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Primary Production in the Ligurian Sea

6.1. Annual cycle of phytoplankton biomass, production and community structure in the Ligurian Sea

6.1.1. Regional context of the area

The availability of earth-orbiting satellite sensors, coupled with past *in situ* observations, allowed the concept of oceanic “*biogeochemical provinces*” to be refined by oceanographers at the end of the 20th Century [LON 98, PLA 91, REY 19]. In the original division of the global ocean into provinces, Longhurst considered the Mediterranean Sea as a single subtropical oceanographic province, without any spatial subdivisions, but regional oceanographic and ecological characteristics were described [LON 98].

For the western Mediterranean Sea region, Morel and André [MOR 91a] performed the first spatiotemporal description of phytoplankton biomass and production from ocean-color satellite data, with images from the coastal zone color scanner (CZCS) experiment sensor and a spectral light–photosynthesis model ([MOR 91a], see textbox). This description, which included the Ligurian Sea, depicted several major seasonal features: the very low chlorophyll-*a* concentration in winter, the phytoplankton spring and fall blooms, and the low chlorophyll-*a* concentration in summer [MOR 91a]. These characteristics of the phytoplankton dynamics in the Ligurian Sea had been first described in the 1960s from transects across the area and related to some physical–biogeochemical processes

[GOS 61, GOS 63]. The MEDIPROD experiments in the 1960–1970s (mostly MEDIPROD I, II and III; [JAC 73]) and more recently the DeWEX experiment in 2012 allowed further (*in situ*) understanding and quantification of the plankton dynamics and biogeochemical budgets for the Northwest Mediterranean and over an annual cycle [CON 18].

Phytoplankton primary production (in gC m^{-2}) can be estimated with empirical or semi-analytical models applied to satellite observations (see the reviews from Babin *et al.* [BAB 15] and Behrenfeld and Falkowski [BEH 97]). The model developed by Morel [MOR 91b] is a “wavelength-resolved model” and corresponds to a light photosynthesis model applied to satellite observations. This type of model evaluates the daily primary production at each depth between the surface and the depth of the productive layer (e.g. 200 m), over the duration of the day and within the spectral limits of the photosynthetic domain (400 and 700 nm). The model, for a day and at a certain depth (z), can be described as follows:

$$PP(z) = P_{\max}^B \times \text{Chla}(z) \int_{t=0}^{24 \text{ h}} \int_{\lambda=400}^{700 \text{ nm}} f(E(z, t, \lambda), a_{ph}^*) d\lambda dt$$

where Chla (mg m^{-3}) is the chlorophyll-a concentration measured by satellite, P_{\max}^B ($\text{gC} [\text{mgChla}]^{-1} \text{h}^{-1}$) is the chlorophyll-normalized maximum rate of carbon fixation at saturating irradiance, E ($\text{mol photons m}^{-2} \text{s}^{-1}$) is the irradiance and a_{ph}^* ($\text{m}^2 \text{mg Chla}^{-1}$) is the chlorophyll-specific phytoplankton absorption coefficient. The function (f) within the integral describes the photosynthesis versus irradiance curve, which could be used to express the relationship between a_{ph}^* and the photosynthetically available radiation (i.e. $E(\lambda)$ integrated between 400 and 700 nm). Therefore, this type of model explicitly includes optical and photosynthetic processes, and can be adapted to different oceanic regions.

Box 6.1. Estimation of phytoplankton primary production using satellite observations

As a brief overview, in winter, deep convection processes reduce the residence time of phytoplankton cells in the surface layer, resulting in very low pigment levels in the central Northwest Mediterranean, in a region known as the “blue hole” [BAR 03]. The phytoplankton spring bloom could be considered as the “reverse figure of the winter pattern” [MOR 91a], with the phytoplankton able to consume the nutrients upwelled in winter as soon as the water column is more stable. In fact, the phytoplankton bloom development in this area is similar to the one described by Sverdrup [SVE 53], with the bloom onset occurring when the turbulent mixing in the upper ocean weakens [LAV 13, MAY 17a]. The low chlorophyll-*a* concentration in summer in the upper surface layer is due to the absence of nutrients in this layer. During this season, phytoplankton cells develop around the euphotic depth and close to the nutricline (nitra- or phosphacline,

[JAC 73]), forming a subsurface chlorophyll maximum (SCM, Figure 6.1). In the Ligurian Sea, light availability and nutrient concentrations are relatively high at the SCM depth, therefore, the SCM is also a subsurface biomass maximum (SBM, [BAR 19]). In early summer, the SBM is intense and located above the euphotic depth, while later in the season, the SBM deepens below the euphotic depth and tends to be less pronounced before shallowing in fall [BAR 19]. The seasonal depth distribution of the SBM is primarily driven by the light availability [BAR 19, MIG 14]. Finally, Morel and André [MOR 91a] and Mayot *et al.* [MAY 17a] suggested that the observed fall bloom was the result of a deepening of the mixed layer depth that spreads the top layer of the SBM and injects some nutrients into the surface layer.

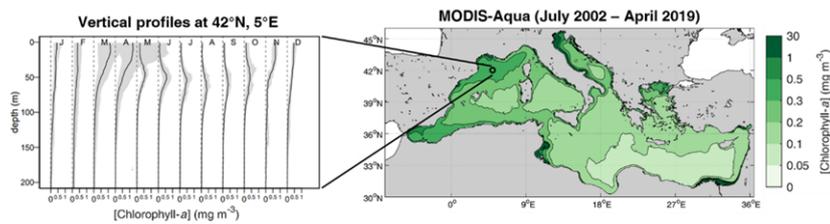


Figure 6.1. Climatologies of chlorophyll-*a* concentration. (Left) Monthly vertical profiles (black line: median value; grey zone: 10–90 percentile range) observed in the water column at the location 42°N, 5°E (modified from Lavigne *et al.* [LAV 15]). (Right) Surface chlorophyll-*a* concentration from the satellite sensor MODIS-Aqua (from NASA Ocean Biology Processing Group). For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip

Recurrent estimations of annual primary production cycles in the euphotic layer of the central Ligurian Sea were obtained at the DYFAMED sampling station [MAR 02a]. The seasonal cycle of primary production followed phytoplankton biomass, with estimates of depth-integrated (0–100 m) daily primary production rate varying between approximately 0.1 gC m⁻² d⁻¹ in winter and approximately 2 gC m⁻² d⁻¹ in summer. The estimates of annual primary production derived from the temporal integration of the daily estimates varied between 86 and 232 gC m⁻² yr⁻¹ [MAR 02a]. These *in situ* estimates are similar to the more recent values obtained from light–photosynthesis models applied to satellite ocean-color data (78–204 gC m⁻² yr⁻¹) [BOS 04, OLI 11, UIT 12].

These general ecological characteristics associated with the Northwest Mediterranean area are different from the rest of the Mediterranean basin. For example, Antoine *et al.* [ANT 95] used the same approach as Morel and André [MOR 91a] to demonstrate that phytoplankton biomass and production were two times higher in the Northwest Mediterranean area than in the Levantine Sea, confirmed later by other investigators [BOS 04, UIT 12]. D'Ortenzio and Ribera d'Alcalà [DOR 09] suggested that the dynamics of the open-ocean area of the Ligurian Sea were similar to the “*mid-latitude nutrient-limited spring production peak*” regime defined by Longhurst [LON 95]. Several studies confirmed the recurrent presence of this typical regime in the Ligurian Sea (e.g. [MAY 16]). Other biogeochemical (e.g. species distribution) and physical (e.g. hydrology and surface currents) characteristics are also well defined and homogeneous in this large area [AYA 18], which supports the idea that the Ligurian Sea, and more generally the Northwest Mediterranean area, is a key region in the Mediterranean Sea.

6.1.2. The diversity of phytoplankton species: the base of community ecology

Quantification of phytoplankton biomass and diversity was originally done by identifying and counting phytoplankton cells in samples collected with plankton nets or bottles. The total volume of phytoplankton cells was used as a proxy for the total phytoplankton biomass. In the early 20th Century, several researchers described and discussed the seasonal variation of phytoplankton species in various parts of the Ligurian Sea: Alexander Nathansohn, Jules Pavillard and Francis Bernard from samples collected around Monaco; Guy Léger from samples collected offshore in the Ligurian Sea; and Achille Forti, Michael Bernhard and Leopoldo Rampi focused on the Italian coast. The next sections provide an overview, instead of an exhaustive assessment, about the micro-, nano- and picophytoplankton species described in these early studies.

6.1.2.1. Micro-phytoplankton (20–200 μm)

Diatoms and dinoflagellates, well differentiated by their morphology and ecology, are the two taxonomic groups that dominate this size class. Diatoms have a rigid siliceous skeleton (frustule). Most diatom species bloom in waters with high nutrient concentrations, although some are able to develop

in more oligotrophic conditions. A substantial spring bloom of diatom cells generally induces the formation and sedimentation of large marine snow aggregates. Dinoflagellates with or without a rigid outer cell covering (or theca) can be autotrophs, as well as mixotrophs or heterotrophs. Dinoflagellate cells always have two flagella but can display very different shapes, from round to long armed. Some species are well known for producing toxins and inducing harmful algal blooms. Nevertheless, as diatoms, dinoflagellates are tracers of changes in the microplankton community.

During winter, the presence of the diatom species *Thalassiothrix frauenfeldii* (now *Thalassionema frauenfeldii*) was noted in the first half of the 20th Century [FOR 22, PAV 37, RAM 38] and was later confirmed, in 1998 and 1999, with observations from the Bay of Villefranche [GOM 03]. In spring, *Nitzschia seriata* was the common diatom species observed in the Ligurian Sea, both in coastal (e.g. Bay of Napoli, La Spezia, San Remo; [BER 67, NAT 09, RAM 38]) and offshore locations [LEG 64, LEG 72]. Later, in the 1970s, an important springtime presence of the diatom genus *Nitzschia* in the Bay of Villefranche was reported [RAS 79]. Claustre *et al.* specifically studied a spring bloom of *Nitzschia seriata* in 1986 and suggested different physiological states of the cells that composed this bloom [CLA 89]. The absence of *Nitzschia seriata* in spring was also noted and reported several times (e.g. around Monaco, [PAV 37]). In summer, although there was a low abundance of diatoms observed in the phytoplankton community, diatoms of the genera *Rhizosolenia* and *Leptocylindrus* were detected [PAV 37, RAM 38]. Another common diatom genus observed, mostly in fall, was *Chaetoceros* [PAV 37, RAM 38], also confirmed by Rassoulzadegan [RAS 79].

Dinoflagellate species collected by a plankton net are as diverse as diatom species. Halim [HAL 60] made an inventory of 198 dinoflagellate species, including the description of seven new species, from samples collected in the Bay of Villefranche. Some species presented strong seasonal variations due to changes in environmental factors [HAL 60]. Tunin-Ley *et al.* [TUN 07], in a careful study of the genus *Ceratium* in coastal waters (Bay of Villefranche), showed that over a year, the dinoflagellate population was dominated by *C. furca* (in spring) and *C. fusus* (in winter). Some species displayed a seasonal cycle that might be linked to water temperature, such as *C. candelabrum* mostly observed

in winter. Tunin-Ley *et al.* [TUN 07] also suggested that seasonal variations of dinoflagellates in the microphytoplankton community were related to competition with diatoms for nutrients and through predation by salps and copepods.

Rampi also observed tychoplanktonic organisms (benthic organisms dispersed through the water column via a disturbance to their habitat, e.g. suspension induced by waves), such as the diatom genus *Licmophora* [RAM 38]. Recently, the tychoplanktonic and harmful dinoflagellate species *Ostreopsis ovata* received more attention in coastal areas of the Ligurian Sea. This dinoflagellate, continuously monitored in Ligurian Sea coastal waters, grows in a mucilaginous layer on macroalgae and can be dispersed in the surface layer from waves. During an *Ostreopsis* bloom, the observed concentration can reach 10^6 cells L^{-1} and the cells can be transported via aerosols into the atmosphere. Cohu and Lemée [COH 12] showed that the presence of this dinoflagellate in summer depends on temperature (>20 °C) and light. Meroni *et al.* [MER 18] also showed that the dynamics of *Ostreopsis* depends on biotic and abiotic parameters, which explains the presence of this species in urban shores and sheltered bays. This species produces a metabolite similar to “palytoxine” (the most powerful toxin produced by marine species) called “ovatoxine”, which might be present among the pelagic and benthic communities, potentially causing human diseases.

6.1.2.2. Nano-phytoplankton (2–20 μm)

In the early 20th Century, observations of phytoplankton cells among the nanophytoplankton were difficult with a standard microscope, and only few characteristics (e.g. flagella) allowed their identification to some taxon levels. However, coccolithophore species were easily identified with their coccoliths (disc-like plates) that surround their cells and form a coccosphere (calcareous skeletons).

Bernard, with observations from two coastal sampling sites (around Banyuls and Monaco), suggested that the volume of the nanoplankton was at a maximum from the end of spring to the end of summer [BER 38]. Then, he gave an early quantitative estimation of the number of coccolithophore species present in the Ligurian Sea [BER 39]. A total of 44 species were recorded and the dominant species were *Oolithotus fragilis*

and *Emiliana huxleyi* (under the names *Coccolithus fragilis* and *Pontosphaera huxleyi*, respectively). Some species were found in deep waters and supposed to be heterotrophs. Bernard emphasized that these species could appear under different shapes over their life cycle [BER 39]. In the eastern part of the Ligurian Sea, around La Spezia (Italy), coccolithophores were also observed to be a major part of the phytoplankton community [BER 67].

Most of these studies were done with samples collected in coastal waters. Léger was one of the first to carry out a survey offshore [LEG 72]. He estimated the abundance of coccolithophores at different seasons in the central part of Ligurian Sea. From his observations, coccolithophores increased in winter and did not produce a bloom. He showed that silicoflagellata, with an annual maximum concentration in winter (to $5.5 \cdot 10^3$ cells L^{-1}) in coastal waters [NIV 65], could also be an important nanoplankton component in offshore water.

The summer season was investigated during a transect off Villefranche [JAC 76]. Although the diatom and dinoflagellate abundances were the same in coastal and offshore waters, the nanoplankton component was dominant offshore, especially *Chrysochromulina* ($0.5 \cdot 10^6$ cells L^{-1}), one coccolithophore species and *Dictyocha fibula* (5000 cells L^{-1}).

6.1.2.3. Pico-phytoplankton (0.2–2 μm)

Sieburth *et al.* [SIE 78] and Waterbury *et al.* [WAT 79] revealed the existence of phytoplankton cells smaller than nanophytolankton cells, passing through 2 μm pore size filters. The cyanobacteria (i.e. photosynthetic bacteria) *Synechococcus* [WAT 86] and *Prochlorococcus* [CHI 92] are the most common picophytoplankton organisms. Vaultot *et al.* [VAU 90] documented the presence of *Prochlorococcus* in the Mediterranean Sea. Their specific photosynthetic pigment, the phycobilin pigment, has an intense fluorescence quantum yield in the orange region of the visible spectrum which is detectable by flow cytometry, and thus can be used to identify the presence of picophytoplankton organisms in a sample. Aside from cyanobacteria, several other picophytoplankton groups have been discovered in other taxonomic groups (i.e. in Chlorophyta: Chlorophyceae and Prasinophyceae; Prymnesiophyceae and Pelagophyceae) with different cell structures and flagella types [LEE 18].

6.1.3. *Phytoplankton community structure*

The development of chlorophyll-*a* concentration measurement techniques allowed a more rapid approximation of the phytoplankton biomass. Nowadays, high-performance liquid chromatography (HPLC) technology is widely used to identify and quantify the concentration of several photosynthetic pigments from a sample. The concentrations of phytoplankton pigments in a sample can be used to detect the presence of different photosynthetic autotrophs by using a diagnostic pigment approach (see text box and Table 6.1).

In addition to chlorophyll-*a*, the dominant photosynthetic pigment, a phytoplankton cell could contain accessory pigments. The pigments associated with chlorophyll-*a* have different functions, for example, photoprotection or to extend the light absorption spectrum. Several accessory pigments exist of different classes (e.g. carotenoids, phycobiliproteins and chlorophylls), and could be specific to a phytoplankton group [BID 90, JEF 74]. Therefore, to study the structure of the phytoplankton community in a sampled area, one can estimate the concentration of accessory pigments and relate this information to the presence of specific phytoplankton taxa.

To this end, Claustre [CLA 94] proposed an approach to detect and quantify the presence of seven phytoplankton groups (i.e. diatoms, dinoflagellates, nanoflagellates, green flagellates, cryptophytes, cyanobacteria and prochlorophytes) based on the concentration of nine accessory pigments, named diagnostic pigments (or biomarker pigments), determined by HPLC analysis. Vidussi *et al.* [VID 01] proposed the possibility of using the typical cell size of the organisms within each taxon to assign taxon to three different phytoplankton size classes: picophytoplankton (< 2 μm), nanophytoplankton (2–20 μm) and microphytoplankton (> 20 μm). This size description of the phytoplankton community is convenient for the study of ocean biogeochemical processes (e.g. phytoplankton photophysiology and biological carbon export [GUI 09, UIT 08]). Therefore, Uitz *et al.* [UIT 06] refined the approach of Claustre [CLA 94] with the three size specific groupings as proposed by Vidussi *et al.* [VID 01].

Box 6.2. *Community structure with HPLC*

In the Ligurian Sea, the diagnostic pigment approach allowed the description of seasonal succession of phytoplankton groups, in relation to the total phytoplankton biomass and production, and the hydrological environment. This description has been made in coastal locations (e.g. in the Bay of Villefranche) and offshore (e.g. the DYFAMED-BOUSSOLE sampling site).

| Taxonomic groups | Diagnostic Pigments | Typical Size Classes proposed by Vidussi <i>et al.</i> (2001) | Genera and species cited in this chapter |
|---|--|---|--|
| <i>Considered in the diagnostic pigment approach of Claustre [CLA 94], Vidussi et al. [VID 01] and Uitz et al. [UIT 06]</i> | | | |
| Diatoms | Fucoxanthin | microphytoplankton (> 20 µm) | <i>Thalassionema</i> , <i>Nitzschia seriata</i> , <i>Rhizosolenia</i> , <i>Leptocylindrus</i> , <i>Chaetoceros</i> , <i>Minidiscus</i> , <i>Licmophora</i> |
| Dinoflagellates | Peridinin | | <i>Ceratium</i> , <i>Ostreopsis</i> |
| Haptophyta (Prymnesiophyceae) | 19'-Hexanoyloxyfucoxanthin 19'-Butanoyloxyfucoxanthin | nanophytoplankton (> 2–20 µm) | <i>Oolithotus fragilis</i> , <i>Emiliana huxleyi</i> <i>Chrysochromulina</i> |
| Cryptophyta (Cryptophyceae) | Alloxanthin | | |
| Chlorophyta (Chlorophyceae, Prasinophyceae) | Total chlorophyll-b | picophytoplankton (< 2 µm) | |
| Cyanobacteria | Zeaxanthin | | <i>Synechococcus</i> , <i>Prochlorococcus</i> |
| <i>Not considered in the diagnostic pigment approach of Claustre [CLA 94], Vidussi et al. [VID 01] and Uitz et al. [UIT 06]</i> | | | |
| Silicoflagellata | 19'-Hexanoyloxyfucoxanthin 19'-butanoyloxyfucoxanthin | microphytoplankton (> 20 µm) | <i>Dictyocha fibula</i> |
| Pelagophyceae | 19'-Butanoyloxyfucoxanthin Fucoxanthin | picophytoplankton (< 2 µm) | |

Table 6.1. *Phytoplankton taxonomic groups targeted by the diagnostic pigment approach presented in the text box, as well as the phytoplankton genera, species and other taxonomic groups mentioned in this chapter*

On average over the annual cycle, the phytoplankton biomass and production in the euphotic zone of the Ligurian Sea is mostly dominated by nanoflagellates (mainly haptophyta), both in coastal [BUS 95] and open-ocean areas [MAR 02b], see Figure 6.2. However, this annual nanophytoplankton domination is challenged in spring. Specifically, the diatom biomass can exceed the nanoflagellate biomass during the phytoplankton spring bloom [MAR 02b]. This classical view of a spring bloom dominated by diatoms has not been observed every year [BUS 95, MAR 02b, VID 00]. Bustillos-Guzman *et al.* [BUS 95] suggested

year-to-year variability in the spring nutrient concentrations and light conditions may explain these observations. Recently, it was proposed that the winter water column mixing influences the spring nitrate to silicate ratio in the surface layer [SEV 17]. Ultimately, a lower (higher) quantity of diatoms in the phytoplankton community can induce a decrease (increase) in the springtime primary production of organic carbon [MAY 17b] (Figure 6.2).

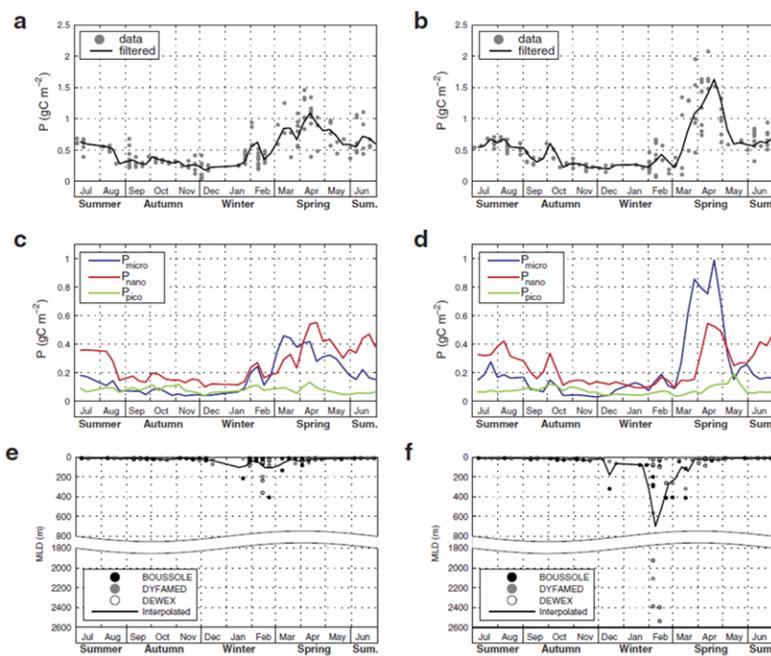


Figure 6.2. Climatological annual cycles of total (top) and class-specific (middle) phytoplankton primary production in the euphotic layer, and of the mixed layer depth (bottom), in the Northwest Mediterranean region (modified from Mayot *et al.* [MAY 17b]). During years with a shallow (a, c and e) or deep (b, c and f) winter water column mixing. For a color version of this figure, see www.iste.co.uk/migon/mediterranean1.zip

After the spring bloom, and when the water column starts to be strongly stratified, the annual biomass peak of nanoflagellates occurs [BUS 95]. Vidussi *et al.* [VID 00] particularly focused on this transition period and reported this switch in the phytoplankton community from diatoms to

haptophyta and an increasing contribution of picophytoplankton groups, mostly cyanobacteria. In general, *Synechococcus* is dominant in the surface layer, while haptophyta and *Prochlorococcus* are located around the SCM [MAR 02b, VID 00]. This vertical distinction was explained by the ability of cyanobacteria to grow under high solar radiation and use regenerated forms of nitrogen [MAR 02b, VID 00]. Overall, the picophytoplankton biomass can overcome the nanophytoplankton biomass in the near surface layer [KHE 14] without dominating integrated phytoplankton biomass over the euphotic zone [MAR 02b, MAY 17b] (Figure 6.2).

During mixing of the water column in winter, the phytoplankton community seems to be mostly dominated by nanophytoplankton groups [MAR 02b, MAY 17b]. However, the diagnostic pigment approach used in these studies relies on the collection of water samples at sea, which is rarely done in harsh winter conditions. Consequently, it is important to develop methods to study the phytoplankton community structure from autonomous platforms (e.g. remote sensing, autonomous underwater vehicles). Studies based on ocean-color [NAV 17, UIT 12] and *in situ* bio-optical data (e.g. from a mooring; [ORG 13]) have already proven the success of these methods, and confirmed the general view of seasonal succession of phytoplankton groups in the Ligurian Sea but with higher spatiotemporal resolution.

However, these approaches prevent, for now, a description of the phytoplankton community at low taxonomic levels, which can be achieved with single cell observations. The introduction of imaging flow cytometers (measuring different parameters of particles: spectral, fluorescent and morphological) offers a way to identify several categories of living particles (e.g. viruses, bacteria, phytoplankton) and their biomasses. Seagoing and autonomous flow cytometers allow the study of short timescale events or processes concerning pico-, nano- and micro-phytoplankton groups. For example, several studies based on single cell imagery systems conducted in the Bay of Villefranche emphasized the importance of pico-eukaryotes, silicoflagellata and nanophytoplankton groups in the first stage of the spring phytoplankton bloom [PED 17, ROM 15, THY 14]. These phytoplankton groups might have a faster response to the favorable spring bloom conditions compared to the large diatoms and dinoflagellates, due to bottom-up processes [ROM 15, THY 14] and zooplankton grazing pressure [ROM 15]. In the open ocean of the Northwest Mediterranean region, a single cell study also emphasized the possibility to observe recurrent spring blooms of a nanoplanktonic diatom species in this area (*Minidiscus*; [LEB 18]).

6.2. From the influence of small spatiotemporal features to the interannual and long-term variability

Associated with the large scale and general (climatological) annual cycle of phytoplankton dynamics, small spatiotemporal processes occur and may play a lead role at local scales. For example, during the MEDIPROD experiment cruises, a sharp boundary between offshore green waters and coastal blue waters was discovered. This boundary is due to the highly dynamic geostrophic frontal jet flow associated with the Ligurian coastal current (i.e. northern branch, [BET 83], see also Chapter 3). Phytoplankton biomass, as well as the abundances of meso- and macro-zooplankton, can be more important in this frontal structure [BOU 87, GOR 00]. The front is characterized by a strong horizontal density gradient and substantial meandering activity [BET 83, PIT 14]. Moreover, geostrophic vertical motions in this frontal structure (convergence and divergence processes) can induce an upwelling of deep-water masses, rich in nutrients, and a downwelling of surface waters containing phytoplankton cells (e.g. [BOU 87]). In fact, several glider surveys detected frontal submesoscale processes that can transport phytoplankton biomass down to 120 m [NIE 08].

Wind and precipitation events can significantly influence vertical water column stability and nutrient concentrations. At some coastal locations and in the spring, nutrients introduced into surface waters by rain events can favor the development of nanophytoplankton groups [KLE 97]. Such local processes can ultimately affect, for example, phytoplankton bloom development [PED 17, ROM 15, THY 14]. Offshore, the occurrence of short-term and intense wind-driven vertical mixing episodes of the water column may stop or delay the typical spring bloom development [MAR 02b, MAY 17a], and be crucial in the amount of organic carbon exported at depth [BER 12, KES 18, ULS 16]. Later in the year, at the transition from the spring bloom to the summer oligotrophic phase, illustrated by the establishment of the SBM, wind events may cause a shoaling of the nutricline and increase nutrient concentrations in the surface layer, as well as primary production [AND 00]. Diatoms can rapidly respond to these short-term summer events, but, ultimately, it is the smaller phytoplankton size classes that are mainly associated with these brief enhancements of the primary production [BUS 95, VID 00].

Physical (sub)mesoscale eddy features are also recurrent in the Ligurian Sea and can influence the phytoplankton dynamics. Mesoscale cyclonic

eddies generated by a recirculation of coastal currents in summer in the Ligurian Sea can generate a horizontal distinction in the distribution of picophytoplankton species in the surface layer [MAR 18]. In spring, eddies that form at the border of the deep convection patch may play a key role in water column stratification and in the phytoplankton spring bloom [LÉV 98b, LÉV 99]. Furthermore, eddies generated in the mixed patch of convected waters (i.e. sub-mesoscale coherent vortices) can persist for an extended period and affect the phytoplankton distribution in summer [BOS 17]. It is still necessary to evaluate the contribution of these small-scale physical features on the larger, sub-basin, description of the phytoplankton dynamics, not only by new field experiments, but also by improving hydrodynamics/biochemistry coupled models (see section 6.3).

Finally, in contrast to these small spatiotemporal variabilities, significant questions remain about the long-term trend of phytoplankton dynamics in the Ligurian Sea, and more generally at the scale of the Northwest Mediterranean basin [THE 11]. As already reported in previous sections, interannual variability in the springtime phytoplankton biomass [LAV 13, MAY 16, VOL 12], community structure [MAR 02a, SAN 71, SEV 14] and production [EST 96, MAR 02a, MAY 17b] occur in the Northwest Mediterranean region. In the open-ocean sector, the principal cause of the interannual variability in the springtime primary production may be the influence of the winter mixing on nutrient availability (concentration and stoichiometry) and zooplankton grazing pressure [MAY 17a, SEV 17]. Although a phytoplankton spring bloom that deviates from the norm has a limited consequence on the annual phytoplankton production (about 6%; [MAY 17b]), the food web structure in Ligurian Sea, as well as the export of particulate organic carbon to depth in this area, might be impacted [LEG 91, RAM 16]. This underlines the importance of predicting the general trends in the Ligurian (e.g. more subtropical or temperate regimes) in the next century, principally in response to the ongoing climate changes [MAR 15].

From nine years of observations (1991–1999), Marty *et al.* [MAR 02b] suggested a general increase in the phytoplankton biomass in the open-ocean area of the Ligurian Sea, driven by an increase in the annual average proportion of pico- and nanophytoplankton in the phytoplankton community. Similar conclusions were derived at coastal locations [PED 17]. When using multiannual satellite-derived surface chlorophyll-a concentration, the interannual variability in the observed seasonal cycle (i.e. year-to-year change in spring bloom intensity) is the most important feature [MAY 16,

SAL 19] with a potential increase in the annual phytoplankton biomass [SAL 19]. Modeling studies of the Northwest Mediterranean region provide insights into future changes that could face the Ligurian Sea. Some studies suggest an increase in water column stratification [ADL 15, SOM 18] that could change the availability of silicon, influencing diatom development and potentially leading to a general reduction of springtime phytoplankton production [HER 13]. However, the physical circulation models are very sensitive to the Atlantic forcing used at the boundary conditions [ADL 15]. In addition, some recent modeling simulations seem to indicate that mesoscale activities [MAC 18] and changes in external nutrient inputs (Atlantic, atmospheric and riverine sources; [LAZ 12, RIC 19]) have crucial roles in the projection of future changes in primary production in the Northwest Mediterranean basin.

6.3. Modeling the impact of the physics on phytoplankton growth and distribution

The biogeochemistry of the Ligurian Sea shares important characteristics with other temperate regions of the ocean, such as the North Atlantic. Modeling studies of this complex system has paved the way for the understanding of the coupling between the physics of the ocean and the response of the biogeochemistry in environments that are prone to strong seasonal variations of the surface mixed layer and to strong mesoscale dynamics.

Unlike the rest of the Mediterranean basin that is predominantly oligotrophic, the productive Ligurian Sea is a typical temperate system characterized by an increase in phytoplankton biomass that starts in the fall, often interrupted in winter, and a stronger, more intense bloom in spring that ends in summer [DOR 14, HOU 16, MAY 16].

It is now fairly well established that the seasonal variations of the mixed layer are a main driver of the seasonal variations in phytoplankton biomass, although there remain some uncertainties regarding the ability of phytoplankton to grow in deep mixed layer and regarding the control that grazing may exert on the onset and decay of the phytoplankton bloom [BEH 18]. The deep-winter convection in the Northwestern Mediterranean plays a key role in the setting the bloom [MAY 16]. It ensures the seasonal replenishment of the euphotic layer with nutrients, which are progressively

being consumed between winter and summer. One-dimensional modeling studies of the phytoplankton phenology in the Ligurian Sea have suggested that the onset of seasonal stratification over the deep-convection area, which is tightly linked to the time at which the net heat flux received by the ocean from the atmosphere becomes positive, drives the onset of the surface bloom [LÉV 98a, LÉV 98b]. This has been confirmed recently thanks to the development of new technologies that have enabled continuous measurements in the field [MAY 17a].

This classical seasonal scenario is, however, strongly modulated by temporal and spatial signals of smaller scale. For instance, high frequency atmospheric events (from one to a few days), such as wind bursts, are sufficient to destroy the stratification and temporarily interrupt the bloom. Similarly, periods of mild weather in winter allow for short periods of stratification that are associated with more elevated phytoplankton biomass at the sea surface [LÉV 98a, MAY 17a].

In addition, mesoscale dynamics have also been shown to strongly modulate the phytoplankton phenology. The first ocean color images over the Ligurian Sea in the early 1980s have revealed phytoplankton heterogeneity at scales similar to mesoscale eddies over this area during winter and spring [MOR 91a], suggesting a strong impact by mesoscale dynamics. The region is indeed the location of intense mesoscale activity, which originates primarily from the baroclinic instability of the current surrounding the deep-convection area. One of the first biogeochemical modeling studies conducted at mesoscale resolution aimed at understanding the physical processes involved in this physical control [LÉV 00, LÉV 98b, LÉV 99]. The model, although highly idealized, was able to reproduce the spatial heterogeneity in the onset of the bloom, which started from the border of the convective area before amplifying in its core. Interestingly, the onset of the bloom around the convective area occurred a few weeks in advance of seasonal stratification. This was due to the **restratifying** action of mesoscale eddies that acted to flatten the isopycnals around the convective area, preventing vertical mixing and enabling an early bloom there. A decade later, this process was very elegantly confirmed by *in situ* observations in the North Atlantic [MAH 12]. Another impact of the mesoscale and sub-mesoscale dynamics is through the associated frontal vertical velocities, which constitute an efficient pathway to supply nutrients to the euphotic layer. Model results suggest that this process constitutes a year-long source of new nutrients to the euphotic layer that adds up to the

Comment [Kce1]: AQ: Should this be "restratifying"?

once-off winter supply associated with deep convection the summer season, and enables to extend the duration of the bloom [LÉV 00]. These small-scale phenomena likely play an important role in the strong year-to-year variability in the timing and amplitude the bloom [MAY 16], which cannot be explained by variations in mixed layer depth alone [LAV 13].

Since these early modeling studies in the 1990s, more complex biogeochemical and dynamical models of the Mediterranean Sea have been developed [RIC 18] and have enabled to tackle the richness of the biogeochemical processes in this small but extremely representative region of the world's ocean. Further development of such models, as increased knowledge of important biogeochemical processes become available, through dedicated field and lab studies, combined with increase in computer capacities in order to better resolve small-scale physical processes, will allow us to better project the future changes that the Ligurian Sea ecosystems are facing in response to climate change.

6.4. References

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