Remotely sensed seasonal dynamics of phytoplankton in the Ligurian Sea in 1997–1999

Nikolay P. Nezlin,[1,2] Genevieve Lacroix,[3] Andrey G. Kostianoy,[1] and Salim Djenidi[4]

Received 7 September 2000; revised 24 March 2004; accepted 23 April 2004; published 17 July 2004.

[1] Remotely sensed data and a one-dimensional hydrophysical model were used to study the seasonal dynamics of surface plant pigments concentration in the Ligurian-Provençal basin. The variations of phytoplankton biomass were estimated from the observations of the Coastal Zone Color Scanner (1978–1986) and Sea-viewing Wide Field-of-view Sensor (SeaWiFS) (September 1997 to October 1999) radiometers. The factors of physical environment analyzed included remotely sensed sea surface temperature (from advanced very high resolution radiometers), wind, air temperature, and atmospheric precipitation. The Geohydrodynamics and Environment Research (GHER) model was used to explain the observed correlations between the physical forcing and the response of phytoplankton biomass. The general pattern of phytoplankton seasonal dynamics was typical to subtropical areas: maximum biomass during cold season from October to April and low biomass during summer months. The intensity of winter/spring bloom significantly varied during different years. The correlation was revealed between the summer/autumn air temperature contrast (expressed as the difference between the air temperatures in August and in November) and the maximum monthly averaged surface chlorophyll concentration during the subsequent winter/spring bloom. The features of seasonal dynamics of phytoplankton are regulated by the physical impacts influencing water stratification. The difference between two seasonal cycles (from September 1997 to October 1999) illustrates the response of phytoplankton growth to local meteorological conditions. In March–April 1999 the vernal bloom was much more pronounced; it resulted from deeper winter cooling and more intensive winter convection. Heating of surface water layer, wind mixing, and freshwater load with rains and river discharge either stimulate or depress the development of phytoplankton, depending on what limiting environmental factor (light or nutrient limitation) prevailed. *INDEX TERMS:* 4227 Oceanography: General: Diurnal, seasonal, and annual cycles; 4845 Oceanography: Biological and Chemical: Nutrients and nutrient cycling; 4842 Oceanography: Biological and Chemical: Modeling; 0933 Exploration Geophysics: Remote sensing; *KEYWORDS:* SeaWiFS, seasonal dynamics, Ligurian Sea

Citation: Nezlin, N. P., G. Lacroix, A. G. Kostianoy, and S. Djenidi (2004), Remotely sensed seasonal dynamics of phytoplankton in the Ligurian Sea in 1997–1999, *J. Geophys. Res.*, *109*, C07013, doi:10.1029/2000JC000628.

1. Introduction

[2] As for other regions of the Mediterranean Sea, the biological production heterogeneity of the Ligurian Sea is closely associated with local and regional hydrodynamical factors, especially those responsible for a high variability of the mixed layer depth in such a strongly stratified environment. This area is typically oligotrophic, and therefore any supply of nutrients is extremely important for the primary production. Moreover, the overall system is dominated by a marked seasonal cycle as a result of the meteorological signal, as well as a significant interannual variability [*La Violette*, 1994; *Marty et al.*, 2002].

[3] If sea surface temperature data provided by the satellite imagery have been extensively used to investigate both seasonal and interannual variability in the western Mediterranean Sea [e.g., *La Violette*, 1994], relatively few were done for chlorophyll patterns, especially in the Ligurian Sea. One can emphasize for instance the analysis made by *Arnone* [1994] for the 1979 Coastal Zone Color Scanner (CZCS) data of the western Mediterranean Sea where the seasonal signal as well as the spatial variability are highlighted. It is shown on the one hand that clear differences in the timing and intensity of the spring and fall blooms occur for different subbasins as a response to local physical events. It is shown on the other hand that subregions with energetic circulation and local wind forcing have higher chlorophyll concentrations (e.g., the Alboran Sea and the Gulf of Lions; see also *Morel and Andre* [1991]). Vertical

[1]P.P. Shirshov Institute of Oceanology, Moscow, Russia.
[2]Now at Southern California Coastal Water Research Project, Westminster, California, USA.
[3]Management Unit of the North Sea Mathematical Models, Royal Belgian Institute for Natural Sciences, Brussels, Belgium.
[4]MARE Oceanographic Research Center, University of Liege, Liège, Belgium.

0148-0227/04/2000JC000628$09.00

mixing of the upper water column by wind events results in enhancement of nutrients at the surface, as observed in the Gulf of Lions in the spring as a response to the Mistral wind [*Millot and Wald*, 1980; *Morel and Andre*, 1991].

[4] We focus here on the general features of spatial distribution and temporal variation of remotely sensed surface chlorophyll concentration in the open part of the Ligurian-Provençal basin, i.e., the rectangle area located between the meridians 6°30′E–11°00′E and to the north of the 42°N latitude. The goal of the study is to correlate the pattern of chlorophyll seasonal variations with the local characteristics of hydrological and meteorological factors influencing water stratification (wind, air temperature, freshwater input with atmospheric precipitation and river discharge, etc.). The influence of local meteorological factors on water stratification is analyzed using a one-dimensional (1-D) hydrophysical model.

[5] The remotely sensed data collected during two recent decades provide oceanographers with a large volume of information on the state of the surface of the World Ocean, although these data are not always accurate enough. The information collected by the optical sensors is especially valuable for biologists because it characterizes the concentration of plant pigments in the most productive surface ocean layer. The absolute values derived from remote sensing characterize not only chlorophyll concentration in algae cells; they also depend on the concentration of *Gelbstoffe* (the colored detritus), concentration of phytoplankton and some products of its excretion, etc. However, all these parameters are related to the biomass of phytoplankton and its life activity. The remotely sensed surface chlorophyll concentration is an important quantity, which can be used for predictions of the type of vertical distribution of chlorophyll [*Morel and Berthon*, 1989] and other properties of the pelagic community [*Vinogradov et al.*, 1992, 1997, 1999], including primary production rate and biomass of different trophic groups of zooplankton.

[6] Since satellite data provide information on surface properties, modeling is meant to be an appropriate complementary tool that can highlight some characteristics within the water body. We use here a model of the mixed layer [*Lacroix and Nival*, 1998] in order to complete the interpretation derived from the observations. The model results should help to understand some processes along the vertical dimension such as the wind mixing that can explain partly some nutrients input in the surface water and the consecutive phytoplankton development [e.g., *Therriault et al.*, 1978; *Klein and Coste*, 1984].

[7] Considering that the establishment and decay of the thermocline are strongly dependent on the atmospheric conditions, the model will be forced by surface wind stress and heat fluxes computed from real meteorological conditions, a high meteorological data rate sampling allowing simulations that give high confidence in the mixed layer dynamics [*Ridderinkhof*, 1992; *Lacroix and Nival*, 1998]. The model results would permit to corroborate some hypotheses derived from the satellite data observation concerning the correlation between the physical forcing and the response of the ecosystem.

[8] In section 2 we describe the general features of hydrology of the western Mediterranean Sea in general and the Ligurian-Provençal Basin in particular with focus on the stratification of water column. In section 3 we describe the remotely sensed, hydrological, and meteorological data we use for the analysis. In section 4 we indicate the general features of spatial distribution of remotely sensed phytoplankton biomass to emphasize the differences between the open sea zone we analyze and the adjacent regions. In section 5 we analyze the historical data on the intensity of spring blooms in the Ligurian Sea and discuss the meteorological forcing influencing the variability we observed during two decades. Then, in section 6, we analyze in detail the time series obtained during two extremely different seasonal cycles (1997–1998 and 1998–1999). To confirm the conclusion on the role of stratification in the formation of phytoplankton production, we use a 1-D model of the upper mixed layer (section 7). The concluding remarks are given in section 8.

2. Ligurian Sea General Features of Hydrology and Surface Circulation

[9] The Mediterranean site is characteristic of a deep sea where the tides are negligible and the dynamics dominated by the exchanges with the atmosphere. At the global scale, momentum and buoyancy fluxes drive a thermohaline general circulation modulated by an energetic seasonal signal, including deep water formation phenomenon.

[10] In the northern part of the western basin, from the Gulf of Lions to the Ligurian Sea, the continental shelf is very narrow (few kilometers width), except for the wide shelves of the French northwestern corner and the Tuscan coast of Italy. Though the physical boundary with the southern Algerian basin is not well defined, the Ligurian-Provençal basin is clearly separated from the Tyrrhenian Sea by the Corsica Channel (see Figures 1 and 2).

[11] The regional climatology is responsible for a negative water balance, the evaporation being much larger than the precipitations and the river supply. In this concentration basin the deficit is compensated for by important inverse estuarine like exchanges through the Gibraltar Strait [e.g., *Bethoux*, 1980; *Bryden*, 1991]. In the western part of the Mediterranean Sea, large cyclonic circulations of incoming surface Atlantic water (Modified Atlantic Water (MAW) is formed as deep as 200 m) are developed throughout the year in the Ligurian-Provençal and in the Tyrrhenian basins [e.g., *Millot*, 1991, 1999; *Send et al.*, 1999]. Transient winds, associated with a complicated bottom topography and coastline geometry, trigger coastal upwelling and a complex mesoscale activity superimposed to the thermohaline circulation patterns [*Millot and Wald*, 1980; *Alberola and Millot*, 2003].

[12] The heating of surface water during late spring progressively establishes a vertical stratification of the upper layer [*Marty et al.*, 2002]. The consequent thermocline is affected by the water motions, giving rise to horizontal temperature gradients particularly visible on infrared images in the form of more or less marked thermal fronts. In the Ligurian Sea a sharp frontal system associated with the prevailing cyclonic circulation separates denser water of the cold core of the central divergence from lighter warm water of the Ligurian shelf/slope current flowing around it (Figure 2). The width of the peripheral strip of less dense water is highly variable at a large range of scales [*Astraldi et al.*, 1994; *Send et al.*, 1999; *Alberola and Millot*,

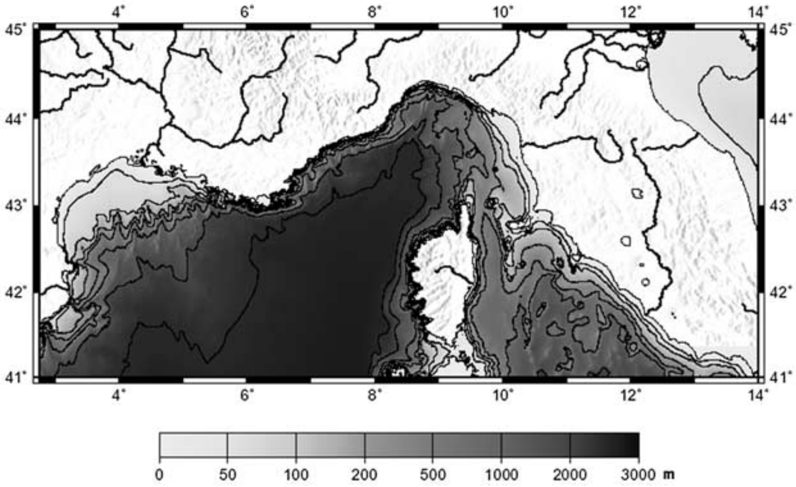

Figure 1. Bottom topography of the Ligurian Sea and the adjacent regions.

2003]. Another active and persistent divergence zone can be found in the northern Tyrrhenian, enhanced by winds blowing eastward between Corsica and Sardinia. According to *Astraldi and Gasparini* [1992] and *Marullo et al.* [1994], a clear seasonality is observed in the exchanges between the Tyrrhenian and Ligurian Seas, the two basins being more or less isolated during the summer, while in winter, surface water is lost to the Ligurian Sea through the Corsica Channel. This flow merges with the southern branch of the Ligurian Current near Cape Corse and reinforces the northern Ligurian Current. In the fall season the progressive erosion of the seasonal thermocline starts, and in winter conditions the thermal signature of the frontal dynamics is obviously much weaker.

[13] During winter, under the effect of dry and cold continental winds and of the temperature contrast between air and sea, evaporation and upward heat transfer become very important. The density of the upper layer strongly increases, inducing baroclinic instability and convective deep water formation. Deep water formation is observed in the Gulf of Lions [e.g., *Leaman*, 1994; *Send et al.*, 1999; *Bethoux et al.*, 2002] and in the eastern Mediterranean Sea [e.g., *Robinson et al.*, 1991]. The water formed in both basins ventilates deep and intermediate layers and develops the core circulation of the Mediterranean Sea.

[14] The cyclonic circulation of the Ligurian Sea produces in its central part a zone of divergence resulting in a doming structure of the isopycnals, evident from sea surface temperature (SST) distribution (Figure 3). This zone of divergence exists there throughout the year, being seasonally modulated, resulting in enrichment of the upper mixed layer by nutrients. Another source of nutrient enrichment seems to be vertical diffusion associated with wind forcing. On the contrary, in the Gulf of Lions, nutrient enrichment results from both convective mixing associated with deep water formation in winter and vertical diffusion associated with wind forcing.

3. Data Used

[15] The remotely sensed data used for analysis are listed in Table 1.

3.1. Advanced Very High Resolution Radiometer Sea Surface Temperature

[16] We used two sources of sea surface temperature measured by infrared sensors AVHRR aboard the NOAA-7, -9, -11, and -14 polar orbiting satellites: multichannel sea surface temperature (MCSST) and climatically averaged sea surface temperature.

[17] MCSST data were processed using the multichannel sea surface temperature algorithm [*McClain et al.*, 1985] at the Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory (PODAAC JPL). The data have been collected since November 1981, averaged weekly, and interpolated (without missing values) over global equal-angle grids of spatial resolution of 2048 pixels/360 degrees (~18.5 km) per degree of longitude and latitude. The nominal accuracy is 0.3°C. We used only the data collected during nighttime (descending pass) to avoid the short-period SST variations resulting from high daytime heating of thin surface layer. These data were used to produce 8-day maps of SST distribution. The intervals we used coincided with the 8-day intervals used in the Goddard Space Flight Center (GSFC) to produce SeaWiFS surface chlorophyll concentration maps (1–8 January, 9–16 January, etc.) rather than the intervals used at JPL to produce MCSST grids. To fit all data (AVHRR SST and SeaWiFS chlorophyll) to similar 8-day intervals, we used weighted averaging of SST data.

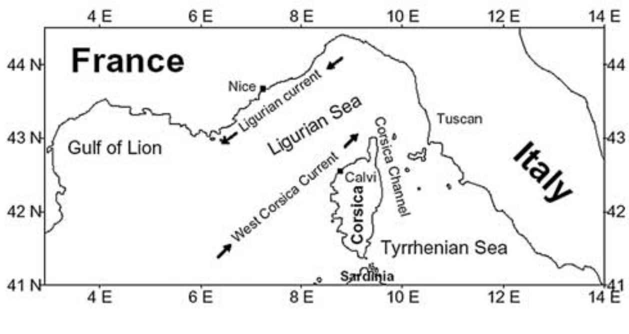

Figure 2. General scheme of circulation in the Ligurian Sea.

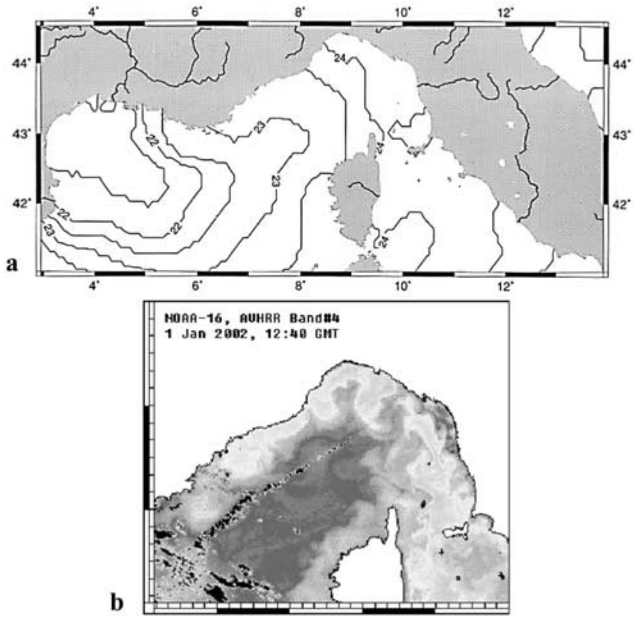

Figure 3. (a) Distribution of climatically averaged (1985–1997) sea surface temperature in the Ligurian Sea, 15–19 July and (b) the AVHRR infrared image obtained 1 January 2002 (courtesy of S.V. Stanichnyi from Marine Hydrophysical Institute, Sevastopol, Ukraine).

[18] The data set on climatically averaged sea surface temperature was created at JPL on the basis of the Pathfinder sea surface temperature data. The latter daily data were processed within the scope of NOAA/NASA AVHRR Oceans Pathfinder Project at JPL. The SST data were derived from the AVHRR radiometers (see above) using the enhanced (as compared with MCSST) nonlinear algorithm [*Walton*, 1988]. The spatial resolution was 4096 pixels/360 degrees (~9.28 km) per degree of longitude and latitude. These data (both daytime and nighttime) were climatically averaged for the period 1985–1997. The details of the process of smoothing and averaging are described by *Casey and Cornillon* [1999]. The obtained from JPL pentad (5-day) climatologies were transformed to 8-day climatologies using weighted averaging to estimate the SST anomalies from the MCSST values and the climatologies.

3.2. NCEP Wind Data

[19] We used the zonal and meridional wind speed values at 10 m from SeaWiFS near-real time NCEP data set (the ancillary wind provided to SeaWiFS users). The data were obtained from the GSFC Distributed Active Archive Center (DAAC). The data were interpolated to equidistant cylindrical images of 1-degree latitude/longitude resolution. The temporal resolution is 6–12 hours. We averaged the absolute values of wind speed over 8-day intervals.

3.3. Coastal Zone Color Scanner

[20] The data were collected from November 1978 to June 1986 by Coastal Zone Color Scanner (CZCS) radiometer [*Hovis et al.*, 1980] on the Nimbus-7 satellite. The ocean surface color was measured at the bands 443, 520, 550, 670, and 750 nm. More than 60,000 images were processed at the Goddard Space Flight Center and summarized as monthly averaged data. These data were stored on compact discs in the form of regular grids of 0.1758° resolution, equivalent to ~18.5 km on the equator. We used these monthly data to analyze the intensities of winter/spring blooms in the region under study.

3.4. Sea-Viewing Wide Field-of-View Sensor

[21] The ocean color data (1997–1999; bands 412, 443, 490, 510, 555, 670, 765, and 865 nm) used in this study were produced by the SeaWiFS project at Goddard Space Flight Center [*Acker et al.*, 2002]. The data were obtained from the Goddard Distributed Active Archive Center under the auspices of NASA. We use this data in accord with the SeaWiFS Research Data Use Terms and Conditions Agreement.

[22] In this study the Level 3 Standard Mapped Data (global grids of the resolution similar to Pathfinder SST) of CZCS-like pigment concentration were used to enable comparing the absolute values with CZCS observations obtained in 1978–1986. The algorithms of optical data processing and calculating plant pigment concentrations are given in the work of *O'Reilly et al.* [1998]. Below we use the terms "chlorophyll concentration" and "phytoplankton biomass," meaning the values calculated by the "old" algorithm used to process both CZCS and SeaWiFS data.

[23] The data grids were processed using the software (DDNPN) specifically designed for this purpose and used in

Table 1. Remotely Sensed Data Used for Analysis[a]

Data	Spatial Resolution	Temporal Resolution	Period of Observations	Source
Multichannel sea surface temperature (MCSST)	2048 pixels/360 degrees (~18.5 km)	weekly averaged	Nov. 1981 to Oct. 1999	JPL PODAAC Product 016
Climatically averaged sea surface temperature	4096 pixels/360 degrees (~9.28 km)	5-day averaged	1985–1999	JPL PODAAC
NCEP Wind data	1 degree	6-hour	March 1997 to Oct. 1999	GSFC DAAC
Coastal Zone Color Scanner (CZCS) surface chlorophyll concentration	2048 pixels/360 degrees (~18.5 km)	monthly	Nov. 1978 to June 1986	GSFC DAAC
Sea-viewing Wide Field-of-view Sensor (SeaWiFS) surface chlorophyll concentration	4096 pixels/360 degrees (~9.28 km)	daily, 8-day, monthly	Sept. 1997 to Oct. 1999	GSFC DAAC
Precipitation	1 degree	monthly	Jan. 1986 to Oct. 1999	GPCC

[a]Abbreviations are as follows: JPL PODAAC, Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory, Pasadena, California; GSFC DAAC, Distributed Active Archive Center at the Goddard Space Flight Center, Greenbelt, Maryland; GPCC, Global Precipitation Climatology Centre, Offenbach, Germany.

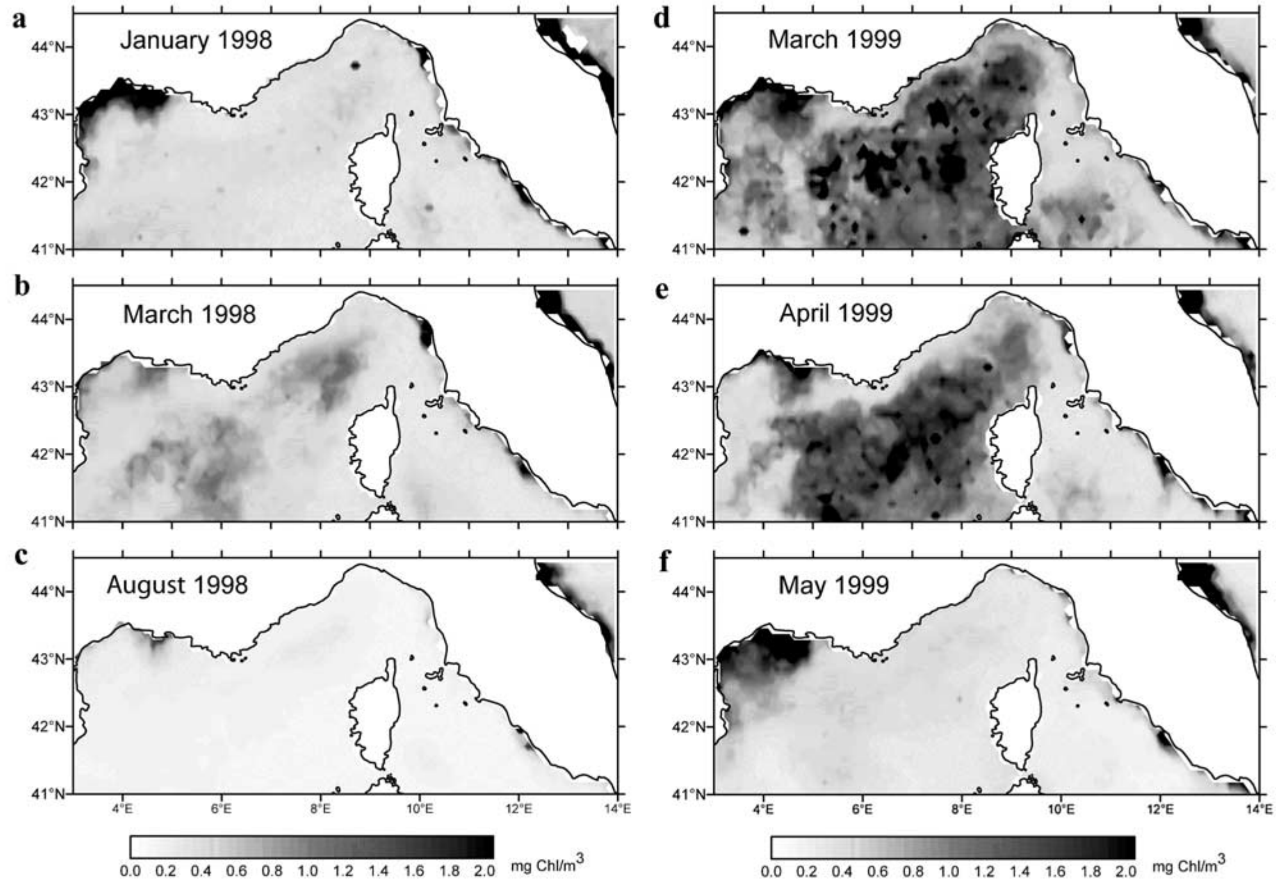

Figure 4. Seasonal variations of plant pigment concentration (monthly means); (a) January 1998; (b) March 1998; (c) August 1998; (d) March 1999; (e) April 1999; (f) May 1999.

our previous studies [*Nezlin et al.*, 1999; *Nezlin*, 2000; *Afanasyev et al.*, 2001; *Nezlin and Li*, 2003]. This software works with files containing SST, CZCS, SeaWiFS, and wind and precipitation data and is a convenient tool to convert the level 3 grids to time series data.

[24] The data on wind speed, SST, and surface chlorophyll concentration were averaged within the rectangle area between 6°30′–11°00′E and to the north of 42°00′N. For the analysis of the chlorophyll concentrations, we calculated the medians instead of arithmetic means. This nonparametric statistic is preferable in this case owing to sharply asymmetrical distribution of surface chlorophyll values [*Banse and English*, 1994].

[25] The data on surface air temperature were collected at the meteorological station in Nice (43°39′N, 7°12′E). We used both monthly averaged data for the period 1978–1999 and daily data for the period January 1995 to September 1999. To produce daily air temperature anomalies, we averaged daily data over the period 1995–1999.

[26] We used conductivity-temperature-depth-measured hydrological profiles (temperature, salinity, and specific density) at two stations in May 1998 and May 1999: station 1 at the transect Calvi-Nice (42°36.25′N, 8°42′E, 28/05/1998, 06:15) and station A (42°37.00′N, 8°42.25′E, 27/05/1999, 10:25). To force the model, we use the meteorological data collected by the automatic weather station located at the end of the Revellata Peninsula (STARESO, Calvi, northwest Corsica) [*Djenidi et al.*, 1999].

4. Spatial Distribution of Sea Surface Temperature and Chlorophyll

[27] The seasonal cycle of chlorophyll concentration (i.e., phytoplankton biomass) in the region under study includes two periods: low values during summer months and high values during autumn/winter/spring period (from October to April). *Morel and Andre* [1991] indicate here a six-fold change in the production rate between February and May; substantial seasonal variability of chlorophyll was registered during 9-year observations at the Dynamique des Flux de Matière en Mediterranée (DYFAMED) station [*Marty et al.*, 2002]. This type of seasonal variation is typical to subtropical regions [*Longhurst*, 1995]. Summer minimum indicates the period of nutrient limitation of phytoplankton growth. Typical to midlatitudes winter minimum resulting from light limitation of phytoplankton growth during winter convection period was never observed with both CZCS (1978–1986) and SeaWiFS (1997–1999) data.

[28] However, during some years of remotely sensed observations in March–April, the phytoplankton biomass significantly increased. These spring blooms were mostly evident in 1982 and 1999. Figure 4 illustrates typical patterns of spatial distribution of chlorophyll in the region

under study in winter, spring, and summer. The chlorophyll concentration in spring 1999 was much higher as compared with 1998 over the whole area of the Ligurian Sea and adjacent regions.

[29] The patterns of seasonal variations of phytoplankton will be discussed later (sections 5 and 6). In this section we analyze the spatial distribution of phytoplankton biomass.

[30] The peculiar feature of the northwest Mediterranean Sea is that in contrast to many other marginal seas, the nearshore zones are not rich in surface chlorophyll, excluding the continental shelf of the Gulf of Lions influenced by the Rhone River (Figure 4). This spatial distribution seems to result from the general pattern of water circulation in the Ligurian Sea (Figures 2 and 3). Flowing from the south, the Tyrrhenian and West Corsica Currents transport water that is poor in phytoplankton and nutrients from the Tyrrhenian Sea and the Western Mediterranean Basin, respectively.

[31] The main reason of low phytoplankton biomass along the shoreline is the extremely low river discharge. Therefore the remotely sensed data (SeaWiFS observations) reflect there the chlorophyll concentration rather than the concentration of *Gelbstoffe* and suspended inorganic matter; *Morel and Andre* [1991] earlier indicated that case 1 waters are largely predominant in that area. The Rhone is the only one big river in the region under study. In the Rhone mouth (the Gulf of Lions) we permanently observed the pronounced plume, where its size varies with the river discharge. In the open part of the Ligurian Sea, in contrast, the seasonal dynamics of phytoplankton is regulated by direct meteorological forcing, i.e., wind mixing and heat and evaporation-precipitation balance.

5. Interannual Variations of the Intensity of Spring Phytoplankton Bloom

[32] The seasonal variation of surface chlorophyll concentration reflects the dynamics of phytoplankton growth limited by the external factors. In the region under study the seasonal cycle of phytoplankton combines two features, typical to both subtropical and midlatitudinal pelagic ecosystems. The general pattern of phytoplankton seasonal variations is obviously typical to subtropical regions [see *Longhurst*, 1995]. The phytoplankton biomass increased in autumn and remained high by late spring/early summer, when the formation of seasonal thermocline resulted in nutrient limitation of phytoplankton growth. During the midwinter seasons we never observed typical to temperate latitude low-chlorophyll values, resulting from light limitation of phytoplankton growth caused by deep winter convection. However, during some years, we observed another typical to midlatitude feature of phytoplankton development: the spring bloom in March–April resulted from the formation of seasonal thermocline. These spring blooms were most intensive in 1982 and 1999. No interannual trend in the intensity of winter/spring blooms was noted; the absence of such a trend in the open Ligurian Sea was also noted by *Goffart et al.* [2002].

[33] We speculate that the differences between the spring bloom intensities observed during different years result from the differences in hydrological conditions. Figure 5 illustrates the correlation (R = 0.68; F = 7.09; d.f. = 1, 8; p = 0.029) between the bloom intensity and seasonal air temperature contrasts. The seasonal air temperature contrast was defined as the monthly averaged air temperature in August minus similar value in November measured in Nice (43°39′N, 7°12′E); the bloom intensity was defined as the maximum monthly averaged plant pigment concentration (measured by CZCS in 1978–1986 and by SeaWiFS in 1997–1999) in the phytoplankton bloom observed during the subsequent winter/spring period.

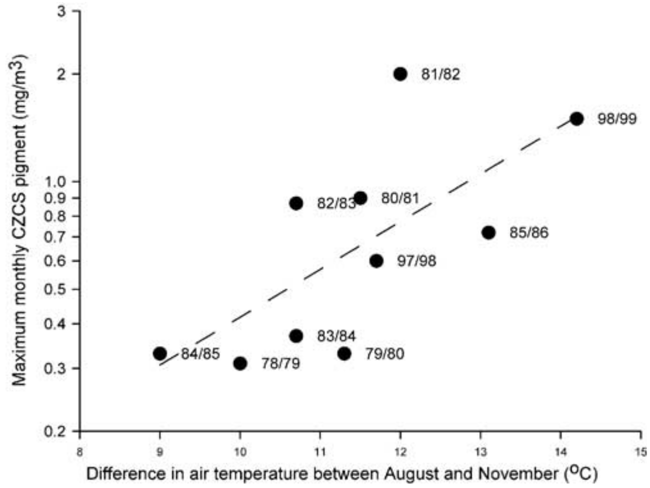

Figure 5. Correlation between the seasonal air temperature contrast (the difference between monthly averaged air temperatures in August and November) measured in Nice (43°39′N, 7°12′E) and the maximum monthly averaged remotely sensed plant pigment concentration during the subsequent winter/spring bloom.

[34] Two aspects are worth attention. On the one hand, a greater difference between summer and autumn air temperatures indicates more intensive cooling of sea surface in the autumn. This cooling, in turn, results in deeper autumn/winter convection, which enriches the upper mixed layer with nutrients. Deeper convection resulting in lower sea surface temperature also could favor earlier formation of seasonal thermocline during the subsequent spring period. On the other hand, the difference between summer and autumn air temperatures seems to be nothing but an index illustrating the entire complex of meteorological factors (winds, precipitation, clouds, etc.) influencing water stratification. We could suppose that more rapid decrease of air temperature is correlated with "stormy weather" (strong winds and heavy rains). However, the influence of these factors on phytoplankton growth requires special explanation. Below we describe the mechanism of influence of hydrometeorological factors on phytoplankton growth, taking into account the stratification within the euphotic layer.

[35] Two main factors limit phytoplankton growth: illumination and nutrients [*Sverdrup*, 1953]. Light limitation is crucial under low stratification (e.g., winter convection) because algae cells are dispersed by turbulent mixing within deep dark layers. Nutrient limitation is crucial under enhanced stratification (e.g., seasonal thermocline in summer) because nutrients do not penetrate into the euphotic (i.e., well illuminated) upper mixed layer. The hydrometeorological factors (air temperature, wind, fresh water load with precipitation, and river discharge) either increase or decrease the stratification within the euphotic layer.

Table 2. Hydrometeorological Factors Influencing Phytoplankton Growth During Different Seasons

Season	Hydrometeorological Factors	Stratification	Phytoplankton Growth
Winter	maximum wind mixing; maximum cooling of upper layer	deep convection	winter minimum resulting from light limitation
Spring	wind mixing weakens; heating of upper layer increases	formation of seasonal thermocline	spring bloom
Summer	maximum heating of upper layer; minimum wind mixing	maximum stratification	summer minimum resulting from nutrient limitation
Autumn	cooling of upper layer increases; wind mixing increases	erosion of seasonal thermocline	autumn bloom

[36] Typical seasonal cycles of phytoplankton result from the combined effect of seasonal cycles of hydrometeorological factors influencing water stratification within the euphotic layer (Table 2). The most illustrative is the phytoplankton seasonal cycle in midlatitudes with two maximums in spring and autumn. In high latitudes (cold and windy) the winter minimum is more pronounced and the summer minimum is less pronounced or absent. In low latitudes (warm and less windy) the winter minimum is less pronounced and the summer minimum is more pronounced (we do not analyze here such seasonal processes as upwelling, monsoons, etc.). We expect the deviations from typical seasonal pattern of hydrometeorological factors to exhibit a response in local phytoplankton biomass.

6. Differences Between the Winter/Spring Phytoplankton Blooms in 1997–1998 and 1998–1999

[37] In this section we compare two seasons, 1997–1998 (no spring bloom) and 1998–1999, when the spring bloom was pronounced. Similar differences between these 2 years are evident also from the DYFAMED time series [*Marty and Chiaverini*, 2002; *Marty et al.*, 2002]. Weaker than typical spring bloom in 1998 in the southern Ligurian Sea was noted by *Goffart et al.* [2002]. Figure 6 illustrates the variations of precipitation, air temperature anomalies, wind, SST anomalies, and surface chlorophyll concentration in the offshore part of the Ligurian Sea during the period from September 1997 to October 1999.

[38] In 1997 the intensive growth of phytoplankton started in October, and in 1998 the autumn bloom was initiated in November. We explain this delay by the difference between the intensity of atmospheric precipitation. In September–October 1997 the precipitation was very low (1–2 mm/day), and during the autumn of 1998 it exceeded climatic values (3.5–4.5 mm/day). Therefore the higher than normal amount of freshwater load into the upper mixed layer in autumn 1998 made water column more stratified, and the autumn convection began as late as in November, induced by strong winds and very cold air (air temperature anomaly in November 1998 was about −5°C). Taking into account that autumn bloom results from the erosion of seasonal pycnocline, the beginning of winter convection induced the development of phytoplankton. In November 1997 the biomass of phytoplankton did not increase. The peaks were observed in December of both 1997 and 1998.

[39] In January–February of both 1998 and 1999 the phytoplankton biomass slightly decreased. We explain it with winter convection resulting in light limitation of phytoplankton growth. Both minimum periods coincided with the periods of strong winds. In February 1998 the wind forcing was weaker than in February 1999; however, the convection seemed to be enhanced by very weak precipitation.

[40] In March–April the spring blooms were observed; we explain them by the formation of seasonal thermocline and the cessation of light limitation. In March–April 1998 the biomass did not exceed the peak observed in December 1997. However, in March–April 1999 the surface chlorophyll concentration was as high as 2 mg/m^3. In 1999 the stronger bloom seemed to result from deeper convection during the preceding autumn/winter period, caused by lower air temperature (resulting in negative SST anomalies) and stronger winds in November and February. The salinity profiles observed in May 1998 and 1999 (Figure 7b) confirm that in 1999, more saline water penetrated from the deep layer to the upper part of water column. Deep convection enriched the upper layer with nutrients. Moreover, we could suppose that during rather warm and not windy March 1999, the seasonal thermocline was formed faster. The temperature and density profiles (Figures 7a and 7c) observed in May 1998 and 1999 support this conclusion. In 1999 the thermocline was two-stepped; this fact indicates that its formation started earlier. In March 1998, SST was slightly higher than normal and the air temperature was close to the climatic average. On the contrary, in March 1999, SST anomaly was negative and the air temperature anomaly reached +2°C. Hence in 1999 the temperature contrast between the atmosphere and water surface was higher and enhanced the formation of seasonal thermocline. This process favored more intensive spring bloom of phytoplankton.

[41] During the period of nutrient limitation (from May to September) the phytoplankton biomass in 1998 was lower as compared with the corresponding period of 1999. In the previous study, *Lacroix* [1998] has shown that the more productive years in the Ligurian Sea are those for which the annual mean concentration of nutrients in the mixed layer is the highest. This is the case for more windy and less sunny years because in this situation the mixed layer is deeper [*Lacroix and Nival*, 1998]. The second condition of high productivity is that the initial distribution of nutrients should be favorable to their entrainment toward the surface [*Lacroix*, 1998].

[42] The winter 1998–1999 is characterized by a substantial deepening of the mixed layer resulting in a high input of nutrients to the surface layer, giving rise to an intense spring bloom. The nutrients entrained into the upper layer constitute a storage for the summer and result (in favorable meteorological conditions) in higher phytoplankton production in deeper layers in summer despite strong stratification. During the winter 1997–1998, the mixing

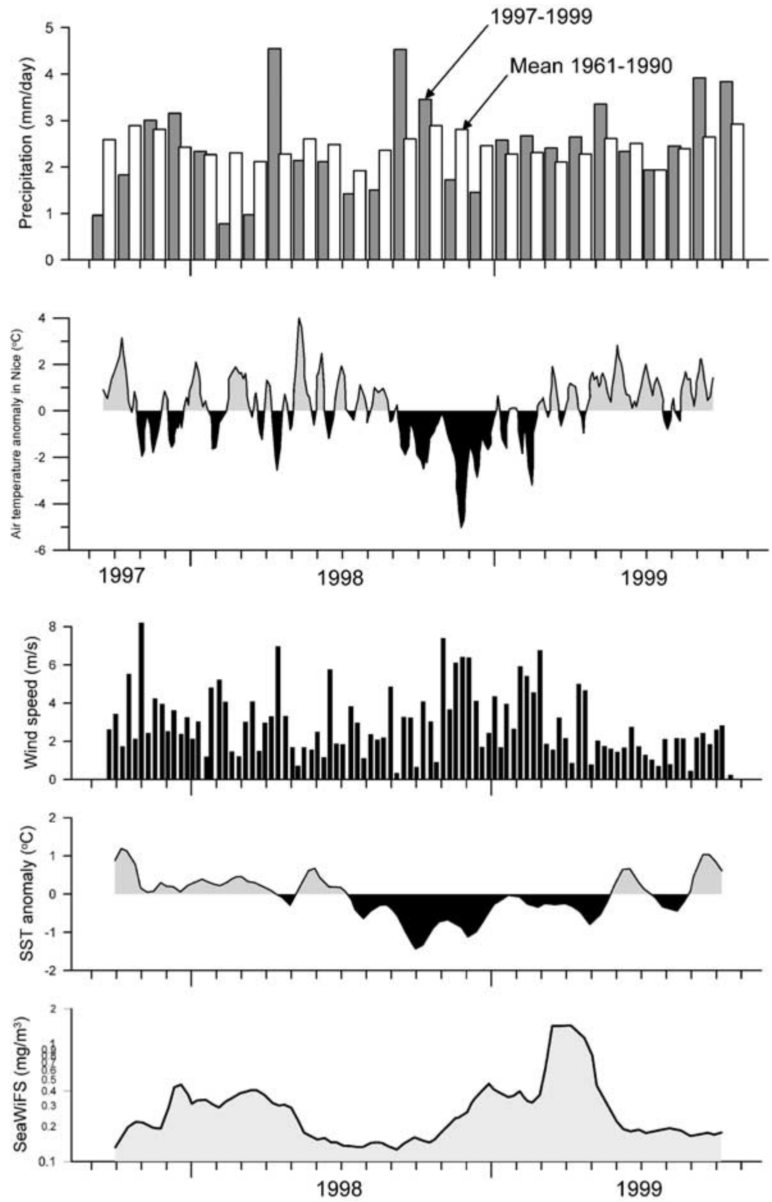

Figure 6. Variations of atmospheric precipitation (mm/day), air temperature anomalies (°C), wind speed (m/s), SST anomalies (°C), and surface chlorophyll concentration (mg/m^3) averaged over the deep part of the Northern Basin (6°30′–9°E).

was less intense and not sufficient to bring up nutrients into the euphotic layer; thus it resulted in weaker phytoplankton production. Our conclusion that deeper winter mixing results in more intensive spring bloom agrees well with the results of *Morel and Andre* [1991], who at the CZCS images observed that in the northwestern Mediterranean algae blooms develop in those places where the phytoplankton concentration was lowest in winter.

7. Numerical Modeling

[43] The model of the mixed layer [*Lacroix and Nival*, 1998] was used to complete the interpretation derived from the data analysis by considering the role of some processes along the vertical dimension such as the vertical mixing. The GHER model is a three-dimensional (multilevel) primitive equation and a free-surface, time-dependent, nonlinear, baroclinic model; it can be used to study both the deep sea and continental shelf hydrodynamics [*Haidvogel and Beckmann*, 1998]. The turbulent closure is ensured by an equation for the turbulent kinetic energy and an algebraic expression of the mixing length as a function of the flux Richardson number. Full equations, parameterizations, boundary conditions, numerical schemes, and early simulations for the western Mediterranean Sea are thoroughly detailed in the work of *Nihoul and Djenidi* [1987], *Djenidi et al.* [1987], *Beckers* [1991], and *Beckers et al.* [1994].

[44] The vertical one-dimensional model is derived from the general 3-D model assuming the horizontal homogene-

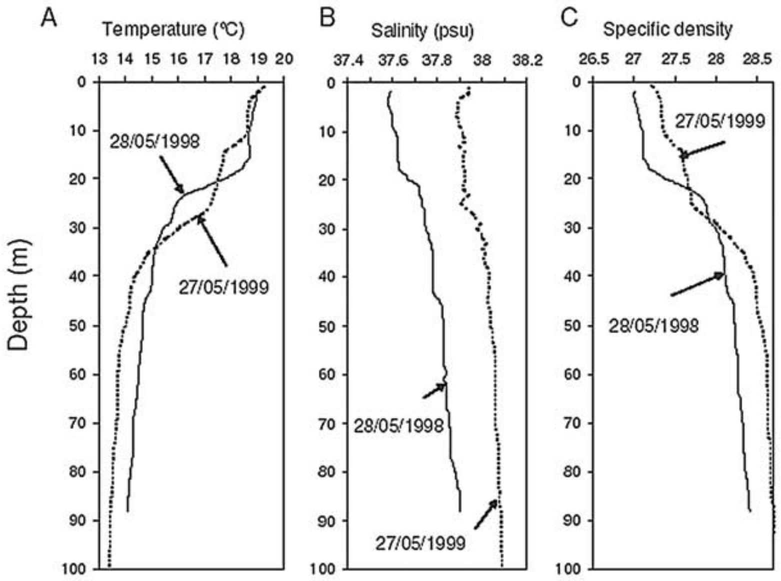

Figure 7. Vertical profiles of (a) temperature, (b) salinity, and (c) specific density in the Ligurian Sea at two stations in May 1998 and May 1999: 42°36.25′N–8°42′E (station 1 transect Calvi-Nice), 28/05/1998 (06:15), and 42°37.00′N–8°42.25′E (station A) 27/05/1999 (10:25).

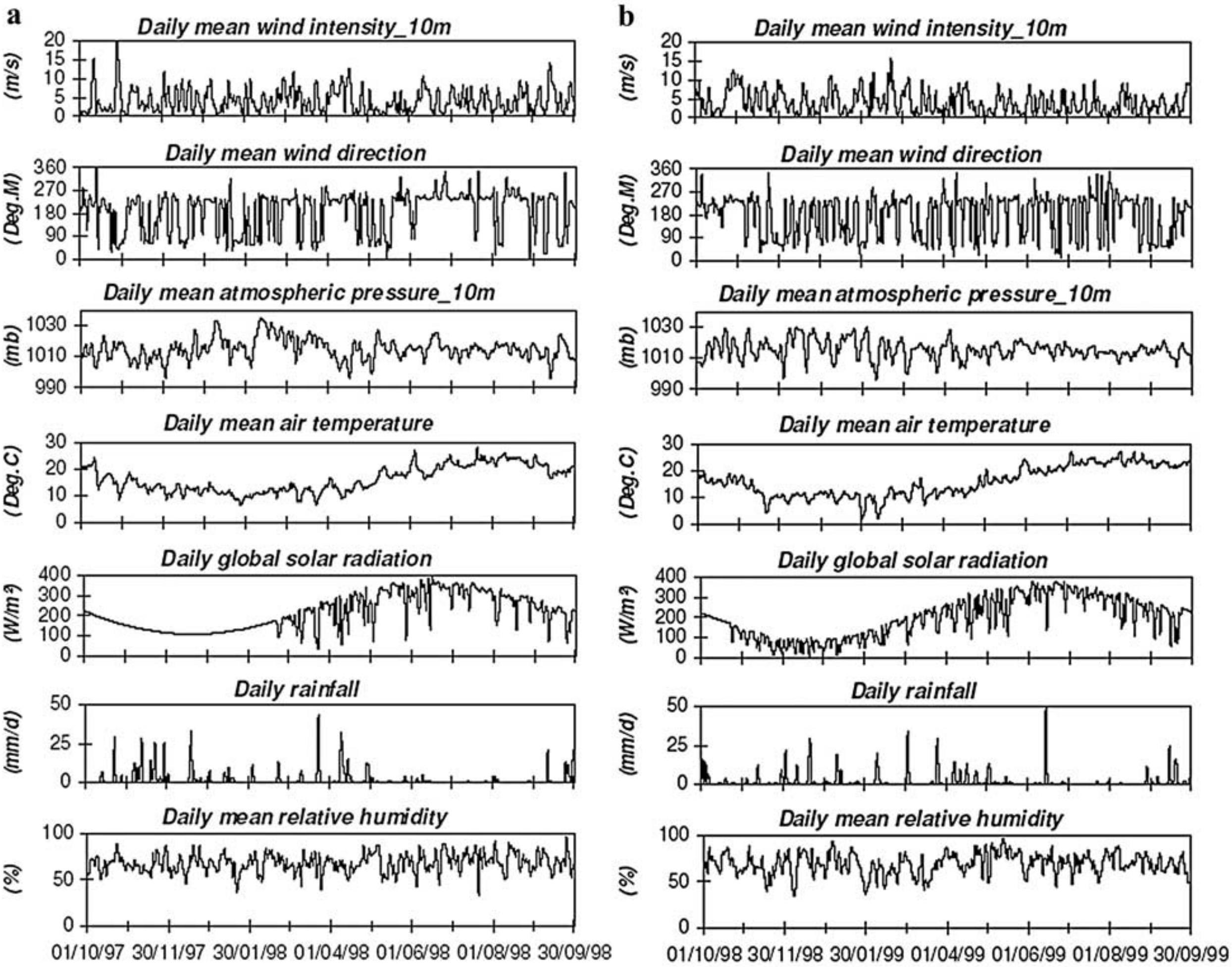

Figure 8. Meteorological data used to force the model: daily mean wind speed, wind direction, atmospheric pressure, air temperature, solar radiation, rainfall, and relative humidity; (a) October 1997 to September 1998 and (b) October 1998 to September 1999.

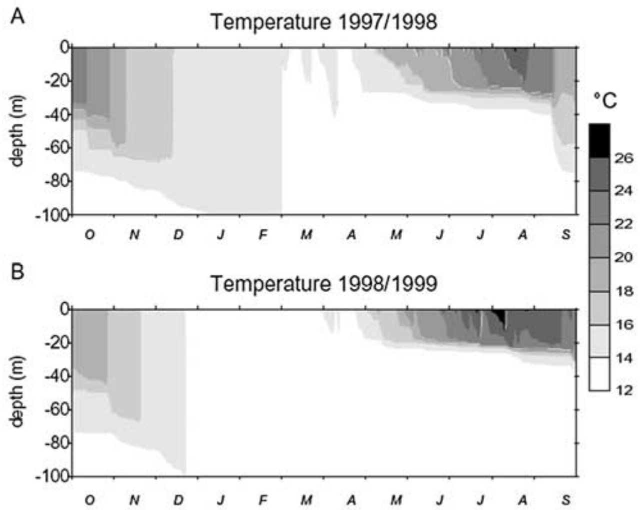

Figure 9. Modeled vertical distribution of temperature; (a) October 1997 to September 1998 and (b) October 1998 to September 1999.

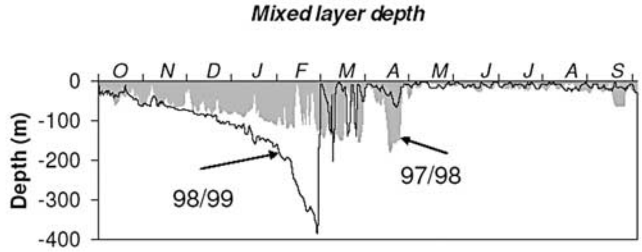

Figure 11. Modeled vertical distribution of the mixed layer depth; October 1997 to September 1998 and October 1998 to September 1999.

ity [*Lacroix and Djenidi*, 1992]. This model has been implemented, calibrated, and validated for the northern Ligurian Sea using the long-term (1984–1988) experimental data from the French Frontal Program surveys (FRONTAL) [*Lacroix*, 1998; *Lacroix and Nival*, 1998].

[45] Taking advantage of the high rate sampling meteorological data measured since fall 1997 from an automatic weather station located at the end of the Revellata Peninsula (Station de Recherches Sous-Marine et Océanographie (STARESO), Calvi, northwest Corsica) where open sea conditions are well represented [*Djenidi et al.*, 1999], two simulations have been performed with the model. The first one covered the period from October 1997 to September 1998 and the second one from October 1998 to September 1999. The meteorological data used to force the model are plotted in Figure 8. The prevailing directions of the regional wind climate were southwesterly (Libeccio) and northeasterly winds. Libeccio was much more frequent in spring and summer than northeasterly winds and more frequent in 1998 than in 1999. It is also worth attention that, while the annual average of wind intensity was higher during 1997–1998 than in 1998–1999 (5.07 versus 4.94 m/s), the year 1997–1998 was characterized by higher winds during autumn, spring, and summer, while during the year 1998–1999 the winter was windier. The winter winds are particularly important for the deepening of the mixed layer. One can then expect a deeper mixed layer in 1998–1999 than in 1997–1998.

[46] We performed the numerical runs of the model for the upper 400 m of the water column, forced by momentum and heat fluxes computed from these measurements. Concerning the choice of this depth, the previous studies for the northern Ligurian Sea [*Lacroix*, 1998] have shown that significant values of the turbulent kinetic energy and eddy diffusivities were found as deep as 300 m in rough conditions of very windy winters, indicating an intense vertical mixing particularly important for the nutrients dynamics and the subsequent primary production.

[47] Among the results of the model we focus on the distributions of temperature (Figure 9), turbulent kinetic energy (Figure 10), and mixed layer depth (Figure 11). The latter is defined here as the depth where the vertical gradient of the turbulent kinetic energy (TKE) changes its sign, indicating the limit between the upper zone of TKE "positive" production and the underlying zone of TKE "negative" production (dissipation of energy). The time series of the depth of the 15°C isotherm is plotted in Figure 12.

[48] The annual cycle of temperature (Figure 9) shows a high interannual variability. In autumn the stratification was still important. In 1997 the thermocline was always very sharp in comparison with autumn 1998. During the winter,

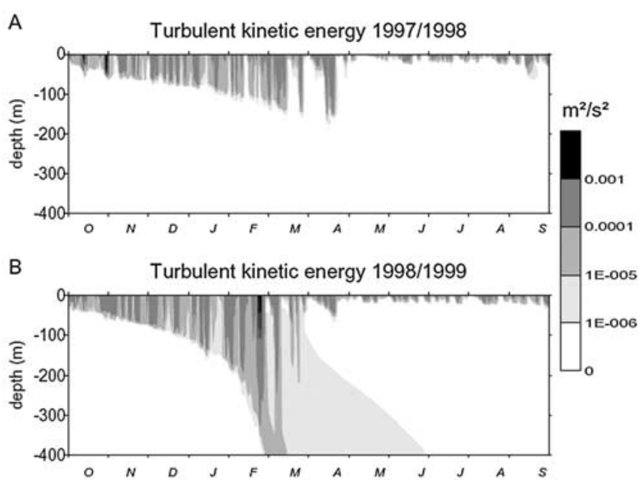

Figure 10. Modeled vertical distribution of turbulent kinetic energy; (a) October 1997 to September 1998 and (b) October 1998 to September 1999.

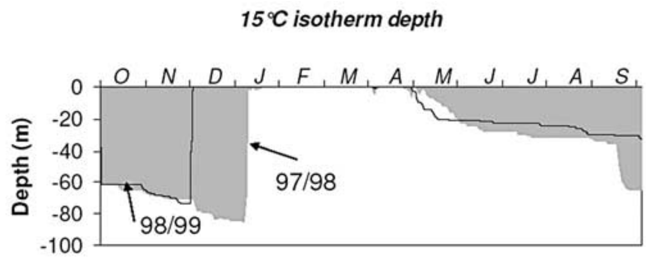

Figure 12. Modeled vertical distribution of the depth of the 15°C isotherm; October 1997 to September 1998 and October 1998 to September 1999.

owing to intense winds and surface cooling, the water column was mixed until a complete homogeneity. It appeared clearly that the complete destratification took place sooner in winter 1998–1999 as compared with the winter 1997–1998; the reason was the windier weather. The homogeneity was observed as soon as December 1998, while during the previous winter (1997–1998), one has to wait the beginning of March. Deeper winter convection in 1998–1999 as compared with the previous years was noted by [*Bethoux et al.*, 2002].

[49] The parallel observation of the turbulent kinetic energy (Figure 10) and the mixed layer depth (Figure 11) indicates that winter mixing was clearly more intense in 1999, when the mixed layer deepened down to 400 m at the end of February. During the winter 1998 the maximum depth of the mixed layer (180 m) was observed in April. The winter mixing decreased suddenly as soon as the end of February 1999, leading to a fast ascent of the mixed layer depth. A first stage of this process was observed at the end of March 1998, followed by a strong mixing event in April. The second stage was noted in April 1999. The beginning of the stratified period started in May and was well illustrated by the deepening of the 15°C isotherm as an indication of the bottom thermocline (Figure 12). This effect was faster in May 1999 (windier than May 1998), while the surface warming was higher in May 1998. As soon as the end of May, this tendency was reversed. In 1999 the summer was less windy that resulted in a higher surface temperature and a steeper thermocline. In summer 1999 the thermocline was shallower than in 1998. The end of September 1998 was marked by a strong wind event followed by a drop of the mixed layer depth and the 15°C isotherm.

[50] These results partly corroborate the hypothesis explaining the higher phytoplankton biomass in 1999 with more intensive mixing of the water column. Despite the fact that the 1-D model could not represent the winter convection, it was able to explain the higher 1999 phytoplankton biomass. The year 1999 showed a very strong (as compared with 1998) winter mixing that could allow an important nutrients input in the surface layer, giving rise to an intense spring bloom. In order to have an estimation of the phytoplankton production due to the mixing, the model should be coupled with a biological one adapted to the situation described in this study.

8. Concluding Remarks

[51] The multidiscipline analysis of remotely sensed physical and biological data using the methods of mathematical statistic and modeling revealed the principle pattern of variations of phytoplankton biomass under the influence of hydrometeorological factors in the area of interest. The shelf there is narrow, and the river discharge is low (except the Gulf of Lions); therefore this region seems to be a good example of the influence of water stratification on phytoplankton development.

[52] The pattern of seasonal variations of phytoplankton in the Ligurian Sea combines the features of subtropical type (high chlorophyll during cold season and low chlorophyll during the summer period of nutrient limitation) with the features typical to midlatitudinal zone (spring bloom resulting from the formation of seasonal thermocline). The intensity of winter/spring bloom depends on the intensity of erosion of seasonal thermocline caused by cooling and wind mixing in autumn. The latter processes result in enrichment of the euphotic layer with nutrients. More nutrients were entrained into the upper layers, more intensive is the spring bloom, and higher is the phytoplankton biomass during the next summer.

[53] **Acknowledgments.** This work was supported in part by the Ministère de l'Education et de la Recherche de la Communauté Française de Belgique (Action de Recherche Concertée 97/02.112), by the Fonds National de la Recherche Scientifique (FRFC 2.4570.97 and 2.4609.99), and by the Project "Shelf-Deep Basin Water Exchange in the Black and Ligurian Seas" of the Russian Ministry of Industry, Science and Technologies (Bilateral Cooperation Program with the Belgian Office for Scientific, Technical and Cultural Affairs (SSTC)). We would like to thank the SeaWiFS Project (code 970.2) and the Distributed Active Archive Center (code 902) at the Goddard Space Flight Center, Greenbelt, MD 20771, for the production and distribution of the data used in this study. These activities are sponsored by NASA's Mission to Planet Earth Program. Critical remarks by two anonymous reviewers are much appreciated useful and helped to improve this paper substantially. This paper is MARE037 publication.

References

Acker, J. G., S. Shen, G. Leptoukh, G. Serafino, G. Feldman, and C. McClain (2002), SeaWiFS ocean color data archive and distribution system: Assessment of system performance, *IEEE Trans. Geosci. Remote Sens.*, *40*(1), 90–103.

Afanasyev, Y. D., N. P. Nezlin, and A. G. Kostianoy (2001), Patterns of seasonal dynamics of remotely sensed chlorophyll and physical environment in the Newfoundland region, *Remote Sens. Environ.*, *76*, 268–282.

Alberola, C., and C. Millot (2003), Circulation in the French Mediterranean coastal zone near Marseilles: The influence of wind and the Northern Current, *Cont. Shelf Res.*, *23*(6), 587–610.

Arnone, R. (1994), The temporal and spatial variability of chlorophyll in the western Mediterranean, in *Seasonal and Interannual Variability of the Western Mediterranean Sea*, *Coastal Estuarine Stud.*, vol. 46, edited by P. E. La Violette, pp. 195–225, AGU, Washington, D. C.

Astraldi, M., and G. P. Gasparini (1992), The seasonal characteristics of the circulation in the north Mediterranean basin and their relationship with the atmospheric-climatic conditions, *J. Geophys. Res.*, *97*(C6), 9531–9540.

Astraldi, M., G. P. Gasparini, and S. Sparnocchia (1994), The seasonal and interannual variability in the Ligurian-Provençal basin, in *Seasonal and Interannual Variability of the Western Mediterranean Sea*, *Coastal Estuarine Stud.*, vol. 46, edited by P. E. La Violette, pp. 93–113, AGU, Washington, D. C.

Banse, K., and D. C. English (1994), Seasonality of coastal zone color scanner phytoplankton pigment in the offshore oceans, *J. Geophys. Res.*, *99*(C4), 7323–7345.

Beckers, J.-M. (1991), Application of the GHER 3D general circulation model to the western Mediterranean, *J. Mar. Syst.*, *1*(4), 315–332.

Beckers, J.-M., P. Brasseur, S. Djenidi, and J. C. J. Nihoul (1994), Investigation of the western Mediterranean's hydrodynamics with the GHER three-dimensional primitive equation model, in *Seasonal and Interannual Variability of the Western Mediterranean Sea*, *Coastal Estuarine Stud.*, vol. 46, edited by P. E. La Violette, pp. 287–324, AGU, Washington, D. C

Bethoux, J.-P. (1980), Mean water fluxes across sections in the Mediterranean Sea evaluated on the basis of water and salt budgets and of observed salinities, *Oceanol. Acta*, *3*(1), 79–88.

Bethoux, J.-P., X. Durieu de Madron, F. Nyffeler, and D. Tailliez (2002), Deep water in the western Mediterranean: Peculiar 1999 and 2000 characteristics, shelf formation hypothesis, variability since 1970 and geochemical inferences, *J. Mar. Syst.*, *33–34*, 117–131.

Bryden, H. L. (1991), Steady 2-layer exchange through the Strait of Gibraltar, *Deep Sea Res.*, *38*, suppl. 1, 445–463.

Casey, K. S., and P. Cornillon (1999), A comparison of satellite and in situ-based sea surface temperature climatologies, *J. Clim.*, *12*, 1848–1863.

Djenidi, S., J. C. J. Nihoul, F. Clément, and D. Salas de Leon (1987), The modem contribution to Medalpex, *Annal. Geophys.*, *5B*(1), 3–12.

Djenidi, S., G. Lacroix, S. Marchandise, S. Ginion, M. Janssens, and A. G. Kostianoy (1999), Contraintes hydrodynamiques sur les écosystèmes pélagique et benthique en site côtier stratifié méditerranéen, approche expérimentale et modélisation, 55 pp., Internal Rep., Commun. Fr. de Belg., Brussels.

Goffart, A., J.-H. Hecq, and L. Legendre (2002), Changes in the development of the winter-spring phytoplankton bloom in the Bay of Calvi (NW Mediterranean) over the last two decades: A response to changing climate?, *Mar. Ecol. Prog. Ser.*, *236*, 45–60.

Haidvogel, D. B., and A. Beckmann (1998), Numerical models of the coastal ocean, in *The Global Coastal Ocean, Processes and Methods.*, edited by K. H. Brink and A. R. Robinson, pp. 457–482, John Wiley, Hoboken, N. J.

Hovis, W. A., et al. (1980), Nimbus-7 Coastal Zone Color Scanner: System description and initial imagery, *Science*, *210*, 60–63.

Klein, P., and B. Coste (1984), Effects of wind-stress variability on nutrient transport into the mixed layer, *Deep Sea Res.*, *31*(1), 21–37.

Lacroix, G. (1998), Simulation de l'écosystème pélagique de la mer Ligure à l'aide d'un modèle unidimensionnel: Étude du bilan de matière et de la variabilité saisonnière, interannuelle et spatiale, Ph.D. dissertation, 256 pp., Univ. of Paris VI, Paris.

Lacroix, G., and S. Djenidi (1992), Extending the GHER 3D model to the modelling of ecosystems in western Mediterranean coastal zones: Results from an exploratory study, in *Water Pollution Research "EROS 2000" (EEC)*, *Rep. 28*, edited by J. M. Martin and H. Barth, pp. 89–104, H.M.S.O., London.

Lacroix, G., and P. Nival (1998), Influence of meteorological variability on primary production dynamics in the Ligurian Sea (NW Mediterranean Sea) with a 1D hydrodynamic/biological model, *J. Mar. Syst.*, *16*, 23–50.

La Violette, P. E. (1994), *Seasonal and Interannual Variability of the Western Mediterranean Sea*, *Coastal Estuarine Stud.*, vol. 46, edited by P. E. La Violette, 373 pp., AGU, Washington, D. C.

Leaman, K. D. (1994), The formation of western Mediterranean deep water, in *Seasonal and Interannual Variability of the Western Mediterranean Sea*, *Coastal Estuarine Stud.*, vol. 46, edited by P. E. La Violette, pp. 227–248, AGU, Washington, D. C.

Longhurst, A. (1995), Seasonal cycles of pelagic production and consumption, *Progr. Oceanogr.*, *36*(2), 77–167.

Marty, J.-C., and J. Chiaverini (2002), Seasonal and interannual variations in phytoplankton production at DYFAMED time-series station, northwestern Mediterranean Sea, *Deep Sea Res. Part II*, *49*(11), 2017–2030.

Marty, J.-C., J. Chiaverini, M.-D. Pizay, and B. Avril (2002), Seasonal and interannual dynamics of nutrients and phytoplankton pigments in the western Mediterranean Sea at the DYFAMED time-series station (1991–1999), *Deep Sea Res. Part II*, *49*(11), 1965–1985.

Marullo, S., R. Santoleri, and F. Bignami (1994), The surface characteristics of the Tyrrhenian Sea: Historical satellite data analysis, in *Seasonal and Interannual Variability of the Western Mediterranean Sea*, *Coastal Estuarine Stud.*, vol. 46, edited by P. E. La Violette, pp. 135–154, AGU, Washington, D. C.

McClain, E. P., W. G. Pichel, and C. C. Walton (1985), Comparative performance of AVHRR-based multichannel sea surface temperatures, *J. Geophys. Res.*, *90*(C6), 11,587–11,601.

Millot, C. (1991), Mesoscale and seasonal variabilities of the circulation in the western Mediterranean, *Dyn. Atmos. Oceans*, *15*(3–5), 179–214.

Millot, C. (1999), Circulation in the western Mediterranean Sea, *J. Mar. Syst.*, *20*(1–4), 423–442.

Millot, C., and L. Wald (1980), The effect of Mistral wind on the Ligurian current near Provence, *Oceanol. Acta*, *3*(4), 399–402.

Morel, A., and J.-M. Andre (1991), Pigment distribution and primary production in the western Mediterranean as derived and modeled from Coastal Zone Color Scanner observations, *J. Geophys. Res.*, *96*(C7), 12,685–12,698.

Morel, A., and J.-F. Berthon (1989), Surface pigments, algal biomass profiles, and potential production of the euphotic layer: Relationship reinvestigated in view of remote-sensing applications, *Limnol. Oceanogr.*, *34*(8), 1545–1562.

Nezlin, N. P. (2000), Remote-sensing studies of seasonal variations of surface chlorophyll-a concentration in the Black Sea, in *Satellites, Oceanography and Society*, edited by D. Halpern, pp. 257–271, Elsevier Sci., New York.

Nezlin, N. P., and B. L. Li (2003), Time-series analysis of remote-sensed chlorophyll and environmental factors in the Santa Monica-San Pedro Basin off southern California, *J. Mar. Syst.*, *39*(3–4), 185–202.

Nezlin, N. P., A. G. Kostianoy, and M. Gregoire (1999), Patterns of seasonal and interannual changes of surface chlorophyll concentration in the Black Sea revealed from the remote sensed data, *Remote Sens. Environ.*, *69*, 43–55.

Nihoul, J. C. J., and S. Djenidi (1987), Perspective in three-dimensional modelling of the marine system, in *Three-Dimensional Models of Marine and Estuarine Dynamics*, edited by J. C. J. Nihoul and B. M. Jamart, pp. 1–33, Elsevier Sci., New York.

O'Reilly, J. E., S. Maritoena, B. G. Mitchell, D. A. Siegel, K. L. Carder, S. A. Garver, M. Kahru, and C. McClain (1998), Ocean color chlorophyll algorithms for SeaWiFS, *J. Geophys. Res.*, *103*(C11), 24,937–24,953.

Ridderinkhof, H. (1992), On the effects of variability in meteorological forcing on the vertical structure of a stratified water column, *Cont. Shelf Res.*, *12*(1), 25–36.

Robinson, A. R., M. Golnaraghi, W. G. Leslie, A. Artegiani, A. Hecht, E. Lazzoni, A. Michelato, E. Sansone, A. Theocharis, and U. Unluata (1991), The eastern Mediterranean general-circulation—Features, structure and variability, *Dyn. Atmos. Oceans*, *15*(3–5), 215–240.

Send, U., J. Font, G. Krahmann, C. Millot, M. Rhein, and J. Tintore (1999), Recent advances in observing the physical oceanography of the western Mediterranean Sea, *Progr. Oceanogr.*, *44*(1–3), 37–64.

Sverdrup, H. U. (1953), On the conditions for vernal blooming of the phytoplankton, *J. Cons. Permanente Int. Explor. Mer*, *18*, 287–295.

Therriault, J.-C., D. J. Lawrence, and T. Platt (1978), Spatial variability of phytoplankton turnover in relation to physical processes in a coastal environment, *Limnol. Oceanogr.*, *23*(5), 900–911.

Vinogradov, M. E., E. A. Shushkina, V. I. Vedernikov, and V. N. Pelevin (1992), The ecological role of organic carbon flux in the waters of different productivity in the North Atlantic, *R. J. Aquat. Ecol.*, *1*(2), 89–101.

Vinogradov, M. E., E. A. Shushkina, V. I. Vedernikov, N. P. Nezlin, and V. I. Gagarin (1997), Primary production and plankton stocks in the Pacific Ocean and their seasonal variation according to remote sensing and field observations, *Deep Sea Res. Part II*, *44*(9–10), 1979–2001.

Vinogradov, M. E., E. A. Shushkina, N. P. Nezlin, V. I. Vedernikov, and V. I. Gagarin (1999), Correlation between different parameters of the ecosystem of the epipelagic zone of the World Ocean, *Oceanology*, *39*(1), 54–63.

Walton, C. C. (1988), Nonlinear multichannel algorithms for estimating sea surface temperature with AVHRR satellite data, *J. Appl. Meteorol.*, *27*(2), 115–124.

S. Djenidi, MARE, University of Liege, B5 Sart Tilman, B-4000 Liège, Belgium.

A. G. Kostianoy, P.P. Shirshov Institute of Oceanology, 36 Nakhimovsky Prospect, Moscow 117997, Russia.

G. Lacroix, Management Unit of the North Sea Mathematical Models (MUMM), Royal Belgian Institute for Natural Sciences (RBINS), Gulledelle 100, B-1200 Bruxelles, Belgium. (G.Lacroix@mumm.ac.be)

N. P. Nezlin, Southern California Coastal Water Research Project, 7171 Fenwick Lane, Westminster, CA 92683, USA.