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► **To cite this version:**

Nicolas Mayot, Paul Nival, Marina Lévy. Primary Production in the Ligurian Sea. Christophe Migon; Paul Nival; Antoine Sciandra. The Mediterranean Sea in the Era of Global Change 1: 30 Years of Multidisciplinary Study of the Ligurian Sea, 1, Wiley, pp.139-164, 2020, 9781786304285. 10.1002/9781119706960.ch6 . hal-03003497

HAL Id: hal-03003497

<https://hal.science/hal-03003497>

Submitted on 27 Nov 2020

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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.

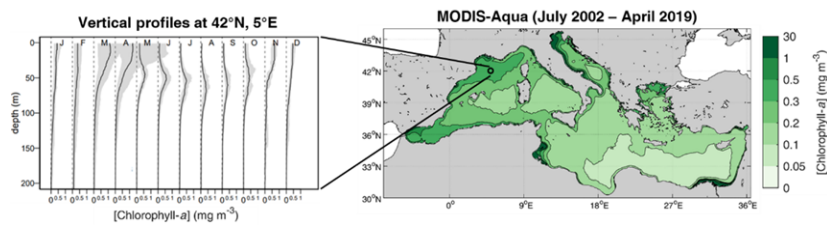


Figure 6.1. Climatologies of chlorophyll-*a* concentration. (Left) Monthly vertical profiles (black line: median value; grey zone: 10–90 percentile range) observed in the water column at the location 42°N, 5°E (modified from Lavigne *et al.* [LAV 15]). (Right) Surface chlorophyll-*a* concentration from 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	Fucoanthin	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).

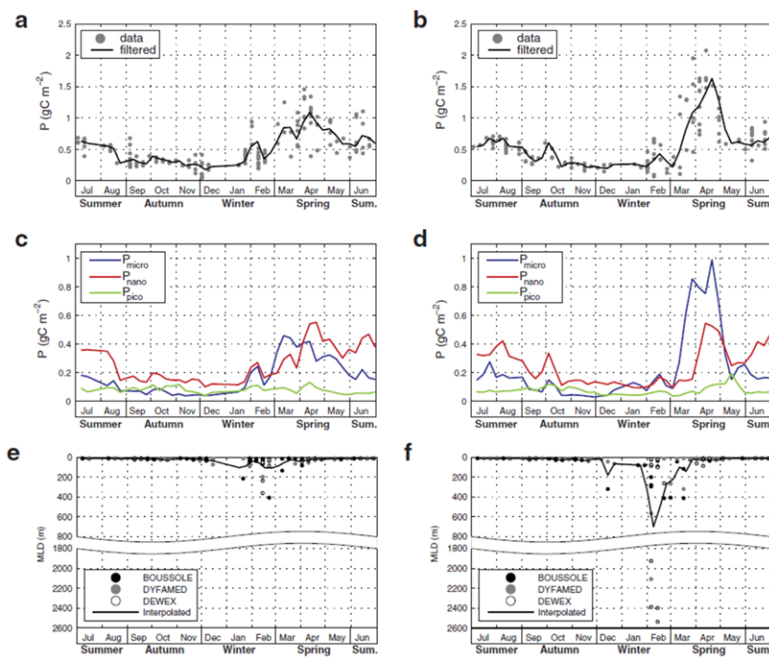


Figure 6.2. Climatological annual cycles of total (top) and class-specific (middle) phytoplankton primary production in the euphotic layer, and of the mixed layer depth (bottom), in the Northwest Mediterranean region (modified from Mayot *et al.* [MAY 17b]). During years with a shallow (a, c and e) or 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

- [ADL 15] ADLOFF F., SOMOT S., SEVAULT F. *et al.*, “Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios”, *Climate Dynamics*, vol. 45, pp. 2775–2802, 2015.
- [AND 00] ANDERSEN V., PRIEUR L., “One-month study in the open NW Mediterranean Sea (DYNAPROC experiment, May 1995): overview of the hydrobiogeochemical structures and effects of wind events”, *Deep-Sea Research Part I-Oceanographic Research Papers*, vol. 47, pp. 397–422, 2000.
- [ANT 95] ANTOINE D., MOREL A., ANDRE J.M., “Algal pigment distribution and primary production in the eastern mediterranean as derived from Coastal Zone Color Scanner observations”, *Journal of Geophysical Research-Oceans*, vol. 100, pp. 16193–16209, 1995.
- [AYA 18] AYATA S.-D., IRISSON J.-O., AUBERT A. *et al.*, “Regionalisation of the Mediterranean basin, a MERMEX synthesis”, *Progress in Oceanography*, vol. 163, pp. 7–20, 2018.
- [BAB 15] BABIN M., BELANGER S., ELLINGSEN I. *et al.*, “Estimation of primary production in the Arctic Ocean using ocean colour remote sensing and coupled physical-biological models: Strengths, limitations and how they compare”, *Progress in Oceanography*, vol. 139, pp. 197–220, 2015.

- [BAR 03] BARALE V., “Environmental remote sensing of the Mediterranean sea”, *Journal of Environmental Science and Health Part a-Toxic/Hazardous Substances & Environmental Engineering*, vol. 38, pp. 1681–1688, 2003.
- [BAR 19] BARBIEUX M., UITZ J., GENTILI B. *et al.*, “Bio-optical characterization of subsurface chlorophyll maxima in the Mediterranean Sea from a Biogeochemical-Argo float database”, *Biogeosciences*, vol. 16, pp. 1321–1342, 2019.
- [BEH 97] BEHRENFELD M.J., FALKOWSKI P.G., “A consumer’s guide to phytoplankton primary productivity models”, *Limnology and Oceanography*, vol. 42, pp. 1479–1491, 1997.
- [BEH 18] BEHRENFELD M.J., BOSS E.S., “Student’s tutorial on bloom hypotheses in the context of phytoplankton annual cycles”, *Global Change Biology*, vol. 24, pp. 55–77, 2018.
- [BER 38] BERNARD F., “Cycle annuel du nannoplancton a Monaco et Banyuls”, *Annales De L’Institut Océanographique*, vol. 17, pp. 349–405, 1938.
- [BER 39] BERNARD F., “Etude sur les Variations de Fertilité des Eaux Méditerranéennes. Climat et Nanoplancton a Monaco en 1937-38”, *Ices Journal of Marine Science*, vol. 14, pp. 228–241, 1939.
- [BER 67] BERNHARD M., RAMPI L., “The annual cycle of the “Utermöhl-phytoplankton” in the Ligurian Sea in 1959 and 1962”, *Pubblicazioni della Stazione Zoologica di Napoli*, vol. 35, pp. 137–169, 1967.
- [BER 12] BERNARDELLO R., CARDOSO J.G., BAHAMON N. *et al.*, “Factors controlling interannual variability of vertical organic matter export and phytoplankton bloom dynamics – a numerical case-study for the NW Mediterranean Sea”, *Biogeosciences*, vol. 9, pp. 4233–4245, 2012.
- [BET 83] BETHOUX J.P., PRIEUR L., “Hydrologie et circulation en Méditerranée Nord-Occidentale”, *Pétrole et techniques*, vol. 299, pp. 25–34, 1983.
- [BID 90] BIDIGARE R., MARRA J., DICKEY T. *et al.*, “Evidence for phytoplankton succession and chromatic adaptation in the Sargasso Sea during spring 1985”, *Marine Ecology Progress Series*, vol. 60, pp. 113–122, 1990.
- [BOS 04] BOSCH E., BRICAUD A., ANTOINE D., “Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations”, *Global Biogeochemical Cycles*, vol. 18, 2004.
- [BOS 17] BOSSE A., TESTOR P., MAYOT N. *et al.*, “A submesoscale coherent vortex in the Ligurian Sea: From dynamical barriers to biological implications”, *Journal of Geophysical Research-Oceans*, vol. 122, pp. 6196–6217, 2017.

- [BOU 87] BOUCHER J., IBANEZ F., PRIEUR L., “Daily and seasonal variations in the spatial distribution of zooplankton populations in relation to the physical structure in the Ligurian Sea Front”, *Journal of Marine Research*, vol. 45, pp. 133–173, 1987.
- [BUS 95] BUSTILLOS-GUZMAN J., CLAUSTRE H., MARTY J.C., “Specific phytoplankton signatures and their relationship to hydrographic conditions in the coastal northwestern Mediterranean Sea”, *Marine Ecology Progress Series*, vol. 124, pp. 247–258, 1995.
- [CHI 92] CHISHOLM S.W., FRANKEL S.L., GOERICKE R. *et al.*, “Prochlorococcus marinus nov. gen. nov. sp.: an oxyphototrophic marine prokaryote containing divinyl chlorophyll a and b”, *Archives of Microbiology*, vol. 157, pp. 297–300, 1992.
- [CLA 89] CLAUSTRE H., MARTY J.-C., CASSIANI L., “Intraspecific differences in the biochemical composition of a diatom during a spring bloom in Villefranche-sur-Mer Bay, Mediterranean Sea”, *Journal of Experimental Marine Biology and Ecology*, vol. 129, pp. 17–32, 1989.
- [CLA 94] CLAUSTRE H., “The trophic status of various oceanic provinces as revealed by phytoplankton pigment signatures”, *Limnology and Oceanography*, vol. 39, pp. 1206–1210, 1994.
- [COH 12] COHU S., LEMÉE R., “Vertical distribution of the toxic epibenthic dinoflagellates *Ostreopsis cf. ovata*, *Prorocentrum lima* and *Coolia monotis* in the NW Mediterranean Sea”, *Cahiers De Biologie Marine*, vol. 53, pp. 373–380, 2012.
- [CON 18] CONAN P., TESTOR P., ESTOURNEL C. *et al.*, “Preface to the Special Section: Dense Water Formations in the Northwestern Mediterranean: From the Physical Forcings to the Biogeochemical Consequences”, *Journal of Geophysical Research: Oceans*, vol. 123, pp. 6983–6995, 2018.
- [DOR 09] D’ORTENZIO F., RIBERA D’ALCALA M., “On the trophic regimes of the Mediterranean Sea: a satellite analysis”, *Biogeosciences*, vol. 6, pp. 139–148, 2009.
- [DOR 14] D’ORTENZIO F., LAVIGNE H., BESSON F. *et al.*, “Observing mixed layer depth, nitrate and chlorophyll concentrations in the northwestern Mediterranean: A combined satellite and NO₃ profiling floats experiment”, *Geophysical Research Letters*, vol. 41, pp. 6443–6451, 2014.
- [EST 96] ESTRADA M., “Primary production in the northwestern Mediterranean”, *Scientia Marina*, vol. 60, pp. 55–64, 1996.

- [FOR 22] FORTI A., “Ricerche sulla flora pelagica (fitoplancton) di Quarto dei Mille (Mar Ligure)”, *Memoria Real Comitato Talassografico Italiano*, vol. 97, pp. 1–248, 1922.
- [GOM 03] GOMEZ F., GORSKY G., “Annual microplankton cycles in Villefranche Bay, Ligurian Sea, NW Mediterranean”, *Journal of Plankton Research*, vol. 25, pp. 323–339, 2003.
- [GOR 00] GORSKY G., PICAL M., STEMMANN L., “Use of the Underwater Video Profiler for the Study of Aggregate Dynamics in the North Mediterranean”, *Estuarine, Coastal and Shelf Science*, vol. 50, pp. 121–128, 2000.
- [GOS 61] GOSTAN J., “Contribution à l’étude hydrologique de la Mer Ligure”, *Bulletin de l’Institut océanographique, Monaco*, vol. 58, pp. 1–47, 1961.
- [GOS 63] GOSTAN J., NIVAL P., “Distribution hivernale des caractéristiques hydrologiques en Mer Ligure et estimation de l’abondance du phytoplancton par la méthode des pigments.”, *Comptes rendus de l’Académie des Sciences, Paris*, vol. 257, pp. 2872–2875, 1963.
- [GUI 09] GUIDI L., STEMMANN L., JACKSON G.A. *et al.*, “Effects of phytoplankton community on production, size and export of large aggregates: A world-ocean analysis”, *Limnology and Oceanography*, vol. 54, pp. 1951–1963, 2009.
- [HAL 60] HALIM Y., “Étude quantitative et qualitative du cycle écologique des dinoflagellés dans les eaux de Villefranche-sur-Mer (1953–1955)”, *Annales De L’Institut Océanographique*, vol. 38, pp. 123–232, 1960.
- [HER 13] HERRMANN M., DIAZ F., ESTOURNEL C. *et al.*, “Impact of atmospheric and oceanic interannual variability on the Northwestern Mediterranean Sea pelagic planktonic ecosystem and associated carbon cycle”, *Journal of Geophysical Research-Oceans*, vol. 118, pp. 5792–5813, 2013.
- [HOU 16] HOUPERT L., DURRIEU DE MADRON X., TESTOR P. *et al.*, “Observations of open-ocean deep convection in the northwestern Mediterranean Sea: Seasonal and interannual variability of mixing and deep-water masses for the 2007–2013 Period”, *Journal of Geophysical Research-Oceans*, vol. 121, pp. 8139–8171, 2016.
- [JAC 73] JACQUES G., MINAS H.J., MINAS M. *et al.*, “Influence des conditions hivernales sur les productions phyto- et zooplanctoniques en Méditerranée Nord-Occidentale. II. Biomasse et production phytoplanctonique”, *Marine Biology*, vol. 23, pp. 251–265, 1973.
- [JAC 76] JACQUES G., MINAS M., NEVEUX J. *et al.*, “Conditions estivales dans la divergence de Méditerranée nord-occidentale. III : Phytoplancton”, *Annales De L’Institut Océanographique*, vol. 52, pp. 141–152, 1976.

- [JEF 74] JEFFREY S.W., “Profiles of photosynthetic pigments in the ocean using thin-layer chromatography”, *Marine Biology*, vol. 26, pp. 101–110, 1974.
- [KES 18] KESSOURI F., ULSSES C., ESTOURNEL C. *et al.*, “Vertical Mixing Effects on Phytoplankton Dynamics and Organic Carbon Export in the Western Mediterranean Sea”, *Journal of Geophysical Research-Oceans*, vol. 123, pp. 1647–1669, 2018.
- [KHE 14] KHEIREDDINE M., ANTOINE D., “Diel variability of the beam attenuation and backscattering coefficients in the northwestern Mediterranean Sea (BOUSSOLE site)”, *Journal of Geophysical Research-Oceans*, vol. 119, pp. 5465–5482, 2014.
- [KLE 97] KLEIN C., DOLAN J., RASSOULZADEGAN F., “Experimental examination of the effects of rainwater on microbial communities in the surface layer of the NW Mediterranean Sea”, *Marine Ecology Progress Series*, vol. 158, pp. 41–50, 1997.
- [LAV 13] LAVIGNE H., D’ORTENZIO F., MIGON C. *et al.*, “Enhancing the comprehension of mixed layer depth control on the Mediterranean phytoplankton phenology”, *Journal of Geophysical Research-Oceans*, vol. 118, pp. 3416–3430, 2013.
- [LAV 15] LAVIGNE H., D’ORTENZIO F., D’ALCALA M.R. *et al.*, “On the vertical distribution of the chlorophyll a concentration in the Mediterranean Sea: a basin-scale and seasonal approach”, *Biogeosciences*, vol. 12, pp. 5021–5039, 2015.
- [LAZ 12] LAZZARI P., SOLIDORO C., IBELLO V. *et al.*, “Seasonal and inter-annual variability of plankton chlorophyll and primary production in the Mediterranean Sea: a modelling approach”, *Biogeosciences*, vol. 9, pp. 217–233, 2012.
- [LEB 18] LEBLANC K., QUÉGUINER B., DIAZ F. *et al.*, “Nanoplanktonic diatoms are globally overlooked but play a role in spring blooms and carbon export”, *Nature Communications*, vol. 9, pp. 953, 2018.
- [LEE 18] LEE R.E., *Phycology*, Cambridge University Press, Cambridge, 2018.
- [LEG 64] LEGER G., “Les populations phytoplanctoniques en mer Ligure (radiale Monaco-Calvi) en juin 1963”, *Bulletin de l’Institut océanographique, Monaco*, vol. 64, pp. 1–32, 1964.
- [LEG 72] LEGER G., “Les populations phytoplanctoniques au point 42°47’ N, 7°29’ E Greenwich. (Bouée laboratoire du COMEXO/CNEXO). Discussion générale”, *Bulletin de l’Institut océanographique, Monaco*, vol. 70, 1972.
- [LEG 91] LEGENDRE L., LE FÈVRE J., “From Individual Plankton Cells To Pelagic Marine Ecosystems And To Global Biogeochemical Cycles”, in DEMERS S. (ed.), *Particle Analysis in Oceanography*, Springer, Berlin, Heidelberg, 1991.

- [LÉV 98a] LÉVY M., MÉMERY L., ANDRE J.M., “Simulation of primary production and export fluxes in the Northwestern Mediterranean Sea”, *Journal of Marine Research*, vol. 56, pp. 197–238, 1998.
- [LÉV 98b] LÉVY M., MÉMERY L., MADEC G., “The onset of a bloom after deep winter convection in the northwestern Mediterranean Sea: mesoscale process study with a primitive equation model”, *Journal of Marine Systems*, vol. 16, pp. 7–21, 1998.
- [LÉV 99] LÉVY M., MÉMERY L., MADEC G., “The onset of the Spring Bloom in the MEDOC area: mesoscale spatial variability”, *Deep Sea Research Part I: Oceanographic Research Papers*, vol. 46, pp. 1137–1160, 1999.
- [LÉV 00] LÉVY M., MÉMERY L., MADEC G., “Combined effects of mesoscale processes and atmospheric high-frequency variability on the spring bloom in the MEDOC area”, *Deep-Sea Research Part I-Oceanographic Research Papers*, vol. 47, pp. 27–53, 2000.
- [LON 95] LONGHURST A., “Seasonal cycles of pelagic production and consumption”, *Progress in Oceanography*, vol. 36, pp. 77–167, 1995.
- [LON 98] LONGHURST A., *Ecological Geography of the Sea*, Academic Press, San Diego, 1998.
- [MAC 18] MACIAS D., GARCIA-GORRIZ E., STIPS A., “Deep winter convection and phytoplankton dynamics in the NW Mediterranean Sea under present climate and future (horizon 2030) scenarios”, *Scientific Reports*, vol. 8, pp. 1–15, 2018.
- [MAH 12] MAHADEVAN A., D’ASARO E., LEE C. *et al.*, “Eddy-driven stratification initiates North Atlantic spring phytoplankton blooms”, *Science*, vol. 337, pp. 54–58, 2012.
- [MAR 02a] MARTY J.-C., CHIAVÉRINI J., “Seasonal and interannual variations in phytoplankton production at DYFAMED time-series station, northwestern Mediterranean Sea”, *Deep Sea Research Part II: Topical Studies in Oceanography*, vol. 49, pp. 2017–2030, 2002.
- [MAR 02b] MARTY J.C., CHIAVÉRINI J., PIZAY M.D. *et al.*, “Seasonal and interannual dynamics of nutrients and phytoplankton pigments in the western Mediterranean Sea at the DYFAMED time-series station (1991–1999)”, *Deep-Sea Research Part II-Topical Studies in Oceanography*, vol. 49, pp. 1965–1985, 2002.
- [MAR 15] MARIOTTI A., PAN Y.T., ZENG N. *et al.*, “Long-term climate change in the Mediterranean region in the midst of decadal variability”, *Climate Dynamics*, vol. 44, pp. 1437–1456, 2015.

- [MAR 18] MARREC P., GREGORI G., DOGLIOLI A.M. *et al.*, “Coupling physics and biogeochemistry thanks to high-resolution observations of the phytoplankton community structure in the northwestern Mediterranean Sea”, *Biogeosciences*, vol. 15, pp. 1579–1606, 2018.
- [MAY 16] MAYOT N., D’ORTENZIO F., RIBERA D’ ALCALA M. *et al.*, “Interannual variability of the Mediterranean trophic regimes from ocean color satellites”, *Biogeosciences*, vol. 13, pp. 1901–1917, 2016.
- [MAY 17a] MAYOT N., D’ORTENZIO F., TAILLANDIER V. *et al.*, “Physical and biogeochemical controls of the phytoplankton blooms in north western Mediterranean Sea: A multiplatform approach over a complete annual cycle (2012–2013 DEWEX experiment)”, *Journal of Geophysical Research-Oceans*, vol. 122, pp. 9999–10019, 2017.
- [MAY 17b] MAYOT N., D’ORTENZIO F., UITZ J. *et al.*, “Influence of the phytoplankton community structure on the spring and annual primary production in the northwestern Mediterranean Sea”, *Journal of Geophysical Research-Oceans*, vol. 122, pp. 9918–9936, 2017.
- [MER 18] MERONI L., CHIANTORE M., PETRILLO M. *et al.*, “Habitat effects on *Ostreopsis cf. ovata* bloom dynamics”, *Harmful Algae*, vol. 80, pp. 64–71, 2018.
- [MIG 14] MIGNOT A., CLAUSTRE H., UITZ J. *et al.*, “Understanding the seasonal dynamics of phytoplankton biomass and the deep chlorophyll maximum in oligotrophic environments: A Bio-Argo float investigation”, *Global Biogeochemical Cycles*, vol. 28, pp. 856–876, 2014.
- [MOR 91a] MOREL A., ANDRÉ J.-M., “Pigment distribution and primary production in the western Mediterranean as derived and modeled from Coastal Zone Color Scanner observations”, *Journal of Geophysical Research*, vol. 96, pp. 12685–12698 1991.
- [MOR 91b] MOREL A., “Light and marine photosynthesis: a spectral model with geochemical and climatological implications”, *Progress in Oceanography*, vol. 26, pp. 263–306, 1991.
- [NAT 09] NATHANSOHN A., “Sur les relations qui existent entre les changements du plankton végétal et les phénomènes hydrographiques, d’après les recherches faites à bord de l’Eider au large de Monaco, en 1907–8”, *Bulletin de l’Institut océanographique de Monaco*, vol. 140, 1909.
- [NAV 17] NAVARRO G., ALMARAZ P., CABALLERO I. *et al.*, “Reproduction of Spatio-Temporal Patterns of Major Mediterranean Phytoplankton Groups from Remote Sensing OC-CCI Data”, *Frontiers in Marine Science*, vol. 4, 2017.

- [NIE 08] NIEWIADOMSKA K., CLAUSTRE H., PRIEUR L. *et al.*, “Submesoscale physical-biogeochemical coupling across the Ligurian Current (northwestern Mediterranean) using a bio-optical glider”, *Limnology and Oceanography*, vol. 53, pp. 2210–2225, 2008.
- [NIV 65] NIVAL P., “Sur le cycle de *Dictyocha fibula* dans les eaux de surface de la rade de Villefranche-sur-Mer”, *Cahiers De Biologie Marine*, vol. 6, pp. 67–82, 1965.
- [OLI 11] OLITA A., SORGENTE R., RIBOTTI A. *et al.*, “Pelagic primary production in the Algero-Provencal Basin by means of multisensor satellite data: focus on interannual variability and its drivers”, *Ocean Dynamics*, vol. 61, pp. 1005–1016, 2011.
- [ORG 13] ORGANELLI E., BRICAUD A., ANTOINE D. *et al.*, “Multivariate approach for the retrieval of phytoplankton size structure from measured light absorption spectra in the Mediterranean Sea (BOUSSOLE site)”, *Applied Optics*, vol. 52, pp. 2257–2273, 2013.
- [PAV 37] PAVILLARD J., “Les Périдиниens et Diatomées pélagiques de la Mer de Monaco de 1907–1914. Observations générales et conclusions”, *Bulletin de l’Institut océanographique de Monaco*, vol. 738, pp. 1–56, 1937.
- [PED 17] PEDROTTI M.L., MOUSSEAU L., MARRO S. *et al.*, “Variability of ultraplankton composition and distribution in an oligotrophic coastal ecosystem of the NW Mediterranean Sea derived from a two-year survey at the single cell level”, *Plos One*, vol. 12, 2017.
- [PIT 14] PITERBARG L., TAILLANDIER V., GRIFFA A., “Investigating frontal variability from repeated glider transects in the Ligurian Current (North West Mediterranean Sea)”, *Journal of Marine Systems*, vol. 129, pp. 381–395, 2014.
- [PLA 91] PLATT T., CAVERHILL C., SATHYENDRANATH S., “Basin-scale estimates of oceanic primary production by remote sensing: The North Atlantic”, *Journal of Geophysical Research*, vol. 96, pp. 147–159, 1991.
- [RAM 38] RAMPI L., “Le diatomee del mare Ligure presso San Remo”, *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, vol. 77, pp. 355–366, 1938.
- [RAM 16] RAMONDENC S., GOUTX M., LOMBARD F. *et al.*, “An initial carbon export assessment in the Mediterranean Sea based on drifting sediment traps and the Underwater Vision Profiler data sets”, *Deep-Sea Research Part I-Oceanographic Research Papers*, vol. 117, pp. 107–119, 2016.

- [RAS 79] RASSOULZADEGAN F., “Cycles annuels de la distribution de différentes catégories de particules du seston et essai d’identification des principales poussées phytoplanctoniques dans les eaux néritiques de Villefranche-sur-Mer”, *Journal of Experimental Marine Biology and Ecology*, vol. 38, pp. 41–56, 1979.
- [REY 19] REYGONDEAU G., DUNN D., “Pelagic biogeography”, in COCHRAN J.K., BOKUNIEWICZ H.J., YAGER P.L. (eds), *Encyclopedia of Ocean Sciences (Third Edition)*, Academic Press, Oxford, 2019.
- [RIC 18] RICHON C., DUTAY J.C., DULAC F. *et al.*, “Modeling the impacts of atmospheric deposition of nitrogen and desert dust-derived phosphorus on nutrients and biological budgets of the Mediterranean Sea”, *Progress in Oceanography*, vol. 163, pp. 21–39, 2018.
- [RIC 19] RICHON C., DUTAY J.C., BOPP L. *et al.*, “Biogeochemical response of the Mediterranean Sea to the transient SRES-A2 climate change scenario”, *Biogeosciences*, vol. 16, pp. 135–165, 2019.
- [ROM 15] ROMAGNAN J.B., LEGENDRE L., GUIDI L. *et al.*, “Comprehensive model of annual plankton succession based on the whole-plankton time series approach”, *Plos One*, vol. 10, 2015.
- [SAL 19] SALGADO-HERNANZ P.M., RACAULT M.F., FONT-MUNOZ J.S. *et al.*, “Trends in phytoplankton phenology in the Mediterranean Sea based on ocean-colour remote sensing”, *Remote Sensing of Environment*, vol. 221, pp. 50–64, 2019.
- [SAN 71] SAN FELIU J.M., MUÑOZ F., “Fluctuations d’une année à l’autre dans l’intensité de l’affleurement dans la Méditerranée occidentale”, *Investigación pesquera*, vol. 35, p. e159, 1971.
- [SEV 14] SEVERIN T., CONAN P., DE MADRON X.D. *et al.*, “Impact of open-ocean convection on nutrients, phytoplankton biomass and activity”, *Deep-Sea Research Part I-Oceanographic Research Papers*, vol. 94, pp. 62–71, 2014.
- [SEV 17] SEVERIN T., KESSOURI F., REMBAUVILLE M. *et al.*, “Open-ocean convection process: A driver of the winter nutrient supply and the spring phytoplankton distribution in the Northwestern Mediterranean Sea”, *Journal of Geophysical Research-Oceans*, vol. 122, pp. 4587–4601, 2017.
- [SIE 78] SIEBURTH J.M., SMETACEK V., LENZ J., “Pelagic ecosystem structure – heterotrophic compartments of plankton and their relationship to plankton size fractions – comment”, *Limnology and Oceanography*, vol. 23, pp. 1256–1263, 1978.

- [SOM 18] SOMOT S., HOUPERT L., SEVAULT F. *et al.*, “Characterizing, modelling and understanding the climate variability of the deep water formation in the North-Western Mediterranean Sea”, *Climate Dynamics*, vol. 51, pp. 1179–1210, 2018.
- [SVE 53] SVERDRUP H., “On conditions for the vernal blooming of phytoplankton”, *Journal du Conseil/Conseil Permanent International pour l’Exploration de la Mer*, vol. 18, pp. 287–295, 1953.
- [THE 11] THE MERMEX GROUP, “Marine ecosystems’ responses to climatic and anthropogenic forcings in the Mediterranean”, *Progress in Oceanography*, vol. 91, pp. 97–166, 2011.
- [THY 14] THYSSEN M., GREGORI G.J., GRISONI J.M. *et al.*, “Onset of the spring bloom in the northwestern Mediterranean Sea: influence of environmental pulse events on the in situ hourly-scale dynamics of the phytoplankton community structure”, *Frontiers in Microbiology*, vol. 5, 2014.
- [TUN 07] TUNIN-LEY A., LABAT J.P., GASPARINI S. *et al.*, “Annual cycle and diversity of species and infraspecific taxa of *Ceratium* (Dinophyceae) in the Ligurian Sea, northwest Mediterranean”, *Journal of Phycology*, vol. 43, pp. 1149–1163, 2007.
- [UIT 06] UITZ J., CLAUSTRE H., MOREL A. *et al.*, “Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll”, *Journal of Geophysical Research: Oceans*, vol. 111, 2006.
- [UIT 08] UITZ J., HUOT Y., BRUYANT F. *et al.*, “Relating phytoplankton photophysiological properties to community structure on large scales”, *Limnology and Oceanography*, vol. 53, pp. 614–630, 2008.
- [UIT 12] UITZ J., STRAMSKI D., GENTILI B. *et al.*, “Estimates of phytoplankton class-specific and total primary production in the Mediterranean Sea from satellite ocean color observations”, *Global Biogeochemical Cycles*, vol. 26, 2012.
- [ULS 16] ULSES C., AUGER P.A., SOETAERT K. *et al.*, “Budget of organic carbon in the North-Western Mediterranean open sea over the period 2004–2008 using 3-D coupled physical-biogeochemical modeling”, *Journal of Geophysical Research-Oceans*, vol. 121, pp. 7026–7055, 2016.
- [VAU 90] VAULOT D., PARTENSKY F., NEVEUX J. *et al.*, “Winter presence of prochlorophytes in surface waters of the northwestern Mediterranean Sea”, *Limnology and Oceanography*, vol. 35, pp. 1156–1164, 1990.
- [VID 00] VIDUSSI F., MARTY J.-C., CHIAVÉRINI J., “Phytoplankton pigment variations during the transition from spring bloom to oligotrophy in the northwestern Mediterranean sea”, *Deep Sea Research Part I: Oceanographic Research Papers*, vol. 47, pp. 423–445, 2000.

- [VID 01] VIDUSSI F., CLAUSTRE H., MANCA B.B. *et al.*, “Phytoplankton pigment distribution in relation to upper thermocline circulation in the eastern Mediterranean Sea during winter”, *Journal of Geophysical Research: Oceans*, vol. 106, pp. 19939–19956, 2001.
- [VOL 12] VOLPE G., BUONGIORNO NARDELLI B., CIPOLLINI P. *et al.*, “Seasonal to interannual phytoplankton response to physical processes in the Mediterranean Sea from satellite observations”, *Remote Sensing of Environment*, vol. 117, pp. 223–235, 2012.
- [WAT 79] WATERBURY J.B., WATSON S.W., GUILLARD R.R.L. *et al.*, “Widespread occurrence of a unicellular, marine, planktonic, cyanobacterium [10]”, *Nature*, vol. 277, pp. 293–294, 1979.
- [WAT 86] WATERBURY J.B., WATSON S.W., VALOIS F.W. *et al.*, “Biological and ecological characterization of the marine unicellular cyanobacterium *Synechococcus*”, in PLATT T., WILLIAN L.W.W. (eds), *Photosynthetic Picoplankton*, Canadian Bulletins of Fisheries and Aquatic Sciences, Ottawa, 1986.