocylindrus*, account also for phytoplankton biomass maxima in mesoscale features such as the Catalan Front (Estrada 1991) and the upwelling of the Alboran Sea (Arin et al. 2002) and for high chl *a* patches at the DCM (Estrada 1985; Estrada et al. 1993; Crombet et al. 2011), sustaining the view that intermittent pulses of growth can occur at the DCM level, originated, for example by hydrographic perturbations that expose bodies of relatively nutrient-rich waters to enhanced irradiance levels (Estrada 1991). In coastal and estuarine areas, the seasonal sequence of diatom assemblages tends to be locally persistent. For example, off the coasts of Barcelona and Castelló, in the NW Mediterranean, Margalef (1969) described the consistent appearance of a winter-spring maximum, dominated by *Chaetoceros* spp., together with cryptomonads and flagellates, a late spring peak, with *Rhizosolenia* and *Pseudo-nitzschia*, and an autumn peak with *Thalassionema nitzschioides*, *Asterionella japonica* and *Thalassiothrix mediterranea*. An autumn diatom assemblage with *Thalassionema nitzschioides* is a recurrent feature in the seasonal cycle in the bay of Els Alfacs, a part of the Ebre Delta (Lebot et al. 2011). In the Bay of Naples, after a winter-spring bloom with *Chaetoceros* spp., *Pseudo-nitzschia delicatissima*, *Thalassionema bacillaris* (in addition to autotrophic

flagellates), there was a substitution of the dominant diatom species by smaller-sized ones like *Skeletonema pseudo-costatum*, *Chaetoceros tenuissimus* and *Chaetoceros socialis*; other species, including *Leptocylindrus danicus*, were generally recorded in autumn. The most abundant taxa succeeded and overlapped each other in a fairly regular pattern, although there was strong interannual variability (Ribera d'Alcalà et al. 2004). Although genera such as *Chaetoceros* and *Thalassiosira* are commonly found in all diatom-dominated blooms, the particular species present of these genera and the co-occurring diatom taxa can vary at different places and times (Estrada 1991; Siokou-Frangou et al. 2010).

In addition to the above-mentioned blooming taxa, diatoms like *Hemidiscus cuneiformis* and *Coscinodiscus radiatus*, have been found consistently within the DCM of the WM, but only in low concentrations. Together with representatives from other groups (*Dictyocha fibula* and *Oxytoxum margalefi*), these species appeared to be part of a “shade flora” assemblage (Estrada 1991). Another group of large-sized diatom species of genera like *Rhizosolenia*, *Proboscia* and *Hemialus* tend to occur in low numbers in the euphotic zone of stratified waters. As noted above, some of these *Rhizosolenia* and *Hemialus* species host the diazotrophic cyanobacterial symbiont *Richelia intracellularis*; their present contribution to nitrogen fixation seems to be small (Krom et al. 2010), but it has been suggested that extensive Rhizosolenid mats and their symbionts may have supported nitrogen fixing during sapropel episodes (Sachs and Repeta 1999; Stambler, this volume). Another diatom typical of relatively oligotrophic conditions is *Leptocylindrus mediterraneus*, which occurs in association with the heterotrophic flagellate *Solenicola setigera* and with potentially diazotrophic unicellular cyanobacteria (Buck and Bentham 1998). More studies are needed also to assess the importance in offshore waters of small-sized species like *Minidiscus trioculatus* and *Arcocellulus* sp., which were abundant in winter samples from the open NW Mediterranean (Delgado et al. 1992; Percopo et al. 2011; Cros and Estrada, unpublished data).

### Dinoflagellates (Dinophyceae)

As a group, the Dinophyceae include a bewildering variety of ecophysiological niches. Dinoflagellates are often very abundant in marine samples but most of them are naked nanoplankton-sized forms that cannot be properly identified in optical microscopy examinations and are often overlooked or lumped in categories such as “small dinoflagellates” or “small gymnodinoids”. Chemotaxonomic analysis may fail to give an accurate measure of dinoflagellate abundance because peridinin, the pigment used as a dinoflagellate biomarker, is not present in many of these organisms. Widespread nano- and microplankton dinoflagellate genera like *Noctiluca*, *Protoperidinium* and *Warnowia*, and species of *Gyrodinium* and *Gymnodinium*,

among others, are heterotrophic and play a functional microzooplankton role. Many genera, like *Ceratium* (*Neoceratium*, a new name recently proposed for the genus by Gómez et al. 2010, is still under discussion) and *Alexandrium* can be mixotrophic (Jacobson and Anderson 1996) while others like *Dinophysis* comprise species with a varying degree of autotrophic capabilities. *Ornithocercus*, *Histioneis* and *Cytharistes*, open water taxa typically present at low concentrations, host endosymbiotic cyanobacteria that could help with nitrogen fixation (Gordon et al. 1994). The variety of trophic strategies and the ability to migrate vertically between the shallow well-illuminated layers and the nutricline underlie the prevalence of dinoflagellates during the stratification period. In general, they are more abundant within the upper layers of the euphotic zone, but species like *Oxytoxum margalefi*, are part of the “shade flora” of the DCM level (Estrada 1991). Some taxa, referred loosely as “red tide dinoflagellates” in Margalef’s Mandala (see section “Generalities on phytoplankton community structure and function”), are frequent producers of blooms when relatively high water column stability, that allows biomass accumulation, is accompanied by nutrient availability. These forms include genera like *Prorocentrum*, *Scrippsiella* and *Alexandrium*, frequently found in coastal waters. Some species or strains of *Alexandrium* and other genera produce toxins that can accumulate in members of higher levels of the trophic web and their proliferations may have noxious effects on human health or on other ecosystem organisms (see section “Harmful algal blooms in the Mediterranean”). In some cases, as happens with several species of *Dinophysis*, a low concentration of individuals is sufficient to cause toxic effects.

### Prymnesiophyceae

Many prymnesiophytes belong to the nanophytoplankton size category, although pigment-based and molecular techniques have recently pointed out their important contribution to the picophytoplankton (Liu et al. 2009). The best studied group is that of the coccolithophores, which possess a cell cover of calcareous platelets. Coccolithophores are well represented in the Mediterranean (Ignatiades et al. 2002; Malinverno et al. 2003; Siokou-Frangou et al. 2010). As mentioned above, they tend to be important in mesotrophic situations, as in the open waters of the NW Mediterranean in winter-spring (Estrada et al. 1999; Latasa et al. 2010) and autumn (Cros 2001). The most widespread species is *Emiliania huxleyi*, which can be dominant both in coastal (Bernardi Aubry et al. 2004; Cerino et al. 2011) and open sea regions (Estrada et al. 1999), a finding perhaps related to the high intraspecific variability of this taxon. There seems to be some ecological differentiation between hetero- and holococcolithophores, with a higher proportion of heterococcolithophores at the DCM level and of holococcolithophores in the more oligotrophic upper part of the euphotic zone (Cros 2001). Curiously, species like *Calyptrosphaera sphaeroidea*,

generally reported in low concentrations, have produced high-density proliferations in zones like the Tarragona Harbour and the Algiers coast (Cros et al. 2002; Illoul et al. 2008). The distributions of non-calcifying prymnesiophytes, which include widespread genera like *Chrysochromulina*, are poorly known with the exception of the colonial forms of species of *Phaeocystis*, which can be very abundant in open waters of the Catalan Sea, in winter (Estrada 1991).

### Other Groups

Cryptophytes are often an important component of the nanophytoplankton (Margalef 1969), but species lists derived from light microscopy should be reconsidered (Cerino and Zingone 2006). Based on microscopic observations or on the detection of alloxanthin, their pigment marker, a substantial contribution of cryptophytes has been found, for example, in offshore waters of the NW Mediterranean in winter-spring (Marty et al. 2002; Latasa et al. 2010) and in relationship with mesoscale fertilization areas (Margalef 1971). Novarino (2005) found 11 morphospecies in samples from Barcelona coastal waters and the Alboran Sea, and noted the abundance of *Plagioselmis prolunga*. In the Gulf of Naples, Cerino and Zingone (2006) used cultures and electron microscopy to identify 16 morphospecies, and reported that the maximum cryptomonad concentration occurred in spring-summer and autumn. The most abundant species was *Hemiselmis* sp., while *Plagioselmis prolunga* was the most frequently found, although at lower concentrations. The regular presence of *Plagioselmis prolunga* was confirmed by McDonald et al. (2007).

The silicoflagellates, a group of Chrysophyceae recognizable by their tubular skeleton of silica, are mainly represented by the genera *Dictyocha* and *Distephanus*. They tend to show population maxima in winter and to be present in subsurface levels during the stratification period (Estrada et al. 1985). Another morphologically recognizable chrysophyte is *Meringosphaera mediterranea* (Cerino et al. 2011).

Other important phytoplankton groups in the Mediterranean Sea are the Prasinophyceae and the Pelagophyceae. Both groups include widespread picoplankton-sized representatives, but the Prasinophyceae comprise also frequent nanoplankton genera, like *Tetraselmis* and *Pyramimonas*, and the striking microplanktonic species *Halosphaera viridis*. Latasa et al. (2010) found that picoplanktonic Prasinophyceae were the most abundant group, after diatoms, during the bloom period in the open NW Mediterranean. Marie et al. (2006) used flow cytometry, gradient gel electrophoresis and quantitative PCR to assess the abundance and composition of picoplankton (cells <3 µm) and the distribution of the prasinophyte genera *Micromonas*, *Bathycoccus* and *Ostreococcus* across a transect between the Morocco upwelling and the EM. The quasi-absence of *Micromonas*, which was replaced mainly by *Bathycoccus* and sporadically by *Ostreococcus*, agreed with the general oligotrophy of the Mediterranean. In contrast,

*Micromonas* was abundant in the coastal waters of the Gulf of Naples (Zingone et al. 1999) and in Blanes Bay, where together with *Bathycoccus* and *Ostreococcus* dominated the sequences obtained in winter and fall (Massana et al. 2004). In fact, *Micromonas pusilla*, the most commonly cited species of the genus *Micromonas*, appears to comprise several independent clades occupying specific niches, as shown by Foulon et al. (2008) for Blanes Bay.

The pigment signature of Pelagophyceae (which they share with chrysophytes) has been found at a number of locations in the Mediterranean (Claustre et al. 1994; Marty et al. 2002). Latasa et al. (2010) reported that pelagophytes were abundant during the winter-spring bloom, but presented also significant concentrations in more oligotrophic periods. In general, Pelagophyceae tended to be more important at depth, a feature that has been related to nutrient availability (Claustre et al. 1994; Barlow et al. 1997; Marty et al. 2002) and low light adaptation (Latasa et al. 2010). Pelagophytes have been investigated by means of molecular methods in coastal areas such as the Gulf of Naples, where they occurred between December and March (McDonald et al. 2007) and Blanes Bay (Massana et al. 2004).

### Generalities on Phytoplankton Community Structure and Function

The available information on large-scale phytoplankton community distribution patterns in the Mediterranean basin is scarce (Siokou-Frangou et al. 2010) and limited to particular times of the year. Based on samples from a cruise that visited nine stations along a longitudinal transect from 4° 95' E to 32° 67' E, Ignatiades et al. (2009) reported that diatoms dominated over the water column (1–120 m depth) in the three westernmost stations (between the Strait of Sicily and the western basin), while dinoflagellates and coccolithophores were more abundant in the eastern stations. These trends coincided with a decrease in water column chl *a* and primary production and an increase of phytoplankton diversity towards the east, in agreement with the more oligotrophic character of the Eastern Mediterranean (EM). In consonance with the generally oligotrophic character of the Mediterranean, the proportion of prokaryotic and eukaryotic picoplankton with respect to total phytoplankton biomass exceeds often 50% (Siokou-Frangou et al. 2010). Picoplankton maxima tend to occur in summer, when temperature is highest and nutrient availability tends to be lowest, although there is substantial spatio-temporal variability (Agawin et al. 1998; Bernardi Aubry et al. 2006; Arin et al. 2002). Superimposed on the picoplankton component, micro and nanoplankton may dominate at particular times of the year or in areas of strong hydrodynamic activity. Margalef (1978) considered the input of external energy, in the form of water convection and

turbulence, and nutrient availability were the main selective factors of the dominant life-forms of phytoplankton, as represented by major taxonomic groups. He proposed a conceptual model, later called the “phytoplankton mandala”, which ordained diatoms, coccolithophores and dinoflagellates along a sequence reflecting the ecological succession of phytoplankton following a fertilization event such as the seasonal mixing of the water column. Diatoms, which grow rapidly in nutrient-rich, turbulent conditions, are the typical dominants in the winter-spring bloom in coastal areas and in deep mixing zones such as the central area of the Ligurian Sea (Estrada et al. 1985; Marty et al. 2002; Siokou-Frangou et al. 2010), but they may also proliferate and form high chl *a* patches within the DCM (Estrada 1985, 1999; Crombet et al. 2011). Dinoflagellates, which may show migratory behaviour and encompass a wide variety of physiological strategies, become relatively more abundant in the nutrient-depleted upper water layers during the stratification period, while coccolithophorids tend to occupy an intermediate position with respect to trophic conditions. Margalef (1978) distinguished a subgroup of red tide dinoflagellates, which would be favoured by situations of high stability and nutrient availability. Later works have proposed modifications or expansions of the mandala (Smayda and Reynolds 2001; Cullen et al. 2002). The relationship of other taxonomic groups with environmental conditions is less known, particularly for nano- and picoplanktonic flagellates, although the situation is rapidly changing with the expansion of the use of chemotaxonomic and molecular techniques (Latasa et al. 2010; Charles et al. 2005).

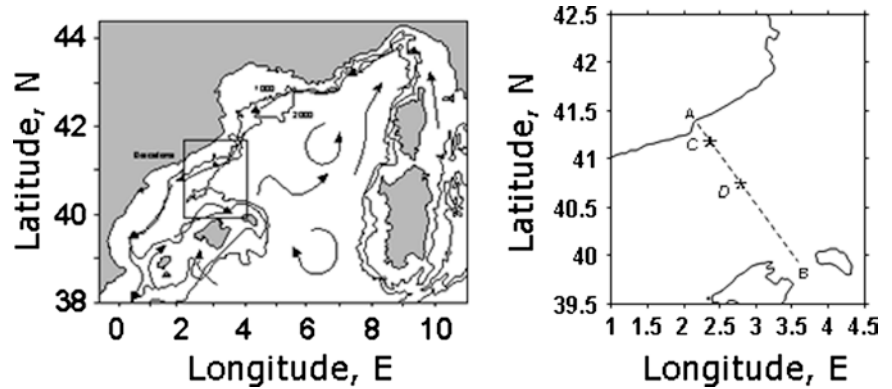
### The Seasonal Succession of Phytoplankton

The seasonal succession of phytoplankton has been investigated in numerous coastal locations of the Mediterranean, but just a small number of them has been followed regularly during more than a few years. In offshore waters, only the DYFAMED station in the Ligurian Sea (Marty et al. 2002) has been studied for more than a decade (Siokou-Frangou et al. 2010), although in some open water regions, the repetition of cruises in different seasons over different years has provided a general picture of the seasonal phytoplankton variability. A case-study for the Catalan Sea (Estrada 1999) will be described below.

Using a pigment chemotaxonomic approach, Marty et al. (2002) reported that the eukaryotic biomass at the DYFAMED site was dominated by prymnesiophytes (containing 19'-hexanoyloxyfuxcoxanthin) except during a short period of diatom dominance (inferred from fucoxanthin), from January to March, generally associated with the period of maximal chl *a* except on some occasions in which it was related to nanoflagellates. The diatom peak

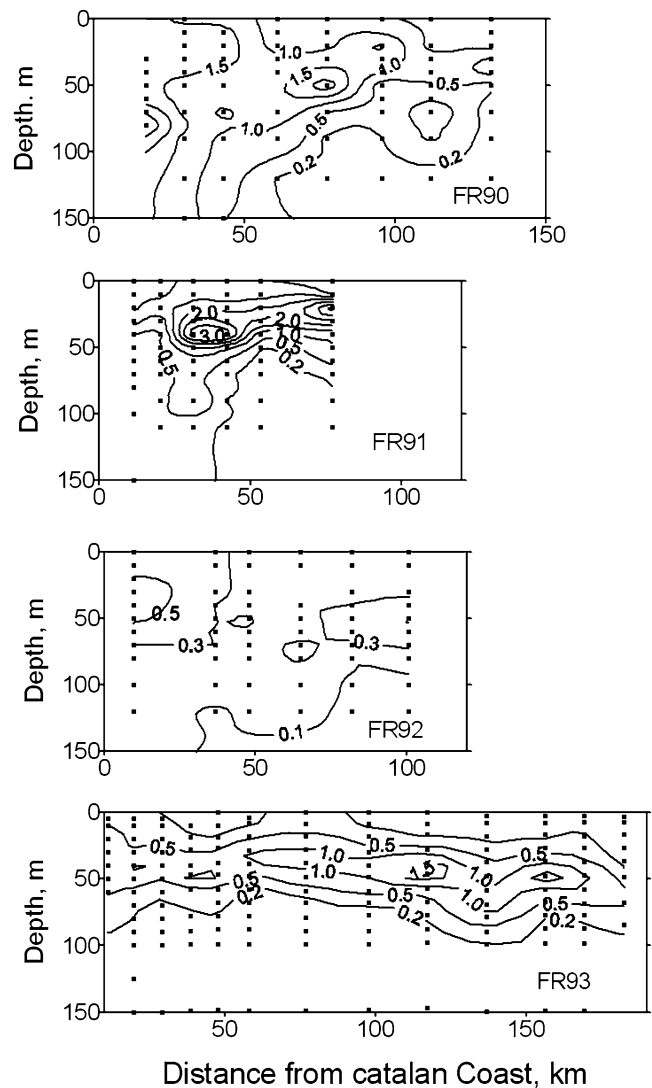


**Fig. 6.1** (Left) Scheme of the circulation in the NW Mediterranean. (Right) Position of the shelf (C) and central divergence (D) stations mentioned in section “Microbial and classical food webs. The example of the Catalan Sea”. The line indicates the situation of the “main transect”



was followed about 1–2 month later by prymnesiophytes and chrysophytes/pelagophytes (these latter, indicated by 19’butanoyloxyfuxcoxanthin). The maximum contribution of prokaryotes, mainly represented by *Synechococcus*, occurred between August and November; prochlorophytes reached their peak abundance at the end of the stratification period, but persisted during the winter. The presence of cryptophytes (alloxanthin) coincided with that of diatoms, and the peridinin (a dinoflagellate marker) maximum occurred in parallel or slightly later than that of prymnesiophytes and chrysophytes/pelagophytes.

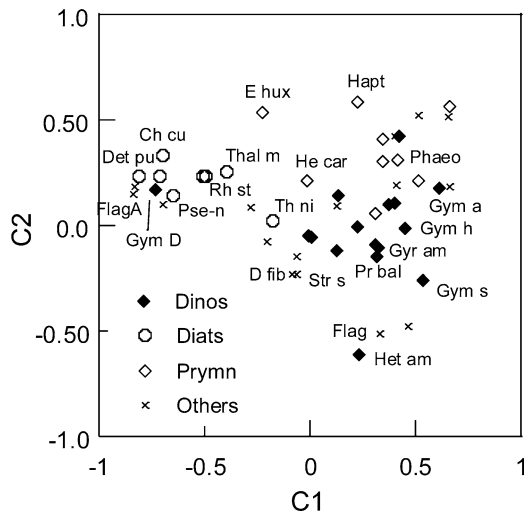
The seasonal variability of phytoplankton composition in the Catalan Sea was described by Estrada (1999), based on data from the cruises FRONTS 90 (FR90, 9–16 February 1990), FRONTS 91 (FR91, 10–21 April 1991), FRONTS 92 (FR92, 15 October–4 November 1992) and VARIMED 93 Phase 2 (FR93, 1–8 June 1993). Studies concerning biological distributions in these cruises can be found in Alcaraz et al. (1994), Margalef (1995), Calbet et al. (1996), Estrada (1996) and Estrada et al. (1999). The surveys visited a variable number of stations within the Catalan Sea, but the phytoplankton data considered here will be those of the transect between Barcelona and the Balearic Islands (“main transect”), which was occupied in all the cruises (Fig. 6.1). The phytoplankton was examined by R. Margalef using the inverted microscope technique, after sedimentation of 100 ml of water in composite chambers. The distribution of physico-chemical variables (data not shown) and chl *a* (Fig. 6.2) along the principal transect featured the characteristic central zone of elevation of the isopycnals, limited in the continental side by the Catalan Front and by the Balearic front in the Balearic Islands side. During FR90, the water column inshore of the Catalan Front was well mixed, but there was already appreciable stratification offshore, with a DCM at 50 m depth. The Catalan Front was also well marked during April 1991 (FR91), but in late spring (FR93) the whole transect was covered by a layer of warm water and featured a well-developed DCM (Fig. 6.2). In the fall (FR92), there was still an appreciable stratification of the upper layers, but the surface waters had been cooling and



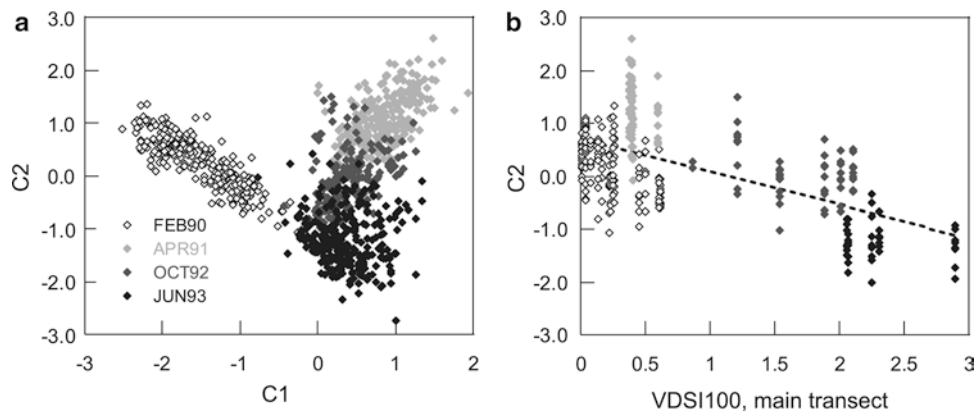
**Fig. 6.2** Cruises FR90, FR91, FR92 and FR93. Distribution of chlorophyll *a* ( $\text{mg C m}^{-3}$ ) along the main transect of Fig. 6.1

the pycnocline had started to erode. A principal component analysis was carried out with the log-transformed abundance data of 49 phytoplankton taxa that occurred in all the cruises and that were present, at least, in 15 % of the

samples. The three first principal components explained 36.1 % of the variance, within the range usually found in this kind of studies. As can be seen in Fig. 6.3, which presents the distribution of the species in the statistical space of the components, the taxa tended to group together according to taxonomic affinities, reflecting a similarity in the ecological response of phylogenetically-related organisms.



**Fig. 6.3** Position of the extremes of the taxa vectors in the space of the first (C1) and second (C2) principal components. Legend: Dinosaurs, Dinoflagellates; Gym a, *Gymnodinium acutissimum*; Gym h, *Gymnodinium hamulus*; Gym s, *Gymnodinium* sp.; Gym D, *Gymnodinium* sp D; Gyr am, *Gyrodinium acutum* “small”; Het am, *Heterocapsa* sp.; Pr balt, *Prorocentrum balticum*; Diats, Diatoms; Ch cu, *Chaetoceros curvisetus*; Det pu, *Detonula pumila*; Pse-n, *Pseudo-nitzschia* spp.; Th ni, *Thalassionema nitzschioides*; Thal m, *Thalassiosira* spp.; Prymn, Prymnesiophytes; E hux, *Emiliana huxleyi*; He car, *Helicosphaera carteri*; Hapt., Unidentified haptophytes; Phaeo, *Phaeocystis* sp.; Others, Other groups; D fib, *Dictyocha fibula*; Flag, Unidentified flagellates; FlagA, Unidentified flagellate A; Str s, *Strombidium* sp. (ciliate)



**Fig. 6.4** (a) Distribution of the points corresponding to the samples of the four cruises in the space of the first (C1) and second (C2) principal components. Cruises, FEB90=FR90 (February 1990), APR91=FR91 (April 1991), OCT92=FR92 (October–November 1992), JUN93=FR93 (June 1993). (b) Relationship between the values of the C2 and a vertical

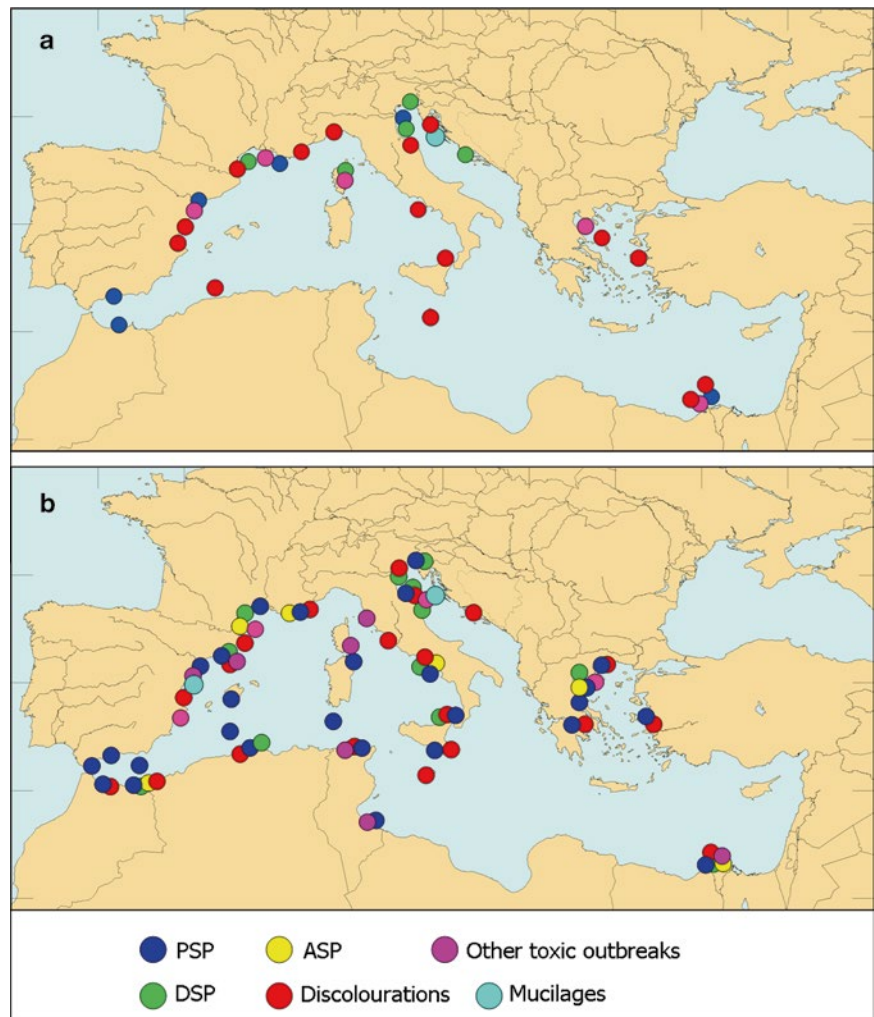
Most diatoms, including *Detonula pumila* and species of *Chaetoceros*, *Pseudo-nitzschia* and *Thalassiosira*, showed negative correlations (or loadings) with principal component 1 (PC1) while dinoflagellates and coccolithophores presented positive correlations. In turn, PC2 was positively correlated with the diatoms, the cryptophyte *Rhodomonas* sp., the coccolithophores, *Phaeocystis* sp. and other non-calcifying prymnesiophytes, and negatively correlated with the silicoflagellate *Dictyocha fibula* and with most dinoflagellates, represented mainly by species of *Heterocapsa*, *Amphidinium*, *Gymnodinium* and *Prorocentrum*. PC3, which was positively correlated with most taxa, reflected the distribution of total cell abundance (data not shown). The position of the sample points in the space of PC1 and PC2 showed a marked division between the samples of FR90 in the negative side of PC1, reflecting the dominance of winter bloom diatoms inshore of the Catalan Front during this cruise, and the samples from the other seasons, grouped in the positive side of PC1 (Fig. 6.4a). With respect to PC2, the sequence FR91–FR92–FR93 (spring, fall, late spring) from the positive to the negative side, can be related to the increasing stratification from FR91 to FR92 and FR93 (Fig. 6.4b). The shift of prymnesiophytes to dinoflagellates from the positive to the negative side of the correlations with PC2 can be interpreted in terms of Margalef’s mandala, as reflecting a successional sequence of better adaptation to decreased turbulence.

In coastal and estuarine areas, seasonal cycles vary depending on local factors, as found by Cloern and Jassby (2010) for data sets from around the world. A winter phytoplankton bloom or at least an increase of biomass, allowed by stable meteorological conditions or stratification of the water column is a common feature in Mediterranean phytoplankton communities (Margalef 1969; Duarte et al. 1999; Bernardi Aubry et al. 2004; Ninčević Gladan et al. 2010).

stratification index, VSI100, calculated as the sum of the absolute values of the differences in water density every 10 m, for a water column between 0 and 100 m depth:

$$VSI100 = \sum_{i=1}^{10} |(\sigma_t(i*10) - \sigma_t((i-1)*10))|, \text{ where } i=1, 2, \dots, 10$$

**Fig. 6.5** Harmful events along Mediterranean coasts (excluding those attributed to *Ostreopsis*). Based on (a) reports up to 1995 (Jacques and Sournia 1978–1979; Honsell et al. 1995) and (b) updated findings (Reproduced from Zingone 2010)



Often, there is also a fall peak, that has been related to higher nutrient availability due to erosion of the thermocline (Margalef 1969) or to stable weather conditions, which allow the exploitation of nutrients of coastal origin (Zingone et al. 2003; Mura et al. 1996). Several zones present peaks driven by nutrient runoff at times like late spring or summer (Bernardi Aubry et al. 2004; Ribera d'Alcalà et al. 2004). In the Gulf of Trieste (Northern Adriatic), during the period 1989–2002, the autumn peak of phytoplankton biomass was the highest one on the annual scale and was related to enhanced freshwater inputs (Mozetič et al. 2012)

### Harmful Algal Blooms in the Mediterranean

Phytoplankton blooms are part of plankton ecosystem dynamics. However, on occasions, microalgal proliferations may be perceived as detrimental due to the production of high accumulations of biomass or of toxicity that can affect other ecosystem organisms or human health. In this case, proliferations are referred to as “harmful Algal Blooms”

(HABs), although it must be taken into account that this is a purely operational designation without any objective ecological meaning. As can be gleaned from Margalef’s mandala, the occurrence of phytoplankton blooms, whether harmful or not, will be favoured by nutrient enrichment, which may enhance phytoplankton growth and low turbulence (or high water residence times), which reduce cell dispersion; another factor may be a reduction of grazing pressure. Until the mid 1980s, HABs, then generally referred to as “red tides”, had been rarely recorded in the Mediterranean and no significant toxic episodes were known (Jacques and Sournia 1978–1979). The first contamination of shellfish by Paralytic Shellfish Poisoning (PSP) toxins, due to *Gymnodinium catenatum*, occurred in 1987 in Southern Spain (Bravo et al. 1990). Since then, HABs have been detected throughout the Mediterranean (Fig. 6.5). The most widespread PSP-producers in the region are *Alexandrium minutum* (Garcés and Camp 2012), and *Alexandrium catenella*, which seems to have increased its geographic distribution on recent years (Vila et al. 2001b; Collos et al. 2009); *G. catenatum* continues to be present, but appears to

be restricted to the SW Mediterranean, including open waters of the Alboran Sea (Calbet et al. 2002). Diarrhetic Shellfish Poisoning (DSP) cases due to species of *Dinophysis* have been reported since the 1980s (Boni et al. 1993; France and Mozetič 2006) and are an important concern for bivalve aquaculture exploitations. Among diatoms, some species of *Pseudo-nitzschia* present in the Mediterranean (Amzil et al. 2001; Quijano-Scheggia et al. 2010) may produce domoic acid, a neurotoxin that has caused Amnesic Shellfish Poisoning events worldwide. Non-toxic species responsible for high biomass blooms include *Noctiluca scintillans* (López and Arté 1971; Fonda Umami 1996) and *Alexandrium taylori*. This last species produces localized brown discolorations that deteriorate the recreational value of some Mediterranean beaches (Giacobbe et al. 2007). In the last decade, reports of fever, respiratory problems and skin irritations in humans have been attributed to proliferations of *Ostreopsis ovata* and *O. cf. siamensis* (Mangialajo et al. 2011), two species of a benthic –epiphytic genus reported in the Mediterranean since the 1970s, which has shown an apparent range expansion in the last years (Zingone 2010). The recent detection in the Mediterranean of *Gambierdiscus* sp., another toxic benthic dinoflagellate, typical of tropical regions has been linked to suggestions of “tropicalization” of the Mediterranean (Aligizaki et al. 2008).

It is difficult to ascertain how much of the HAB increase is due to better study and monitoring and how much of it reflects a real trend (Garcés and Camp 2012). Eutrophication could be a potential factor in some areas. During part of the twentieth century, the increment of nitrate and phosphate discharges in coastal waters may have driven increases of chl *a* concentrations (Šolić et al. 1997) and high biomass blooms in some coastal zones but, after about 1990, the reduction of nutrient sources (for example, of phosphate from detergents), the expansion of wastewater treatment and, in some cases, the decrease of river discharges, reversed the eutrophication trend in many locations (Garcés and Camp 2012; Mozetič et al. 2010) but not in others (Wyatt 2010; Polat 2010). Often, however, there is no clear relationship between high biomass or toxic blooms and eutrophication (Zingone 2010). In the Northern Adriatic, for example, the absence of red tides since the late 1980s has been associated to a decrease in nutrient availability, but other changes such as the return of mucilage or “mare sporco” events, apparently not related to eutrophication (see section “Long-term temporal variability”), point out to hydrological and ecological changes that could be related to large-scale climate drivers (Conversi et al. 2010). In the Thau Lagoon, the increment of temperature and the reduction of phosphate loads resulted in a decrease of phytoplankton biomass but increased the abundance of *Synechococcus* and promoted the development of the toxic *Alexandrium minutum*, which apparently preyed on the cyanobacteria (Collos et al. 2009). Other anthropogenic factors affecting the occurrence of

HABs in the Mediterranean are the human spreading of noxious species and the building of coastal infrastructures (Garcés and Camp 2012). While increasing transfers of ballast water and shellfish stocks may have been responsible for some introductions of species into new regions, the increment of the number or size of confined water bodies suitable for HAB development due to constructions in the coastline may have been the most significant cause of HAB increase in areas like the Catalan Coast (Garcés et al. 2000).

### Long-Term Temporal Variability

In a context of global change, the collection of long time series of physico-chemical and biological ecosystem data with adequate resolution is a necessary tool to uncover temporal patterns of variability and to detect signatures of long-term trends. The availability and characteristics of biological time series in the Mediterranean were examined in CIESM Workshops held in 2003 (CIESM 2003) in Split (Croatia) and in 2009 (CIESM 2010) in Tunis. A special issue of Estuaries and Coasts (Zingone et al. 2010a) with papers arising from the AGU-Chapman Conference carried out in 2007, in Rovinj (Croatia), contained research results and comparative information concerning several Mediterranean phytoplankton time series. As noted in the executive summary of CIESM (2003), there are more non-biological than biological Mediterranean time series and, among the later, the frequency decreased from higher to lower trophic levels. A list with information on some ongoing Mediterranean time series sites measuring microbial plankton variables is presented in Table 6.1. In addition, water quality parameters and plankton composition are being sampled at many littoral locations (not included in the table) as part of monitoring requirements (Le Bec et al. 1996; Goberville et al. 2010; Vila et al. 2001a).

Corresponding to the interannual and seasonal patterns in forcing variables, the available Mediterranean time series exhibit strong interannual and within-year variability. Ascertaining long-term signals that could be caused by climate change is difficult due to strong interannual fluctuations and the relatively short length of the available series. However, some consistent trends have been reported. For example, Marty et al. (2002) attributed an increase of pico- and nanoplankton biomass during the period 1990–1999, at the DYFAMED station, to a lengthening of the stratification period. A latter work (Marty and Chiavérini 2010) confirmed an increment of chl *a* biomass between 1995 and 2006, but the responsible organisms for the most recent years were mainly diatoms, rather than flagellates. Marty and Chiavérini (2010) related the strong winter-spring bloom of 2006 to the enhanced introduction of nutrients to the surface waters caused by the intense deep water convection of the winter

**Table 6.1** Information on some ongoing long time series in estuarine, coastal and open waters of the Mediterranean sea

Location	Variables sampled (non-exhaustive list)	Approximate starting date	Representative publications
NW Mediterranean, DYFAMED site (43° 25' N, 7° 52' E)	Hydrography, nutrients, phytoplankton pigments	1991	Marty (2002), Marty et al. (2002), and Marty and Chiavérini (2010)
Northern Adriatic Sea, Italy/Slovenia/Croatia (several sites)	Hydrography, nutrients, chlorophyll <i>a</i> , phytoplankton	1970–1999, (gaps)	Bernardi Aubry et al. (2004), Viličić et al. (2009), and Mozetič et al. (2010)
Mid-Adriatic Sea, Croatia Kaštela Bay (43° 31' N, 16° 22' E), Offshore station (43° 00' N, 16° 20' E)	Hydrography, nutrients, bacterioplankton, chlorophyll <i>a</i> , primary production (PP), phytoplankton (Phyto), zooplankton	1950s (Phyto) 1962 (PP) 1960s–1980s (other variables)	Šolić et al. (1997), Marasović et al. (2005), and Ninčević Gladan et al. (2010)
Tyrrhenian, Gulf of Naples, Italy (40° 48.5' N 14° 15' E)	Hydrography, nutrients, phytoplankton, zooplankton	1984	Ribera d'Alcalà et al. (2004) and Zingone et al. (2010a, b)
NW Mediterranean, Blanes Bay (41.67° N, 2.80° E)	Hydrography, nutrients, Bacterioplankton (B), chlorophyll <i>a</i> (Chl <i>a</i> ), primary production (PP), phytoplankton (Phyto),	1992 (Chl <i>a</i> ) 1998 (B, PP, Phyto)	Duarte et al. (1999), Galand et al. (2010), and Gasol (2007)
NW Mediterranean, Thau Lagoon, France (43° 24' N – 3° 36' E)	Hydrography, nutrients, phytoplankton >5 μm (Phyto), picophytoplankton (Pico)	1971 1987 (Phyto) 1991 (Pico)	Collos et al. (2009)
NW Mediterranean, Point B, Villefrance-sur-mer, France (43° 41' N, 07° 19' E)	Hydrography, nutrients, zooplankton	1974 (with gaps) 1995	García-Comas et al. (2011)
NW Mediterranean, els Alfacs Bay (Ebre Delta), Spain	Hydrography, chlorophyll <i>a</i> , phytoplankton	1990	Llebot et al. (2011) and Fernández-Tejedor et al. (2010)
Eastern Mediterranean, Aegean Sea, Saronikos Gulf, Greece	Hydrography, nutrients, chlorophyll <i>a</i> , zooplankton	1989	Christou 1998
NW Mediterranean, Balears transect, Mallorca, Spain (39.48° N, 39.40° N, 39.34° N, all at 2.43° E)	Hydrography, nutrients, chlorophyll <i>a</i> , zooplankton	1993	Fernández de Puelles et al. (2007) and Fernández de Puelles and Molinero (2008)

2005/2006, and associated the greater intensity of recent convection events to drought episodes decreasing the input of freshwater to the NW Mediterranean. In the Gulf of Naples, Zingone et al. 2010b related a negative trend in phytoplankton biomass with meteorological changes causing a decrease in water column stability, while Tunin-Ley et al. (2009) reported that some likely stenothermic *Ceratium* species had disappeared from the surface layers in response to water warming. As described in section “Harmful algal blooms in the Mediterranean”, the decrease in phytoplankton abundance and biomass found in the Adriatic Sea over the last 20 years (Mozetič et al. 2010) has been related to a reduction of nutrient loads and to a lower river outflow, reflected in positive anomalies of the surface salinity. The changes in the Northern Adriatic encompassed also higher trophic levels (mesozooplankton and gelatinous plankton). The proposed scenario (shift in trophic control and identification of drivers) is presented in Mozetič et al. (2012). Variations in river discharge have also produced shifts in the appearance of the phytoplankton maximum (Viličić et al. 2009; Mozetič et al. 2010). In contrast to the Northern Adriatic, Ninčević Gladan et al. (2010) did not find modifications in the timing of the winter and spring phytoplankton maxima of a 30 year phytoplankton series in Kaštela Bay

(Middle Adriatic), but reported an increase of phytoplankton abundance, in particular of dinoflagellates, from the mid-1980s to the 1990s, coinciding with years of high North Atlantic Oscillation (NAO) index and with a large scale change in the Northern Hemisphere (Conversi et al. 2010). These authors found that the relationship between chl *a* and primary production with the NAO index varied in different seasons, reflecting the NAO influence on local weather factors (such as temperature, winds and precipitation).

## Viruses and Heterotrophic Microbes

### Viruses

Studies on viruses in open and coastal waters of the Mediterranean Sea are still scarce. To date most of Mediterranean works have addressed the viral effects on bacterial biomass and production rather than the characterization of the viral community. Several publications (Table 6.2) reveal that viral abundances in the surface of coastal waters vary from  $0.3 \times 10^7$  to  $3.9 \times 10^7$  viruses mL<sup>-1</sup>, while lower values occur in off-shore surface waters ( $0.02 \times 10^7$  to  $2.5 \times 10^7$  viruses mL<sup>-1</sup>) and still lower ones in

**Table 6.2** Site, sampling data depths and variables measured and source of the studies considered in this review

Location	Date	Depth (m)	N	Variables	References
NW Mediterranean	September 2001	4 (coastal)	25	BA, VA, VBM, VBR	Bettarel et al. (2002)
	May 2005–April 2007	5 (coastal)	24	Chl <i>a</i> BA, VA, VBM, VBR	Boras et al. (2009)
	June 1995	5–200	42	Chl <i>a</i> BA, VA, VBM, VBR	Guixa -Boixereu et al. (1999a, b)
	June 1999	5–200	10	BA, VA, VBM, VBR	Weinbauer et al. (2003)
Alboran Sea	October and November 2004	1–200	6	BA, VA, BP, VBR	Magagnini et al. (2007)
W Mediterranean	October and November 2004	1–200	16	BA, VA, BP, VBR	Magagnini et al. (2007)
	June–July 2008	1–200	16	BA, VA, BP, VBR	Christaki et al. (2011)
Thyrranean Sea	October and November 2004	1–200	11	BA, VA, BP, VBR	Magagnini et al. (2007)
Sicily channel	October and November 2004	1–200	15	BA, VA, BP, VBR	Magagnini et al. (2007)
Adriatic Sea	May 1991–November 1992	0.5 (coastal)	5	Chl <i>a</i> BA, VA, VBR	Weinbauer et al. (1993)
	January–February 2001	1–200	2	BA, VA, BP, VBR	Corinaldesi et al. (2003)
	April–May 2003	0.5 (coastal)	1	BA, VA, BP, VBR	Bongiorni et al. (2005)
Ionian Sea	October and November 2004	1–200	19	BA, VA, BP, VBR	Magagnini et al. (2007)
	June–July 2008	1–200	17	BA, VA, BP, VBR	Christaki et al. (2011)
Levantine basin	June–July 2008	1–200	17	BA, VA, BP, VBR	Christaki et al. (2011)

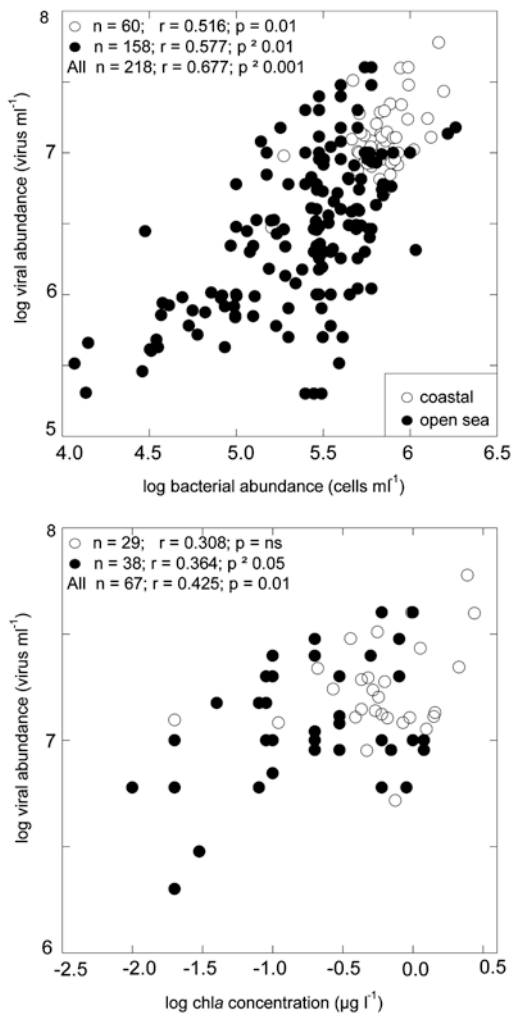
*Chl a* chlorophyll *a* concentration, *BA* bacterial abundance, *VA* Viral abundance, *BP* bacterial production, *VBR* ratio of viral abundance respect to bacterial abundance, *VBM* viral mortality on bacteria, *N* number of data corresponding to viral abundance

deep waters (Magagnini et al. 2007). In the Mediterranean, as elsewhere, viral abundances increase from oligotrophic to more eutrophic areas. This means from coastal to open sea waters, and from the western to the eastern basin (Siokou-Frangou et al. 2010; Christaki et al. 2011).

Existing data (Table 6.2) show that bacterial and viral abundance are more coupled with chl *a* in open than in coastal waters (Fig. 6.6a, b). Furthermore, correlations between bacterial and viral abundance are higher ( $n=218$ ,  $r=0.677$ ,  $p<0.001$ ) than between virus abundance and chl *a* concentration ( $n=67$ ,  $r=0.425$ ,  $p<0.01$ ). This suggests that bacteria are more probable virus hosts than phytoplankton. The virus to bacteria ratio (VBR) varied between 7 and 69 ( $20\pm 11$ ) inshore and between 1 and 93 ( $19\pm 20$ ) in the upper 200 m of the open sea. Similar values of virus abundances and VBR could be found in other marine systems with comparable levels of fertility (Weinbauer 2004). The strong variability of the VBR may be due to factors such as (1) viruses may belong to different types of hosts, and or (2) viruses are in different phases of infection, increasing or decreasing in the water column as a consequence of their release from or their entrance into host cells at a particular sampling time. For instance, in the North Adriatic Sea an increase of VBR covaried with an increase of released viruses per cell (burst size) (Weinbauer et al. 1993), while the opposite relationship was observed by Bongiorni et al. (2005). Furthermore, based on data from Table 6.2, bacterial production (BP) increased from oligotrophic to eutrophic waters, and was positively and significantly correlated with viral ( $n=97$ ,  $r=0.556$ ,  $p<0.05$ ) and bacterial abundances ( $n=97$ ,  $r=0.698$ ,  $p<0.01$ ). Weinbauer et al. (1993) found a similar trend in the Adriatic Sea.

Along a gradient from eutrophy to oligotrophy in the Adriatic Sea, viral infection, estimated from viral lysis production, affected from 40 to 1.3 % of bacteria (Bongiorni et al. 2005). In the same study, burst size increased with the productivity of the system. The few available data indicate that lysogenic infection is lower than could be expected for the oligotrophic Mediterranean conditions. Reported values oscillate between 2 and 14 % of the total active bacteria (Bongiorni et al. 2005). Viral infection in open and coastal waters of the NW Mediterranean accounted for less than 20 % of the total bacterial mortality, suggesting that grazing by protists was the dominant pathway of bacterial losses (Guixa-Boixereu et al. 1999a, b; Bettarel et al. 2002). However, viral activity can occasionally prevail over grazing by HNF, for example in coastal waters with high bacterial abundances (Weinbauer and Peduzzi 1995; Boras et al. 2009).

Using enriched cultures, Alonso et al. (2002) isolated and characterized 26 bacteriophages from the W Mediterranean Sea. Morphological studies revealed that most of them were included in two of the three tailed families (Siphonviridae, Myoviridae) of the Caudovirales order, while viruses belonging to the Podoviridae (the third family) were not observed. All bacteriophages had icosahedral heads. Based on protein patterns, phages were grouped in 11 classes. Sizes oscillated between 30 and >100 nm (Weinbauer and Peduzzi 1994; Alonso et al. 2002) and it was observed that bacteria with different morphotypes hosted viruses with different sizes. Thus, viruses between 30 and 60 nm were mainly infecting rods (74 %) and spirillae bacteria (100 %), while viruses sized between 60 and 110 nm were found inside of cocci (65.5 %).



**Fig. 6.6** Relationships between (a) bacterial and viral abundances, and (b) chlorophyll *a* concentration and viral abundance for coastal and open sea Mediterranean waters

In studies carried out in the Gulf of Naples, Zingone et al. (1999, 2006) found a highly dynamic seasonal fluctuation between the abundance of the picoeukaryote *Micromonas pusilla* and that of the viruses infecting it. Although changes of *M. pusilla* concentrations could be influenced by viral infection, there was no evidence that viruses could terminate host blooms, and the decline of *M. pusilla* populations did not appear to be related to viral impact. *M. pusilla* virus strains sampled on different dates showed distinct molecular characteristics, indicating that viral diversity for a single host can be very high. Zingone et al. (2006) isolated two different viruses (MpVN1 and MpVN2) infecting *M. pusilla*. Both viruses had similar sizes (100–130 nm) and icosahedral shape, but MpVN1 attached to the host with a tail of about 0.2 µm that was absent in MpVN2. The infectivity of these two viruses, tested in 11 *M. pusilla* isolates, showed no relationships with the geographic origin or the phylogenetic diversity of the host strains. A host strain cultured after recovery

became resistant to infection from the same virus. This observation indicates that acquired immunity could have important implications concerning susceptibility of host strains to infection and host-virus dynamics in the natural environment. A potential consequence is that viral infection could change host diversity, although there are not yet studies of this effect in the Mediterranean Sea.

## Heterotrophic Prokaryotes

Due to space limitations, this subsection will focus mainly on heterotrophic bacteria. However, it must be remembered that marine prokaryotes, including both bacteria and archaea, may present a rich variety of trophic strategies, including photoheterotrophy and chemolithotrophy. One of the firsts studies of bacterial distribution in the open Mediterranean, carried out in ultra-oligotrophic waters of the Levantine Sea (Zohary and Robarts 1992), showed that bacterial abundance at ( $3 \times 10^8$  cells L<sup>-1</sup>) was around the lower threshold of the world ocean (Cho and Azam 1990). It was suggested that some key factor like the availability of inorganic nutrients, in particular phosphorus, could limit bacterial production in the Mediterranean Sea, and several experimental approaches were implemented (revision of Siokou-Frangou et al. 2010, and references therein) to test the nutrient control of bacterial production. In a Lagrangian experiment in surface waters of the Levantine Sea, the addition of phosphate produced a surprising response: a decline in chl *a* concentration and a rise in bacterial production. It was hypothesized that while phytoplankton was concurrently nitrogen- and phosphorus- limited, bacterial growth was mainly phosphorus- limited (Thingstad et al. 2005; Pitta et al. 2005; Zohary et al. 2005). Nevertheless, while phosphorus is usually the limiting nutrient, nitrogen and carbon limitation or co-limitation also occurs, and the type of limitation can vary with slight changes in competition, nutrient concentrations and grazing pressure (Sala et al. 2002; Van Wambeke et al. 2002, 2009). As a result, large changes in abundance, production and proportions of particle-attached to free-living bacteria have been documented over time scales of only a few hours (Mével et al. 2008).

The identification of the existing bacterial phylotypes and their temporal succession is a necessary first step to understand their role in the functioning of the system. Fingerprinting techniques such as DGGE, TRFLP, SSCP or ARISA (see, Dorigo et al. 2005 for an overview of methodologies) have been used to compare bacterial communities and establish their scales of variability. However, although, we have advanced in the current knowledge of prokaryotic diversity, these molecular studies are still far from answering specific questions on the ecosystem functioning worldwide (see review, Höfle et al. 2008). Since the late 1990s, a number of

molecular studies carried out in the Mediterranean have improved our understanding of different aspects of bacterial community structure (Ghiglione et al. 2005; Coll et al. 2010, and references therein). The first microbial diversity studies from Mediterranean Sea microcosm experiments revealed an important variety of unknown microorganisms (Pukall et al. 1999) and allowed the unexpected detection of a high number of isolates that were phylogenetically close to *Sulfitobacter pontiacus*, a species only represented until then by two strains from the Black Sea (Sorokin 1995). Later, Schauer et al. (2000) were the first to provide a seasonal study of the bacterioplankton composition coastal sites of the NW Mediterranean, using the DGGE technique (denaturing gradient gel electrophoresis). They found marked seasonal changes of the bacterial assemblages and reported that spatial variability among some of the stations was consistent with different hydrographic conditions. In a new study determining the time-scale of changes in the dominant bacterial populations of Blanes Bay, Schauer et al. (2003) reported the taxonomic composition of the main bacterioplankton groups over time. Alonso-Saez et al. (2007) continued the work of Schauer et al. (2003) in the same station, and presented a comprehensive assessment of seasonal changes in bacterial diversity by means of different approaches (PCR-based and the direct CARD-FISH method).

In investigations realized by Acinas et al. (1997), community fingerprinting by 16S rDNA restriction analysis applied to Western Mediterranean offshore waters showed that the free-living pelagic bacterial cells were very different from those aggregated or attached to particles of more than about 8  $\mu\text{m}$ . Acinas et al. (1999) studied also free and attached assemblages from three depths (5, 50, and 400 m) by cloning and sequencing the 16S rDNA obtained from the same samples, and used scanning electron microscopy to detect morphological patterns. As expected, the sequences retrieved from free or attached assemblages were very different. The subsample of attached bacteria contained low diversity, with close relatives of a well-known marine species, *Alteromonas macleodii*, representing the vast majority of the clones at every depth. On the other hand, the free-living assemblage was highly diverse and varied with depth. At 400 m, close relatives of cultivated Proteobacteria predominated, but near the surface most clones were related to phylotypes of the SAR11 cluster of the Proteobacteria. Moesender et al. (2001) found that the composition of surface and deep-water free bacterial communities was highly complex and reported pronounced differences among the attached and free-living bacterial communities throughout the water column (10–1,200 m) of the open EM (Aegean Sea). All studies, whether based on PCR-based clone libraries, metagenomic studies or fluorescence *in situ* hybridization, concur to identify members of the SAR11 group as some of the most abundant Mediterranean bacteria, with

contributions of 25–45 % of the sequences (Zaballos et al. 2006; Alonso-Saez et al. 2007; Feingersch et al. 2010). These are commonly followed by other Alphaproteobacteria, such as the members of the Rhodobacteriaceae, particularly *Roseobacter*, which tend to be more common in coastal regions and during algal blooms. Apart of phototrophic Cyanobacteria (*Prochlorococcus* and *Synechococcus*), diverse culturable (Alteromonadales) and unculturable Gammaproteobacteria and Bacteroidetes represent the remaining bacterial diversity, with some differences with depth and distance to land. Rather similar community structures have been described at the Aloha station in the Pacific (Feingersch et al. 2010) and in surface waters of the Greenland Sea (Zaballos et al. 2006), although these latter authors found a larger share of Alteromonadales in the Ionian Sea, an observation that was not corroborated by Feingersch et al. (2010) in waters further East. Blümel et al. (2007) focused on the depth-specific distribution of Bacteroidetes in the EM, while García-Martínez and Rodríguez-Valera (2000) examined the microdiversity of the SAR11 and the Crenarchaeota group I in the WM. The number of studies addressing the distribution of Archaea in Mediterranean waters has increased substantially in the last decade, but the abundance patterns, diversity and metabolic activity of these prokaryotes are still poorly known. For example, Yakimov et al. (2009) found Mediterranean-specific archaeal ecotypes in bathypelagic waters, and Tamburini et al. (2009) in the Tyrrhenian, and De Corte et al. (2009) in the EM examined the depth distribution of bacteria and of different archaeal groups. Galand et al. (2010) found a strong seasonality of archaeal assemblages in Blanes Bay (NW Mediterranean), matching the variability of the environment and the rest of the planktonic community.

### Heterotrophic Pico- and Nanoflagellates

Colourless and pigmented eukaryotic pico- and nanoflagellates in open and coastal marine systems are mainly dominated by small cells (70–80 %  $<5 \mu\text{m}$ ) with total abundances between  $10^5$  and  $10^6$  cells  $\text{L}^{-1}$  (Zohary and Robarts 1992; Christaki et al. 1999, 2001) and  $10^5$ – $10^7$  cells  $\text{L}^{-1}$  (Massana 2011), respectively. For instance, in the Blanes Bay Microbial Observatory, along a time-series of 9 years, abundances of pigmented and colorless flagellates  $\leq 3 \mu\text{m}$  (called picoeukaryotes) averaged  $4.9 \times 10^6$  cells  $\text{L}^{-1}$  and  $9.4 \times 10^5$  cells  $\text{L}^{-1}$ , respectively. Both groups showed a clear seasonality, with phototrophic picoeukaryotes (PPE) being higher in winter, and heterotrophic picoeukaryotes (HPE) peaking in summer (Fig. 2 of Massana 2011). Picoeukaryotes accounted for the largest fraction of eukaryotes year-round: PPE explained on average 82 % of total pigmented cells and heterotrophic picoeukaryotes represented 83 % of total colourless cells. In



contrast, smaller eukaryotic cells ( $\leq 2 \mu\text{m}$ ) constituted a more variable and minor fraction of pigmented (PPE) and colourless (HPE) cells, respectively (Massana 2011). Similar picoeukaryote abundances were found in other sites (Jürgens and Massana 2008). The ubiquity and relative stability of the picoeukaryotes appears to be related to bottom-up forcing, including environmental constraints and resource availability, and top-down effects such as predation and viral infection, which may control the realized abundances. In general, it seems that microbial eukaryotes in oligotrophic systems are controlled by resources, while predation control is more common in productive systems (Gasol 1994). Both, bottom up and top-down control could operate on individuals and populations, so that intrinsic specific differences in resource acquisition and predation-viral susceptibility may affect the final observed trends (Saura et al. 2011).

Heterotrophic nanoflagellates  $\leq 5 \mu\text{m}$  are important bacterivores. For example, bacterivory consumed from 45 to 87 % of bacterial production in an east–west Mediterranean transect (Christaki et al. 2001). Large variability of bacterivory (<10–100 % consumption of bacterial production) was reported by Vaqué et al. (2001) for two different transects in the NW-Mediterranean Sea. These authors also showed that bacterivory was positively correlated with the abundance of bacteria with a high DNA content. A study in the Aegean Sea showed that mixotrophic nanoflagellates were relatively abundant (10–15 % of the stock). However, BP consumption by these protists was of the order of only 5 % (Christaki et al. 1999). A similar percentage of mixotrophic nanoflagellates was found in coastal waters (11–18 % of the NW Mediterranean Sea, but with a contribution of 50 % to the total grazing by flagellates (Unrein et al. 2007). This activity was relatively high throughout the year (35–65 %) and was negatively correlated with soluble reactive phosphorus concentrations, suggesting that mixotrophic flagellates would be using their phagotrophic capability when nutrients such as P were limiting (Unrein et al. 2007).

Reports on heterotrophic pico- and nanoflagellate diversity are scarce in the Mediterranean Sea (Review of Massana 2011 and references therein). For instance, Massana et al. (2004) constructed genetic libraries of picoeukaryotes from surface coastal picoplankton of Blanes Bay (NW Mediterranean Sea, 41°40'N, 2°48'E) and found that the best-represented phylogenetic groups were novel alveolates-I (36 % of clones), dinoflagellates (17 %), novel marine stramenopiles or MAST (10 %), prasinophytes (5 %) novel alveolates-II (5 %), and cryptophytes (4 %). In the Mediterranean-wide study of Marie et al. (2006) cited in section “The seasonal succession of phytoplankton”, the picoplankton displayed characteristics typical of oligotrophic oceanic areas with concentrations down to 1,000 cells  $\text{mL}^{-1}$  in the Eastern Basin. The most abundant eukaryotic sequences recovered by gradient gel electrophoresis

represented uncultivated heterotrophic marine groups: alveolates I (16 %) and II (26 %) and a newly discovered group (env Nansha, 17 %) that could be related to Acantharians. Prasinophyceae (photosynthetic green algae) accounted for 10 % of the sequences, whereas Cercozoa, Stramenopiles, Polycystinea, dinoflagellates and ciliates provided minor contributions.

## Ciliates

In the Mediterranean Sea, as anywhere in coastal and open marine environments, planktonic ciliates are dominated by the order Oligotrichida (Lynn and Small 2000). Within that order, the naked aloricate forms are the most important group (Margalef 1963; Travers 1973; Rassoulzadegan 1977, 1979; Vaqué et al. 1997). In one of the few studies dealing with the Mediterranean open waters, Dolan and Marrasé (1995) found that ciliate concentrations in the Catalan Sea averaged 230 cells  $\text{L}^{-1}$  at surface and about 850 cells  $\text{L}^{-1}$  at the DCM, with a total ciliate biomass of about 125  $\text{mg C m}^{-2}$  for the 0–80 m layer, and reported a significant correlation between heterotrophic ciliate abundance and the chl *a* concentration. Pérez et al. (2000) studied the daily vertical distribution of planktonic ciliates in open waters of the Ligurian Sea and found average abundances  $\sim 3.3 \times 10^3$  cells  $\text{L}^{-1}$ , with a maximum in May of  $\sim 10^4$  cells  $\text{L}^{-1}$ . These authors showed also that a portion of the heterotrophic ciliate population was able to migrate from 20 to 30 m depth during the day to the surface at night or in early morning and that ciliate abundance was positively correlated to zeaxanthin concentration, implying the possibility that ciliates concentrated around *Synechococcus maxima* and fed on them. Also in the open Ligurian Sea, Tanaka and Rassoulzadegan (2002) studied water column profiles and found that the abundance of ciliates, heterotrophic nanoflagellates and bacteria decreased by three, two and one order of magnitude over depth (5–2,000 m), respectively.

Since most of the primary production in the Mediterranean is due to nano- and picophytoplankton, one can expect that ciliates feed mainly on these size groups, as found in coastal and laboratory studies (i.e. Pierce and Turner 1992; Rassoulzadegan 1978; Sherr et al. 1986; Ferrier and Rassoulzadegan 1991; Christaki et al. 1999). Along a Mediterranean transect, Dolan et al. (1999) found changes in both ciliates and chl *a* concentration with a sevenfold W-to-E decline (2.8–0.4 and 0.48–0.07  $\text{mg C m}^{-3}$ , for ciliates and chl *a*, respectively), although the lower chl *a* concentrations (0.1  $\text{mg chl a m}^{-3}$ ) of the eastern basin stations corresponded to a relatively high stock of ciliates (0.5  $\text{mg C m}^{-3}$ , approx. 40  $\text{mg C m}^{-2}$ ). Pitta et al. (2001) reported a twofold decrease in ciliate concentration from west to east (26.9–11.2  $\times 10^6$  cells  $\text{m}^{-2}$  and

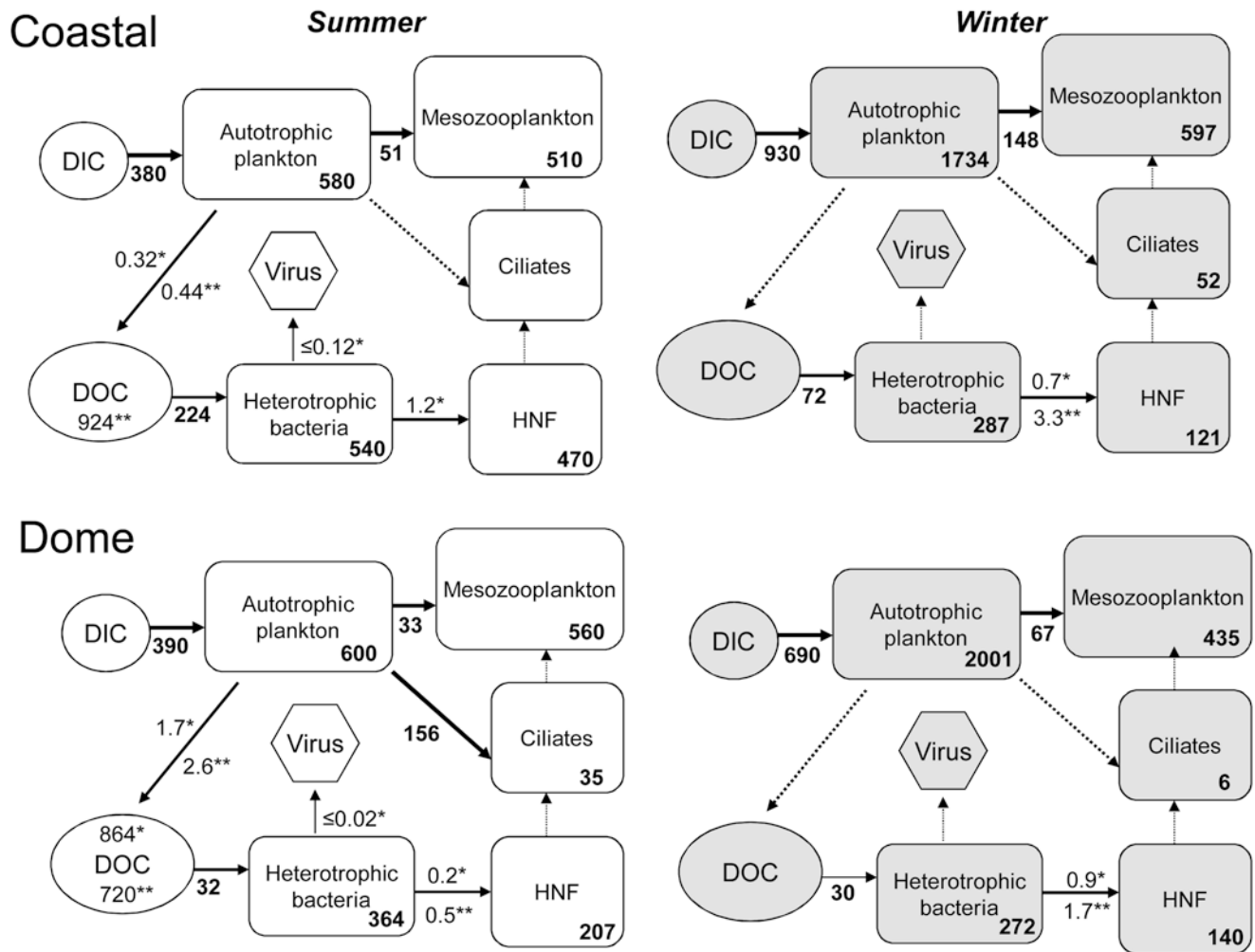
84.8–41.5 mg C m<sup>-2</sup>) in abundance and biomass, respectively. The relationship between ciliate abundance and chl *a* concentration (Dolan and Marrasé 1995; Pitta et al. 2001) was stronger in the west than in the east (Siokou-Frangou et al. 2010), suggesting a better coupling with the phytoplankton stock in the west. Dolan and Marrasé (1995) reported that ciliates could have a grazing impact reaching 50 % of the primary production in the Catalan Sea and Pitta et al. (2001) found similar values in stations of the WM. Pérez et al. (2000) showed that ciliates were able to consume between 8 and 40 % of a primary production varying between 11 and 5.5 mg C m<sup>-3</sup> day<sup>-1</sup> in the Ligurian Sea. The estimates of ciliate consumption of primary production reported in Dolan et al. (1999) were lower than those measured by Pitta et al. (2001), especially in the EM; however, both studies seemed to be in agreement regarding the increasing importance of ciliates as primary production consumers towards the east.

The taxonomic diversity patterns of ciliates have been investigated with regard to tintinnids. Although they represent only a small fraction of the ciliate community, generally <10 % of total cell numbers or biomass (Dolan and Marrasé 1995; Vaqué et al. 1997; Dolan 2000; Dolan et al. 2002), their distinctive morphology makes them ideal organisms for the study of changes in the structure of microzooplankton communities (Thompson et al. 1999; Dolan 2000). A west-to-east increasing gradient of tintinnid diversity in the Mediterranean Sea was positively related to the depth of the DCM and inversely related to the chl *a* concentration (Dolan 2000; Dolan et al. 2002). In contrast, Pitta et al. (2001) did not observe any obvious west–east trend in tintinnid diversity but noted a peak in species richness in central stations. The size-class diversity of potential phytoplankton prey was identified by Dolan et al. (2002) as a major mechanism influencing tintinnid richness, suggesting that tintinnid diversity reflects that of the resources rather than competitive interaction or predation. No clear relationship between tintinnid diversity, chl *a* concentration and water column stability was found by Cariou et al. (1999) in the NW Mediterranean, and recent studies confirmed that water column structure alone appeared to be a poor predictor of temporal changes in tintinnid diversity, supporting the view that it could be directly linked to characteristics of food resources (Dolan et al. 2006).

### Microbial and Classical Food Webs. The Example of the Catalan Sea

The general oligotrophy of the Mediterranean has been associated with a widespread dominance of small phytoplankton and the channelling of an important proportion of the carbon fluxes through the microbial food web (Siokou-Frangou et al. 2010). However, there is a large variability associated with the west to east gradient of oligotrophy and

with the intermittent occurrence of fertilization events linked to the seasonal cycle, mesoscale features or other processes. In agreement with the increasing oligotrophy towards the east, heterotrophic to autotrophic biomass ratios ranged in general from 0.5 to 3.0 in the WM (Christaki et al. 1996; Pedrós-Alió et al. 1999) and from 0.9 to 3.9 in the Aegean Sea (Siokou-Frangou et al. 2002, 2010). Phytoplankton production tends to be several times higher than bacterial production (Pedrós et al. 1999; Christaki et al. 2011), although the strong variability typical of metabolic rate estimates (Christaki et al. 2011) and differences in methodology make it difficult to compare values from different studies. The contribution of bacterioplankton in the open sea tends to be more important than near the coast, but there are exceptions (see below). For example Krstulović et al. (1995) report that BP amounted 9–28 % of PP in eutrophic Kaštela Bay and 10–40 % in an open sea station in the middle Adriatic. The dominance of picoplankton may be interrupted by proliferations of nano and microplankton, and activation of the classical or herbivorous food web, after nutrient enrichment events. These pulses of growth tend to be short-lived and difficult to sample, leading to a probable underestimation of their contribution. The intermittent dominance of the herbivorous pathway may occur also within the DCM layers, in particular where the chlorophyll maximum is relatively shallow, as happens in the central divergence of the NW Mediterranean (Estrada 1996). Some of these characteristics can be appreciated in Fig. 6.7, based in part on data from Pedrós-Alió et al. 1999, which represents major biomasses and fluxes of the microbial food web in two stations located on the shelf and in the central divergence of the NW Mediterranean (marked C and D in Fig. 6.1). As can be expected, phytoplankton biomass (PB) and production (PP) were higher during the winter phytoplankton bloom than during the summer stratification period. At the same time, bacterial biomass (BB) and production (BP) were lower in winter, specially on the shelf, contributing to the higher PB/BB and PP/BP ratios in winter. The flux of carbon to metazooplankton through the herbivorous food web was also greater in winter, although the metazooplankton biomass was similar during both seasons, presumably because metazooplankton had not yet experienced a substantial increase in response to the phytoplankton bloom. The standing stocks and C fluxes of the shelf and the divergence stations were fairly similar in winter, while a seasonal phytoplankton bloom was happening at both stations. In summer, BB did not change much from the coast to the open sea, while BP was higher on the shelf, probably in response to dissolved organic carbon inputs from land, while in contrast what could be expected for an open sea location. PB and PP were also similar in both stations, although diatom abundance and mesozooplankton ingestion rates were higher on the shelf. The summer enhancement of the classical food web activity in the central divergence can



**Fig. 6.7** Summary of microbial biomasses and fluxes in the planktonic ecosystem of the Catalan Sea, for two reference stations, one located on the shelf (*C* in Fig. 6.1) and another above the central divergence (*D* in Fig. 6.1). Boxes represent depth-integrated biomasses over 0 to 60–80 m (mg C m<sup>-2</sup>) and arrows indicate fluxes (\* and \*\*, surface and DCM values, respectively, in mg C m<sup>-3</sup> d<sup>-1</sup>; bold numbers refer to depth-integrated values in mg C m<sup>-2</sup> day<sup>-1</sup>). The summer figures are based on pooled data from cruises carried out in late spring of 1993, 1995 and 1996, and

the winter ones are taken from a cruise in March 1999. DOC concentrations are from Doval et al. (1995); phytoplankton and bacterial data from Pedrós-Alió et al. (1999), Morán and Estrada (2005), Vaqué et al. (2001) and Vaqué (unpublished data); ciliate predation rates were derived from Dolan and Marrasé (1995); mesozooplankton biomass was taken from Calbet et al. (1996, 2002), Saiz et al. (1999) and Alcaraz (unpublished data); predation rates were calculated from the gut content or from egg production rates assuming a gross growth efficiency of 40 %

be explained, as noted in section “Fertilization mechanisms in the Mediterranean”, because the shallow level of the nutricline in this zone facilitates the introduction of nutrients into relatively well-illuminated water layers (Estrada 1996). Siokou-Frangou et al. (2010) have highlighted the potential flexibility and efficiency of the planktonic food web in the Mediterranean Sea, characterized by a high diversity of trophic roles and with connections spanning a continuum between the microbial loop and the classical food web. These features may contribute to the maintenance of a higher heterotrophic biomass per unit of primary production and a more efficient energy transfer to the upper trophic levels in the Mediterranean and other oligotrophic seas, than in more eutrophic marine systems (Margalef 1986; Alcaraz et al. 1985).

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