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# Typology of environmental conditions at the onset of winter phytoplankton blooms in a shallow macrotidal coastal ecosystem, Arcachon bay (France).

Corine Glé[1,*], Yolanda Del Amo[1,*], Béatrice Bec[1], Benoît Sautour[1], Jean-Marie Froidefond[2], Francis Gohin[3], Danièle Maurer[4], Martin Plus[4], Pierre Laborde[2] and Pierre Chardy[1]

[1] CNRS, Université Bordeaux 1, UMR 5805-EPOC, ECOBIOC, Station Marine, d'Arcachon, 2 Rue Du Professeur Jolyet, 33120 Arcachon, France
[2] CNRS, Université Bordeaux 1, UMR 5805-EPOC, ECOBIOC, Avenue Des Facultés, 33405 Talence Cedex, France
[3] IFREMER Centre de Brest, BP 70 29280 Plouzané, France
[4] IFREMER DEL/AR, Quai du Commandant Silhouette, 33120 Arcachon, France

*: Corresponding author : c.gle@epoc.u-bordeaux1.fr (G.C.) or y.delamo@epoc.u-bordeaux1.fr (D.A.Y.)

**Abstract:**

Phytoplankton dynamics were assessed in the macrotidal ecosystem of Arcachon Bay through high-frequency surveys over a 5-year period in order to characterize typology of environmental conditions at the onset of the productive period. Temporal variations of hydrological and biological parameters were examined in external and internal waters of the lagoon, during the winter–spring periods from 1999 to 2003. An additional survey was performed during winter–spring 2005 in order to study the vertical structure of the water column. The occurrence of winter phytoplankton blooms between January and March emerged as a recurrent event. The early onset of the productive period is influenced by the biological functioning of adjacent Bay of Biscay oceanic waters. It is hypothesized that under a propitious hydrodynamic regime, phytoplankton inocula from the Bay of Biscay enter in the Arcachon Bay where cells presumably find favourable conditions for their fast development. The timing of the onset of those winter blooms in Arcachon Bay seems to be mainly influenced by the presence of anticyclonic weather conditions (associated with an increase in incident irradiance) during late winter (i.e. by February), while the water column does not show any particular stabilization nor stratification liable to facilitate the onset of these blooms. Moreover, these winter blooms dominated by diatoms led to an early nutrient depletion which could have inevitable consequences on the structuration of the food web during spring and summer.

**Keywords:** winter blooms, onset, phytoplankton inoculum, macrotidal ecosystem.

## INTRODUCTION

In coastal temperate ecosystems, the basic scheme of the plankton dynamics shows a productive period with an important initial phytoplankton bloom during spring (Margalef, 1958) based on new production and characterized by large cells (>20 µm) on which the classical herbivorous food chain reposes. These spring blooms are a characteristic feature of temperate North Atlantic open waters (Harrison et al., 1993; Waniek, 2003), as well as coastal and estuarine waters in temperate latitudes (Cloern, 1996). However, since a few years, the increasing quantities of nutrients produced by anthropogenic activities on the edges of coastal areas (Howarth et al., 1996) as well as the climatic variability (Edwards et al., 2002) have strongly modified the primary production calendar, its extent, and the nature of the phytoplankton communities (Cloern, 2001; Edwards and Richardson, 2004).

In a few coastal ecosystems, the phytoplankton dynamics pattern occasionally or recurrently shifts on the seasonal scale with early blooms starting by late winter (Herbland et al., 1998; Labry et al., 2001; Townsend and Thomas, 2001; Winder and Schindler, 2004). This is the case observed in coastal waters of the Bay of Biscay and specially in the plumes of the Gironde and Loire estuaries where late winter phytoplankton blooms are observed by February (Labry et al., 2001; Lunven et al., 2005). Those early blooms have been observed within hydrographic fronts during the establishment of halostratification and/or decrease of light vertical attenuation coefficient (Labry et al., 2001). The major consequence of the early phytoplankton development in the Bay of Biscay is a precocious nutritive limitation (Labry et al., 2002) leading to a spring phytoplankton community dominated by small cells (Herbland et al., 1998) and thus mainly grazed by microzooplankton (Sautour et al., 2000). The timing of the onset of the productive period is therefore one of the essential factors determining its duration as well as the total annual primary production rate. Moreover, as phytoplankton represents the first step of the food chain, the timing of bloom initiation has inevitable effects on the trophodynamic fate of bloom products, including life cycle of grazers (Edwards and Richardson, 2004).

Arcachon Bay (France) is a semi-enclosed embayment, situated on the east coast of the Bay of Biscay below the Gironde estuary (100 km). This bay sustains a high exploitation of *Crassostrea gigas* and the phytoplankton community structure conditions necessarily the success of oyster larvae recruitment (Maurer et al., 2003). In such systems, it appears essential to understand the ecosystem functioning and to specify under what conditions the productive period starts and its chronology. More fundamentally, the main objective of this paper is to characterize the phytoplankton dynamics in this coastal lagoon during the winter-spring period. In this paper, we address the following questions: 1) What is the pattern of the phytoplankton dynamics in Arcachon Bay during this period: do early blooms exist in this system, as they do in the Bay of Biscay and if

so, is this a recurrent phenomenon? ; 2) Is there any coupling link between the adjacent Bay of Biscay winter blooms and phytoplankton dynamics within Arcachon Bay? And 3) What are the climatic and hydrological conditions that characterize the onset of the productive period?

## METHODS

### Study area

Arcachon Bay (44°40'N 01°10'W; Fig. 1) is a semi-enclosed embayment of 174 $km^2$ on the southwest coast of France, connected to the Bay of Biscay (Atlantic Ocean) by a large opening (3 km). In the inner lagoon (156 $km^2$), channels (41 $km^2$) penetrate between large intertidal areas (115 $km^2$), mostly covered by seagrass beds. This shallow lagoon is a macrotidal environment (maximum tidal range 4.35 m) characterized by semi-diurnal tides enabling important water exchanges with the ocean through the southwest entrance of the lagoon. Those are estimated at 384 $10^6$ $m^3$ for an average spring tide and 264 $10^6$ $m^3$ for an average neap tide. Continental inputs also participate to the distribution of the water masses but to a lesser degree as the volume of seawater exchange with Bay of Biscay waters during one single tide is higher than the total annual river discharge to the Bay. Annual freshwater inputs average 1.25 $10^6$ $m^3$ with a major part (4/5) coming from the Leyre estuary located in the south-eastern part of the bay. The remaining 1/5 is provided by secondary canals, e.g the Lège Canal, at the northeast area (Carruesco, 1989).

The influence of both oceanic inputs derived from the Bay of Biscay and freshwater runoff due to the river Leyre and secondary canals permits to distinguish clearly two distinct geographical areas in the bay according to hydrological parameters (Vincent, 2002): (1) the external waters, directly influenced by the oceanic waters; (2) the internal waters, particularly influenced by continental inputs. The bay is therefore an heterogeneous ecosystem according to its hydrology.

Arcachon Bay is submitted to a typical oceanic temperate climate where prevailing winds were westerly (Manaud et al., 1997).

### Sampling strategy

Two sampling locations were chosen in order to compare external and internal part of the bay: the first one is located in the external waters (EW; station 'Bouée 13'; 44°38 N, 1°14 W; Fig. 1), characterised by a flushing time of about 4 days in winter (Plus et al., 2006). This station is situated in a channel of 17 m of depth, characterised by neritic coastal water masses at high tide. It is therefore considered as representative of the Bay of Biscay waters entering the bay at high tide (Guillocheau, 1988).

A second sampling site is located in the internal waters (IW; station 'Comprian'; 44°40 N, 1°05 W; Fig. 1), near continental inputs (i.e. river Leyre), and is characterised by a flushing time of about 13

days in winter (Plus et al., 2006). This station is situated in the south-eastern channel of the bay and is characterized by a depth of 7 m.

Sampling was performed at the two stations during the winter-spring periods (from January to May) during 5 consecutive years, from 1999 to 2003. Samples were collected three times a week from 1999 to 2002 and two times a week in 2003. Each sampling was performed in sub-surface (-1 m) and centred on high tide, providing the best chances to sample neritic water masses entering the bay. In order to study the vertical structure of the water column, an additional study was performed in 2005 at both stations, during high tide and with a monthly sampling strategy from January to April.

**Climatic and physical environment**.

Data on daily-integrated irradiance (i.e. incident irradiance) were provided by the meteorological station of Arcachon Bay (Météo France).

Seawater salinity and temperature measurements were obtained with a thermosalinometer (WTW Tetracon 325). Discrete sampling was carried out at subsurface (1 m below the surface) by using 5-L Niskin samplers, fitted with non-toxic silicone tubings. In 2005, temperature and salinity profiles were measured on the whole water column with a CTD probe (Sea Bird, SBE-19). The system was also equipped with light sensors (Biospherical/Licor) to measure photosynthetically available radiation (PAR; 400 to 700 nm). Density vertical distribution was determined from temperature, salinity and pressure profiles.

The vertical attenuation coefficient K for PAR was calculated from the relation between irradiance (Ez), surface irradiance (Eo) and depth z using PAR data: $Ez = Eo^* e^{-KZ}$. K is the slope of the linear regression between ln Ez and depth Z. Depth of the euphotic layer Ze was assumed to be the depth of 1% of surface irradiance and was determined by $Ze = -(\ln 0.01)/K$.

**Chemical and biological variables**

All seawater samples were collected in sub-surface waters (1 m below the surface) by using 5-L Niskin samplers and kept on a l0 L polypropylene (PP) carboy. Nutrient and phytoplankton subsamples were performed on board and the remaining water was kept in an icebox until return to the laboratory for chlorophyll a (Chl a) filtrations and primary production incubations.

For nutrient measurements, seawater was directly filtered either on glass fibre filters (Whatman GF/C for nitrate+nitrite and phosphate) or on cellulose acetate filters (for silicic acid) with a syringe filtration system, and stored in 100 mL glass bottles (nitrate+nitrite and phosphate) or in 100 mL PP bottles (silicic acid). Nutrient samples were then either stored at 4°C for silicic acid, or frozen (-20°C) for nitrate+nitrite and phosphate. Ammonium was immediately fixed by the addition of

working reagents (Koroleff, 1969) and kept in the dark. Phosphate (Murphy and Riley, 1962), nitrate+nitrite (Bendschneider and Robinson, 1952) and silicic acid (Mullin and Riley, 1955) concentrations were measured on a Technicon Auto Analyser II. Ammonium was analyzed according to Koroleff (1969).

For chlorophyll a (Chl a) and phaeopigment determinations, 0.5 L of seawater were filtered through Whatman GF/F membrane filters. Filters were immediately frozen (-20°C) until further analysis by the fluorimetric method (Yentsh and Menzel, 1963), using a calibrated Turner Design 700 fluorometer.

Samples for the identification of phytoplankton species composition were preserved on board with an acid lugol solution. Phytoplankton species were identified and counted by microscopic examination on an inverted microscope (ZEISS) in accordance with Utermöhl method (Utermöhl, 1958) for the years 2000, 2001 and 2003. A minimum of 400 cells was counted leading to an accuracy range of 10% (Lund et al., 1958).

Primary production rates were also measured in sub-surface during winter-spring 2003 in the EW and IW. The experimental design was based on the measurement of C incorporation with the $^{14}C$ method of Steeman-Nielsen (Steeman-Nielsen, 1952) and using *in situ* simulated incubations. Unprefiltered seawater was dispensed into 250 mL translucent polycarbonate bottles and inoculated with 1 mL (ca 5.6 µCi) of $NaH^{14}CO_3$ solution (Carbon 14 Centralen ®, Denmark). Dark incubations were periodically performed for control. Bottles were then incubated in an outdoor tank filled by a continuous flow of seawater directly pumped from Arcachon Bay in order to maintain ambient water temperature. This outdoor tank received during the incubation time the natural incident daylight irradiance (i.e. solar radiation). After 24 h incubation, samples were filtered onto 0.4 µm Nucleopore filters which were immediately covered with 250 µL of HCl 0.5 M and scintillation vials were stored at room temperature until counting. Initial specific activities of each sample were counted from 250 µL of sample collected from incubation bottles and stored in a vial with 100 µL of NaOH (1 N). Before counting, 10 mL of liquid scintillation cocktail (Ultima Gold Packard) was added to each vial and activity was counted after 24 h in the dark with a Beckmann LS 6500 liquid scintillation counter. Primary production rates were calculated using usual equations converting DPM values to daily production rates, using 25000 mgC $m^{-3}$ for DIC concentration following the JGOFS protocol (JGOFS, 1988). As incubations were rarely dawn-to-dawn due to the tide-dependent sampling times, daily primary production rates (mgC $m^{-3}$ $d^{-1}$) were corrected according to Moutin's model (Moutin et al., 1999) which takes geographical position, length of sunshine and incubation start deferred into account.

The biomass-specific primary productivity (P/B, mg C mg Chl $a^{-1}$ $h^{-1}$) was calculated as the carbon fixation rate (P) per unit of Chl a biomass (B).

In order to verify how hydrodynamism can affect particle dispersion (phytoplankton cells) within the lagoon, we have tested the hypothesis that a given phytoplankton biomass present in the external waters can attain the internal waters of the bay by using a bidimensional hydrodynamic mathematical model. Phytoplankton biomass dispersion was calculated by the MARS model (horizontal resolution: 235 m) developed by IFREMER - French Research Institute for Exploitation of the Sea- (Salomon et al., 1995) and calibrated for Arcachon Bay (Plus and Durand, 2004). Briefly, the algorithm calculates surface elevation and barotropic currents, as well as dissolved and suspended elements transported by currents. In this model, phytoplankton biomass is assimilated to a passive tracer, i.e. mortality, sedimentation and growth rates are not taken into account. The simulation is forced by real conditions of tide, river run-off, and wind using 2003 data.

For a larger assessment of phytoplankton dynamics in the adjacent oceanic waters, ocean colour data was used. Daily maps of Chl a concentrations of the Bay of Biscay surface waters, during February 2003, have been provided by IFREMER (MarCoast project) from SeaWiFS data. Briefly, the SeaWiFS radiances have been processed by an empirical algorithm adapted to coastal waters (i.e. modifications of the SeaWiFS Ocean Colour 4 band algorithm = OC4 by including the 412 and 555 channels) to avoid overestimations of Chl a concentration owed to yellow substances and suspended matter. The complexity of the parameterisation of the relationship between the OC4 ratio and the 412 and 555 bands led to the creation of a "look up table" that was applied to SeaWiFS data, to provide realistic chlorophyll concentration maps in the mixed coastal-clear water area (Gohin et al., 2002). For a full description of the algorithms, see Gohin et al. (2002).

## RESULTS

### Physical and climatic environments

The general pattern of the Leyre river flow rates recorded during the five study periods (i.e. winter-spring; Table I) reveals a high interannual variability. The winter-spring 2001 exhibited the highest mean flow rates (45 $m^3 s^{-1}$). On the contrary, the winter-spring 2002 was especially dry and river flow rates remained very low (8 $m^3 s^{-1}$).

As evidenced by salinities (Table I), the EW (external waters) behaves as a typical marine ecosystem with salinity mean values generally >33. In the IW (internal waters), due to its geographical position near to freshwater inputs, salinities were lower than those of the EW but generally >25. In these two water masses, lower mean salinities were observed in 2001 when high river discharges led punctually to important decreases (down to 29.9 in the EW and 20.3 in the IW). Conversely, the very dry 2002 winter-spring exhibited the highest mean salinities (average >34.6 and 32.7 in the EW and IW respectively).

Average temperatures of the five winter-spring periods (Table I) did not show great differences between the EW and IW. A comparison of the five years showed slightly lower temperatures during the 2000 study period (<12°C) than during the other years in the two water masses. Seasonal variations of water temperatures in the EW and IW followed the usual seasonal cycle, characterized by minimal winter values in January-February and maximal values during May (Table I, Fig. 2). Temperatures in the IW (Fig. 2) were generally lower than those recorded in the EW during January-February (mean difference = 1.3°C) and higher from March to May (mean difference = 0.7°C). These two water masses were at the same temperature (homothermous period) during a short period observed generally in March (from 5$^{th}$ to 12$^{th}$ March 1999, 25$^{th}$ February to 8$^{th}$ March 2000, 14$^{th}$ March to 2$^{nd}$ April 2001, 15$^{th}$ to 20$^{th}$ March 2002 and 6$^{th}$ to 20$^{th}$ March 2003). Based on this seasonal pattern of temperature differences between the EW and IW, two periods have been distinguished (Fig. 2) : 1) the winter period (22$^{nd}$ January-5$^{th}$ March 1999, 17$^{th}$ January-25$^{th}$ February 2000, 19$^{th}$ January-14$^{th}$ March 2001, 21$^{st}$ January-15$^{th}$ March 2002 and 16$^{th}$ January-6$^{th}$ March 2003) marked by higher temperatures in the EW than in the IW and 2) the spring period until the end of the studied period, when temperatures in the EW were generally lower than in the IW.
In order to assess the influence of incident irradiance on phytoplankton and considering our 3-days interval sampling strategy, we have summed the daily-integrated irradiance for the three days before each sampling date (Fig. 2). The 3-days cumulated irradiance followed the classical seasonal evolution of temperate areas with lowest values in January and maximum values in May. During winter, some periods were characterized by anticyclonic weather conditions (i.e. anticyclonic window = consecutive days with relatively high irradiance), especially during February when 3-days cumulated irradiance exceeded 3000 J cm$^{-2}$. During spring periods, a clear step-like increase was observed during March for the year 1999, 2000, 2002 and 2003, while for the year 2001, irradiance raised in a more progressive way from January to May.

**Structure of the water column and light conditions**

The vertical structure of temperature and salinity was studied during the winter-spring 2005. In both water masses, temperature and salinity differences between surface and bottom waters (Fig. 3) were weak during the 2005 winter-spring period, generally less than 0.8°C and 0.5 salinity units, respectively. The corresponding vertical gradient of density shows that from January to April, the Arcachon Bay waters exhibited an homogeneous vertical structure. The maximal vertical density difference, reaching 0.23, was observed in the IW on 31$^{st}$ March.
Values of the vertical attenuation coefficient (K, Table II) do not show pronounced spatial variability between the EW and IW except in April 2005 when K was higher in the IW (0.55 m$^{-1}$) than in the EW (0.29 m$^{-1}$). In the two water masses, values of K decreased from January to April,

affecting the euphotic layer depth (Ze). In the EW, Ze was shallower than the maximum water depth during January, and became deeper (or equal) to the maximum water depth from February to April. In the IW, Ze was always deeper than the maximum water depth.

**Nutrients**

For the five study years, just before the productive period beginning, the average DIN (nitrate + nitrite + ammonium) and Si concentrations in the ENW were the highest (ranges from 3.7 to 9.1 µM for DIN and from 2 to 7.1 µM for Si; Table III) but remained all the same low for a typical coastal embayment. Similarly, in the INW, average DIN and Si levels were maximal before the start of the productive period and due to the proximity of the Leyre River, levels were higher than in the ENW (ranges from 4.2 to 30 µM for DIN and from 4 to 22.5 µM for Si). In the two water masses during 2002, silicic acid concentrations reached their lowest values (2 µM in the EW and 4 µM in the IW), as a consequence of low Leyre River flow rates. Average phosphate concentrations were generally low in the two water masses (<1 µM) except in 2001 when they reached 1.3 µM in the EW.

During the productive period (from February to May), the start of the productive period coupled with weaker freshwater inputs led to a drastic decrease of nutrient concentrations in both stations, except during March when freshwater inputs, following spring rainfalls, led to punctual nutrient enrichments.

**Seasonal plankton cycle and biomass parameters**

In order to facilitate the study of the productive period onset, we have splitted Chl a series in two periods: the first bloom called “winter bloom” and secondary blooms called “spring blooms”. The distinction of “winter” and “spring” periods was based on the seasonal pattern of temperature differences between the EW and IW as described previously.

In the two water masses, Chl a concentrations were generally less than 2 µg $L^{-1}$ by mid January (Fig. 4). Afterwards, the seasonal pattern of Chl a concentrations showed an early start of the productive period (>2 µg $L^{-1}$) with a rapid increase of the phytoplankton biomass (excepted in 2000) as early as February. Globally, the winter Chl a maxima were higher in the EW than in the IW (5-years average of Chl a winter maxima = 5.6 and 4.2 µg $L^{-1}$ in the EW and IW, respectively). In the two water masses, the lowest winter blooms were observed during 2000 (2.5 µg $L^{-1}$ in the EW and IW) and the greatest in 2002 (9.4 µg $L^{-1}$ in the EW and 7.4 µg $L^{-1}$ in the IW). The onset of winter blooms in the EW and in the IW are either delayed in time (earlier in the EW, in 1999 and 2003) or synchronous (2000, 2001 and 2002) . The spring period was then evidenced by successive Chl a peaks showing variable intensities in the two water masses. Chl a concentrations remained

low during 1999 (below 2.5 µg $L^{-1}$ in the EW and IW) whereas they reached their maximum during 2002 spring (14.9 µg $L^{-1}$ in the EW and 7.1 µg $L^{-1}$ in the IW). Phaeopigment concentrations were generally lower than Chl a values and their temporal evolution was close to that of Chl a (data not shown).

Phytoplankton species determinations showed that winter blooms were dominated by diatoms (60%) and abundant autotrophic nanoflagellates (>30%) as Cryptophyceae and Prymnesiophyceae in both stations. The dominant diatom populations during the winter bloom were the same in the EW and IW, and mainly composed of *Lauderia spp*., *Skeletonema costatum* and *Thalassiosira spp.* in winter 2000, *Chaetoceros spp*. and *Asterionella glacialis* in winter 2001 and *Asterionella glacialis* in winter 2003. During the spring period, in the two water masses, diatoms accounted for as much as 80% of the total phytoplankton abundances and were essentially represented by *Leptocylindrus danicus*, *Pseudonitzschia spp.*, *Chaetoceros spp.* and *Asterionella glacialis*.
In 2003, the pattern of P/B (carbon fixation rates per unit of biomass based upon Chl a) shows several increases starting from mid-February in both water masses (Fig. 5). During the 2003 winter bloom, P/B of 1.1 mg C mg Chl $a^{-1}$ $h^{-1}$ were observed in the EW (on 27$^{th}$ February) and of 1.8 mg C mg Chl $a^{-1}$ $h^{-1}$ in the IW (on 6$^{th}$ March). The maximum P/B values were reached during the spring period: on 31$^{st}$ March in the EW (2.8 mg C mg Chl $a^{-1}$ $h^{-1}$) and on 22$^{nd}$ April in the IW (4.9 mg C mg Chl $a^{-1}$ $h^{-1}$).
For the 2003 winter-spring period, P/B and levels of daily-integrated incident irradiance (Fig. 5) show a significant correlation in the EW ($r = 0.63$, $p < 0.001$, $n = 37$; Pearson test) and IW ($r = 0.66$, $p = 0.001$, $n = 37$; Pearson test).

**Dispersion of chlorophyll biomass in the lagoon**

We have chosen to simulate the Chl a biomass dispersion in the lagoon during the winter 2003 when Chl a concentrations show the clearest delay (7 days) between winter peaks in the EW (on 27$^{th}$ February) and IW (on 6$^{th}$ March; Fig. 4). Phytoplankton biomass dispersion was modelled from 27$^{th}$ February to 6$^{th}$ March 2003, under real (i.e. *in situ*) tide, river run-off and wind conditions. Fig. 6a presents the initial conditions of the simulation in Arcachon Bay on 27$^{th}$ February 2003: Chl a concentrations attributed to the EW and IW at the start of the simulation correspond to *in situ* Chl a measured in these water masses (7 µg $L^{-1}$ and 1.3 µg $L^{-1}$, respectively). The simulation shows that in 7 days, the main part of the initial phytoplankton biomass present in the EW was ejected towards the ocean (Fig. 6b). Nevertheless, a part of this initial phytoplankton biomass is transported towards the internal part of the lagoon, reaching by 6$^{th}$ March 2003 concentrations ranging from 3 to 4 µg $L^{-1}$ in the IW, i.e. lower than those measured in these water masses (5 µg $L^{-1}$).

**Chl a concentrations derived from SeaWiFs data**

Chl a images from SeaWiFS data showed an increase of surface Chl a in the Bay of Biscay coastal waters by mid-February 2003 (Fig. 7), i.e. simultaneously to the EW winter bloom. From 18$^{th}$ to 21$^{st}$ of February, the Chl a concentrations increase in time and from South to North along the Biscay east coast, in the direction of Arcachon Bay. The 21$^{st}$ February 2003, the Chl a concentrations derived from satellite data reached up to 10 mg $m^{-3}$ (10 µg $L^{-1}$) along the Biscay coast while during early March, the Chl a concentrations dropped down to <2 mg $m^{-3}$ (2 µg $L^{-1}$; data not shown).

**DISCUSSION**

**Oceanic influence on the onset of winter phytoplankton bloom in Arcachon Bay**

In Arcachon Bay waters, the increase of Chl a concentrations between January and February from 1999 to 2003 shows the occurrence of a late winter phytoplankton bloom, which appears as a recurrent seasonal event (Fig. 4). Winter blooms were initiated as early as February for the five study years and usually persist over periods of several weeks (from 2 to 5 weeks) in Arcachon Bay. Although winter phytoplankton blooms are now recognized as a common feature of the annual phytoplankton cycle in the adjacent Bay of Biscay waters (Herbland et al., 1998; Beaufort and Heussner, 2001; Labry et al., 2001; Lampert, 2001; Gohin et al., 2003) and in faraway systems as the Massachusetts Bay (Kelly and Doering, 1997; Keller et al., 2001), the Gulf of Maine (Durbin et al., 2003), the Narragansett Bay (Oviatt et al., 2002) or the Chesapeake Bay (Glibert et al., 1995), this is the first time it is documented within Arcachon Bay waters.

A well more significant result of our study concerns the relationships that can be evidenced among a macrotidal coastal lagoon and the adjacent oceanic waters in terms of combined phytoplankton dynamics. Winter phytoplankton species dominating in Arcachon Bay were essentially composed of diatoms larger than 20 µm (*Lauderia spp.*, *Thalassiosira spp.*, *Chaetoceros spp.*, *Skeletonema costatum*) and large colonies (*Asterionella glacialis*), typical of spring phytoplankton populations (Margalef, 1958) that grow under rich nutrient conditions. These populations correspond to those blooming during late winter and early spring in the Bay of Biscay waters and more generally along the French coasts e.g. *Thalassiosira spp*, *Asterionella glacialis, Chaetoceros danicus* (Beliaeff et al., 2001; Labry et al., 2001; Gailhard et al., 2002; Gohin et al., 2003). Satellite estimates of surface Chl a in the oceanic waters adjacent to the lagoon, at the timing of the 2003 winter bloom in the EW (i.e. February), corroborated the existence of great phytoplankton developments (10 µg $L^{-1}$) during early winter on the continental shelf waters (Bay of Biscay), close to Arcachon Bay (Fig. 7). This observation is consistent with the hypothesis that the biological functioning of adjacent oceanic waters may influence the timing and the chronology of the productive period in Arcachon Bay. The

hypothesis made here is that horizontal transport of water masses at each high tide can be a source of phytoplankton (i.e. phytoplankton inocula) when oceanic adjacent blooms are advected into the lagoon.

In terms of internal functioning of Arcachon Bay, the comparison of temporal variations of Chl a concentrations between the EW and IW (Fig. 4) showed that some years, under some particular conditions (i.e. tidal coefficient, wind, oceanic phytoplankton dynamics), winter bloom started first in the EW and secondarily in the IW (in 1999 and 2003; Fig. 4). Additionally, the intensity of winter blooms in the EW was always higher than those of the IW and the dominant phytoplankton species characterizing these winter blooms are similar in the two water masses. The simulation of the Chl a biomass advection within the lagoon (for the 2003 scenario; Fig. 6) has shown that the dispersion and advection of phytoplankton from the EW towards the IW could be in part responsible of the winter bloom observed in the inner part of the bay and could explain the decreasing gradient of Chl a observed every year from the EW to the IW. However, these single hydrodynamic processes do not seem sufficient to explain the 5 $\mu g\ L^{-1}$ of Chl a measured in the IW. The increase of the biomass-specific primary productivity (P/B) at the time of the winter bloom in the IW (1.8 mg C mg Chl $a^{-1}\ h^{-1}$) proved that Chl a levels observed in the IW during the winter bloom were not only the result of cells advection but were also originated from local phytoplankton production (Fig. 5). This local production could be supported by phytoplankton inoculum from EW finding favourable conditions for blooming in the inner part of the bay, as well as by autochthonous phytoplankton, which could explain that some years winter bloom was synchronous in the two water masses.

To conclude, horizontal transport can be a source of phytoplankton when outer blooms are advected into macrotidal coastal systems by a propitious hydrodynamic regime. The occurences of these phenomena may vary seasonally and spatially with hydrodynamic forcing such as wind, freshwater flow and tidal currents (Lucas et al., 1999) and could also explain that some years, delay between the onset of winter bloom in the EW and IW has not be evidenced. Finally, phytoplankton inocula that enter into Arcachon Bay necessarily finds favourable climatic (light, wind regime) and hydrological (nutrients, temperature, turbulence) conditions in this bay for their fast development.

**Typology of environmental conditions at the onset of the winter bloom**

In coastal ecosystems, the conditions that determine the timing of the onset of the productive period are the result of the conjunction of several favourable factors as temperature, nutrient and light availability, as well as low grazing pressure (Thórdardóttir, 1986).

Nutrient concentrations in the two water masses were at their highest levels before the start of the productive period. Compared to typical French coastal embayment (Wafar et al., 1983; Del Amo et

al., 1997; Strusky et al., 2006), ranges of concentrations (Table III) appeared to be low for the ENW (ranges: 3.7 to 9.1 µM for DIN, 2 to 7.1 µM for Si, 0.2-1.3 µM for P) and moderate in the INW (ranges: 4.2 to 30 µM for DIN, 4 to 22.5 µM for Si, 0.2-0.5 µM for P). However, in the two water masses, nutrient levels were well above half-saturation constants for nutrient uptake (Ks) reported by Fisher et al. (Fisher et al., 1988) for natural populations in coastal temperate ecosystems (DIN = 1-2 µM, silicic acid = 1-5 µM, phosphate = 0.1-0.5 µM). Moreover, amongst the five study periods, the greater winter bloom was observed when nutrient concentrations were at their lowest levels (i.e. 2002). These observations support the idea that winter nutrient stocks were sufficient to sustain a fast development of phytoplankton cells at this period but not a triggering factor acting on the early onset of the productive period in Arcachon Bay as shown in the Gironde plume estuary (Labry et al., 2001).

In Narragansett Bay, the onset of the winter bloom has been shown to be the result of grazing pressure relaxation (Pratt, 1965; Martin, 1970). In Arcachon Bay, planktonic metazoa abundances are usually at their lowest levels during winter (Castel and Courties, 1982; D'Elbée and Castel, 1995; Vincent, 2002), and increase only by March after the decline of winter blooms. However, grazer abundances can definitely play a major role on the magnitude of those winter blooms, as shown by the minor winter bloom recorded in 2000 (Fig. 4). Higher mesozooplancton abundances than other years and an atypical *Noctitula scintillans* bloom were indeed observed in 2000 (data not shown). This top-down control of winter blooms, already reported in some coastal areas (Keller et al., 1999; Keller et al., 2001; Oviatt et al., 2002; Oviatt, 2004), could have important consequences on trophic levels, and more specially on benthic-pelagic coupling, by reducing the detrital carbon supply available for benthic organisms (Townsend and Cammen, 1988; Oviatt et al., 2002; Oviatt, 2004).

The most determining factor for the onset of the productive period in coastal temperate areas is usually depth-integrated solar radiation as a function of stratification, vertical attenuation coefficient and incident irradiance (Thórdardóttir, 1986). In Arcachon Bay, no vertical density stratification was observed during the 2005 winter-spring (Fig. 3). In such well-mixed waters, more influenced by tidal stirring than by freshwater discharges, the mixed layer corresponds to the whole water column. Consequently, the increase of light availability in the water column does not depend on the establishment of a persistent density stratification of the water column as shown in numerous coastal and estuarine systems (Cloern, 1984; Levasseur et al., 1984; Thórdardóttir, 1986; Ingram et al., 1985; Pennock and Sharp, 1994; Yin et al., 1996; Labry et al., 2001).

Despite a perpetual well-mixed water column, light seems to be sufficient to sustain photosynthesis as early as February as the water column was entirely euphotic. Two major factors are liable to

control the depth-averaged quantity of light available for phytoplankton: the vertical attenuation coefficient K and surface irradiance levels (Riley, 1957).

In macrotidal shallow systems poorly influenced by freshwater inputs such Arcachon Bay, K essentially depends on cyclic tidal currents and punctual wind events that provoke sediment resuspension (Allen et al., 1980; de Jonge and Beusekom, 1995). This high variability of K controlled by short-term fluctuations and punctual events cannot therefore be the triggering factor of recurrent winter blooms whose onset is periodically observed by February. The prevailing factor is this case is obviously a seasonal-fluctuating factor such as the incident irradiance level.

Anticyclonic weather conditions (i.e. high incident irradiance) were observed during the ~3 days preceding the onset of the winter blooms in the EW (Fig. 2). The 3-days cumulated incident irradiance before the onset of the winter bloom range from 3794 to 2263 J $cm^{-2}$. The minimum value was observed in 2000 and can also explain the minor winter bloom observed this year (<2.5 µg $L^{-1}$). On the contrary, the highest 3-days cumulated incident irradiance (>3000 J $cm^{-2}$) lead to well developed winter blooms as such observed in 1999, 2001, 2002 and 2003.

Riley (Riley, 1957) equation permits to calculate the depth-averaged irradiance (I) received by phytoplankton in the water column during February-March (at the onset of winter blooms): $I = (Io - Io * e^{-KZ})/KZ$ where Io is the total surface incident irradiance (in W $m^{-2}$), Z is water depth (in m) and K is the vertical attenuation coefficient (in $m^{-1}$). Using a 3-days irradiance value of 3000 J $cm^{-2}$ as a threshold for biomass accumulation, a daily value of Io = 1000 J $cm^{-2}$ $d^{-1}$ (= 116 W $m^{-2}$) can be calculated; K = 0.25 (corresponding to the average of K measured during February-March 2005 in Arcachon Bay), then I = 27 W $m^{-2}$. This value is higher than the empirical critical irradiance suggested by Riley (Riley, 1957) of 0.03 g cal $cm^{-2}$ $min^{-1}$ (= 20.9 W $m^{-2}$) required for blooming in temperate coastal waters. Inversely, this empirical value of 20.9 W $m^{-2}$ would led to a 3-days cumulated incident irradiance of 2330 J $cm^{-2}$ with our conditions, that explains the quasi-absence of winter bloom in 2000 (coupled with high zooplankton abundances).

We could conclude that in Arcachon Bay, initiation of winter blooms seems to be triggered when incident irradiance reaches a threshold value as observed in other coastal systems characterized by relatively clear waters (Hitchcock and Smayda, 1977; Båmstedt, 1985; Townsend et al., 1992; Townsend et al., 1994; Townsend and Thomas, 2001). Under such conditions, incident irradiance seems to prevail upon vertical attenuation coefficient in the initiation processes of winter phytoplankton bloom. The correlation between the biomass-specific primary productivity (P/B) and daily-averaged incident irradiance observed in 2003 corroborates this hypothesis. This situation, typical of clear waters, is different to that of the dilution plume of the Gironde estuary and other turbid coastal ecosystems affected by freshwater inputs where the onset of the productive period is typically associated with an increase of depth-averaged quantity of light available due to a decrease

of the vertical attenuation coefficient and a vertical density stratification/gradient induced by freshwater runoff (Labry et al., 2001; Thórdardóttir, 1986; Cloern, 1991; Ragueneau et al., 1996). Finally, although the increase of light availability is one of the main factors controlling the outburst of phytoplankton bloom during winter, water temperature could also play an important role during this season, by influencing the P/B (Eppley,1972; Harrison and Platt, 1980). From 1999 to 2003, winter blooms were generally initiated when temperatures ranged from 9.5 to 11.5°C in the EW and from 8.2 to 10.3°C in the IW (Fig. 2). These lowest temperatures characterizing the IW could explain the delay of the onset of winter blooms observed between the outer and inner water masses in 1999 and 2003 (considering that depth-integrated irradiance is similar in the two water masses, i.e. same incident irradiance and identical seasonal variations of K). For the year 1999 and 2003, when winter blooms were initiated in the EW but not yet in the IW, water temperature were inferior to 8°C in the IW while they were above 9°C in the EW, suggesting that the overtaking of a temperature threshold of 8-9°C could be necessary for an increase of phytoplankton growth. Obviously, this temperature threshold need to be clarified and used with some caution as temperature optima are highly variable and species specific (Goldman and Ryther, 1976). Moreover, some diatoms are known to be eurythermal species and therefore are able to develop in a large range of temperatures. For instance, *Asterionella glacialis* (that dominated the 2003 winter blooms) are present from 0.8 to 23°C in Narragansett Bay (Karentz and Smayda, 1984). By consequence, this temperature threshold is also considered as region-dependent.

**Trophic consequences of the early phytoplankton blooms**

In Arcachon Bay, a major consequence of the presence of phytoplankton blooms early in the year was a nutrient depletion that occured as early as March-April (Table III) and led to nutrient limitations of phytoplankton primary production rates by spring (Glé et al., in press). The consequences of these precocious nutrient limitations could be similar to those observed in the dilution plume of the Gironde Estuary, which means the structuration of the planktonic food web towards the dominance of small phytoplankton cells (Herbland et al., 1998) and grazing mainly realized by microzooplankton (Sautour et al., 2000). The size-class structure of summer phytoplankton developments appears to be specially determinant for the success of the development and recruitment of bivalves larvae as *Crassostrea gigas* which are particularly demanding as regards of food (Robert and Trintignac, 1997). Indeed, in Arcachon Bay, low abundances of nanoplankton in summer could limit the food supply to bivalves larvae and thus could be a cause of weak settlement as observed some years (Maurer, pers. comm.).

In shallow coastal ecosystem rich in suspension feeders as Arcachon Bay, early phytoplankton blooms could sustain a great pelagic-benthic coupling. Indeed, in Arcachon Bay, there is typically a

mismatch between the winter-spring diatom bloom and the mesozooplankton abundance peak which occurs by March-April (data not shown) when water temperatures are favourable (Castel and Courties, 1982; Vincent, 2002). By consequence, phytoplankton could not be efficiently consumed by the zooplankton but instead sinks, providing a large supply of organic matter which serves as a rich food source for benthic organisms as shown in Narragansett Bay (Townsend and Cammen, 1988; Keller et al., 2001; Oviatt, 2004), in the North Sea (Nielsen and Richardson, 1989) or in Northern Baltic Sea (Lignell et al., 1993).

Moreover, the massive sedimentation of spring diatom blooms could also impact the Si cycle, with potential implications on the summer functionning of the bay. Indeed, it has been shown recently in the Bay of Brest that the activity of suspension feeders during early spring (filtration and subsequent production of quantities of biodeposits) led to temporary retention of biogenic silica (BSi) in the sediments of the Bay (Ragueneau et al., 2002; Ragueneau et al., 2005). The subsequent BSi dissolution during late spring and summer, enhanced by increasing temperature and elevated bacterial activity, would provide the necessary dissolved silicon required by diatoms to maintain their dominance throughout the productive period (Chauvaud et al., 2000).

## CONCLUSION

This study has shown that winter blooms, initiated as early as February, are a recurrent pattern observed in Arcachon Bay. In this macrotidal system, the beginning of the productive period seems to be highly influenced by the phytoplankton dynamics of the adjacent oceanic waters. This oceanic influence, by affecting firstly the external waters of the lagoon, led to an uncoupling of the biological functioning between the external and internal waters of the lagoon at the start of the productive period, evidenced by the recurrent lowest magnitude of winter blooms in the IW and by the delayed onset of the winter bloom observed in the IW.

The essential environmental condition for the onset of winter blooms in Arcachon Bay seems to be an increase of light availability. Due to the low turbidity of these water masses, incident irradiance seems to prevail upon any particular vertical structure of the water masses (e.g. stratification, decrease of extinction coefficient) in the initiation process of winter phytoplankton bloom. However, the influence of temperature on phytoplankton growth during winter should not be underestimated, especially in the cooler internal waters.

As most typical spring blooms, winter blooms in Arcachon Bay are dominated by diatoms that accumulated under rich nutrient environment. However, the early nutrient depletion that will encompass the winter bloom collapse by spring could have inevitable consequences on the structuration of the food web during spring and summer as shown in the dilution plume of the Gironde estuary (Herbland et al., 1998; Sautour et al., 2000). Further studies are therefore needed to

characterize such consequences on nutrient dynamics and consequently, on the following community and size structure of plankton in Arcachon Bay.

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**LEGENDS FOR TABLES AND FIGURES**

Table I. Average and range salinities and temperatures (°C) in the External (EW) and Internal waters (IW) of Arcachon Bay and average Leyre flow rates for the 5 study periods (from January to May).

Table II. Mean value of the vertical attenuation coefficient $K$ ($m^{-1}$) and the depth of the euphotic layer $Ze$ (m) in the External waters (EW) and Internal waters (IW) of Arcachon Bay during winter-spring 2005.

Table III. Average nutrient concentrations (in µM) in the External waters (EW) and Internal waters (IW) of Arcachon Bay for the 1999, 2000, 2001, 2002 and 2003 study periods. The average nutrient concentrations observed before the beginning of the productive period have been calculated from 22nd January to 12th February 1999, from 17th January to 2nd February 2000, from 19th January to 21st February 2001, from 21st January to 13th February 2002 and from 16th January to 20th February 2003. The average concentrations during the productive period have been calculated from the onset of the winter blooms to the end of the study periods (i.e. May). DIN=nitrate+nitrite+ammonium except *: ammonium not available.

Fig. 1. Sampling locations in Arcachon Bay (●): External waters EW ('Bouée 13') and Internal waters IW ('Comprian').

Fig. 2. Time course variations of temperatures (°C) in the External waters (EW) and Internal waters (IW) and 3-days cumulated incident irradiance (J $cm^{-2}$) from January to May during 1999-2003. Vertical dashed lines delimit the winter and spring periods (see text for details).

Fig. 3. Vertical structure of temperature, salinity and density during winter-spring 2005 in the External waters (EW) and Internal waters (IW) of Arcachon Bay.

Fig. 4. Time course variations of chlorophyll a (in µg $L^{-1}$) in the External waters (EW) and Internal waters (IW) of Arcachon Bay during winter-spring 1999, 2000, 2001, 2002 and 2003.

Fig. 5. Time course variations of the biomass-specific primary productivity (P/B in mg C mg Chl $a^{-1}$ $h^{-1}$) in the External waters (EW) and Internal waters (IW) and incident irradiance in ($J.cm^{-2}.d^{-1}$) in Arcachon Bay during winter-spring 2003.

Fig. 6. Phytoplankton cell dispersion calculated by the hydrodynamic model MARS-2D developed by IFREMER (Salomon et al., 1995) and calibrated for Arcachon Bay (Plus and Durand, 2004) with a horizontal resolution of 235 m from 27th February 2003 (a) to 6th March 2003 (b). See text for details.

Fig. 7. Daily Chl a concentrations estimated by SeaWiFS maps along the Biscay coast for 18th and 21st February 2003. The spot (A) is located 50 km South from the Arcachon Bay.

Table I. Average and range salinities and temperatures (°C) in the External (EW) and Internal waters (IW) of Arcachon Bay and average Leyre flow rates for the 5 study periods (from January to May).

| | | Salinity mean (range) | Temperature (°C) mean (range) | Average Leyre flow rates ($m^3$ $s^{-1}$) |
|---|---|---|---|---|
| 1999 | EW | 33.7 (31.5-34.7) | 12.2 (9.5-15.8) | 21 |
| | IW | 28.9 (24.9-30.6) | 12.4 (8.0-18.9) | |
| 2000 | EW | 33.8 (32.3-34.7) | 11.6 (6.3-16.8) | 28 |
| | IW | 29.3 (26.7-33.1) | 11.5 (6.1-19.3) | |
| 2001 | EW | 33.3 (29.9-36.5) | 12.6 (8.6-17.4) | 45 |
| | IW | 26.5 (20.3-32.8) | 12.4 (7.2-21.5) | |
| 2002 | EW | 34.6 (33.8-35.1) | 12.5 (10.6-16.5) | 8 |
| | IW | 32.7 (30.1-33.7) | 12.6 (8.2-17.8) | |
| 2003 | EW | 34.0 (31.1-35.0) | 12.3 (8.8-15.9) | 17 |
| | IW | 30.7 (20.3-33.3) | 12.4 (6.0-18.7) | |

Table II. Mean value of the vertical attenuation coefficient *K* (m–1) and the depth of the euphotic layer *Z*e (m) in the External waters (EW) and Internal waters (IW) of Arcachon Bay during winter-spring 2005.

| Dates | Stations | K ($m^{-1}$) | Ze (m) |
|---|---|---|---|
| 31/01/2005 | EW | 0.50 | 9.2 |
| | IW | 0.46 | 10.0 |
| 03/02/2005 | EW | 0.30 | 15.4 |
| | IW | 0.30 | 15.4 |
| 31/03/2005 | EW | 0.19 | 24.2 |
| | IW | 0.15 | 30.7 |
| 14/04/2005 | EW | 0.29 | 15.8 |
| | IW | 0.55 | 8.4 |

Table III. Average nutrient concentrations (in µM) in the External waters (EW) and Internal waters (IW) of Arcachon Bay for the 1999, 2000, 2001, 2002 and 2003 study periods. The average nutrient concentrations observed before the beginning of the productive period have been calculated from 22nd January to 12th February 1999, from 17th January to 2nd February 2000, from 19th January to 21st February 2001, from 21st January to 13th February 2002 and from 16th January to 20th February 2003. The average concentrations during the productive period have been calculated from the onset of the winter blooms to the end of the study periods (i.e. May). DIN=nitrate+nitrite+ammonium except *: ammonium not available.

| Year | Periods | DIN (µM) | | Silicic acid (µM) | | Phosphate (µM) | |
|---|---|---|---|---|---|---|---|
| | | EW | IW | EW | IW | EW | IW |
| 1999 | Before productive period | 5.9 | 10.3 | 4.3 | - | 1.0 | 0.5 |
| | During productive period | 2.9 | 5.3 | 2.1 | - | 0.8 | 0.7 |
| 2000 | Before productive period | 4.9 | - | 4.2 | - | 0.2 | - |
| | During productive period | 5.2 | - | 2.6 | - | 0.4 | - |
| 2001 | Before productive period | 4.6 * | 20.2 * | 7.1 | 20.9 | 1.3 | 0.3 |
| | During productive period | 3.1 * | 11.1 * | 1.9 | 10.6 | 0.5 | 0.2 |
| 2002 | Before productive period | 3.7 | 4.2 | 2.0 | 4.0 | 0.3 | 0.2 |
| | During productive period | 3.1 | 3.2 | 1.4 | 3.6 | 0.2 | 0.1 |
| 2003 | Before productive period | 9.1 | 30.0 | 6.4 | 22.5 | 0.3 | 0.3 |
| | During productive period | 2.4 | 7.7 | 2.2 | 7.7 | 0.2 | 0.2 |

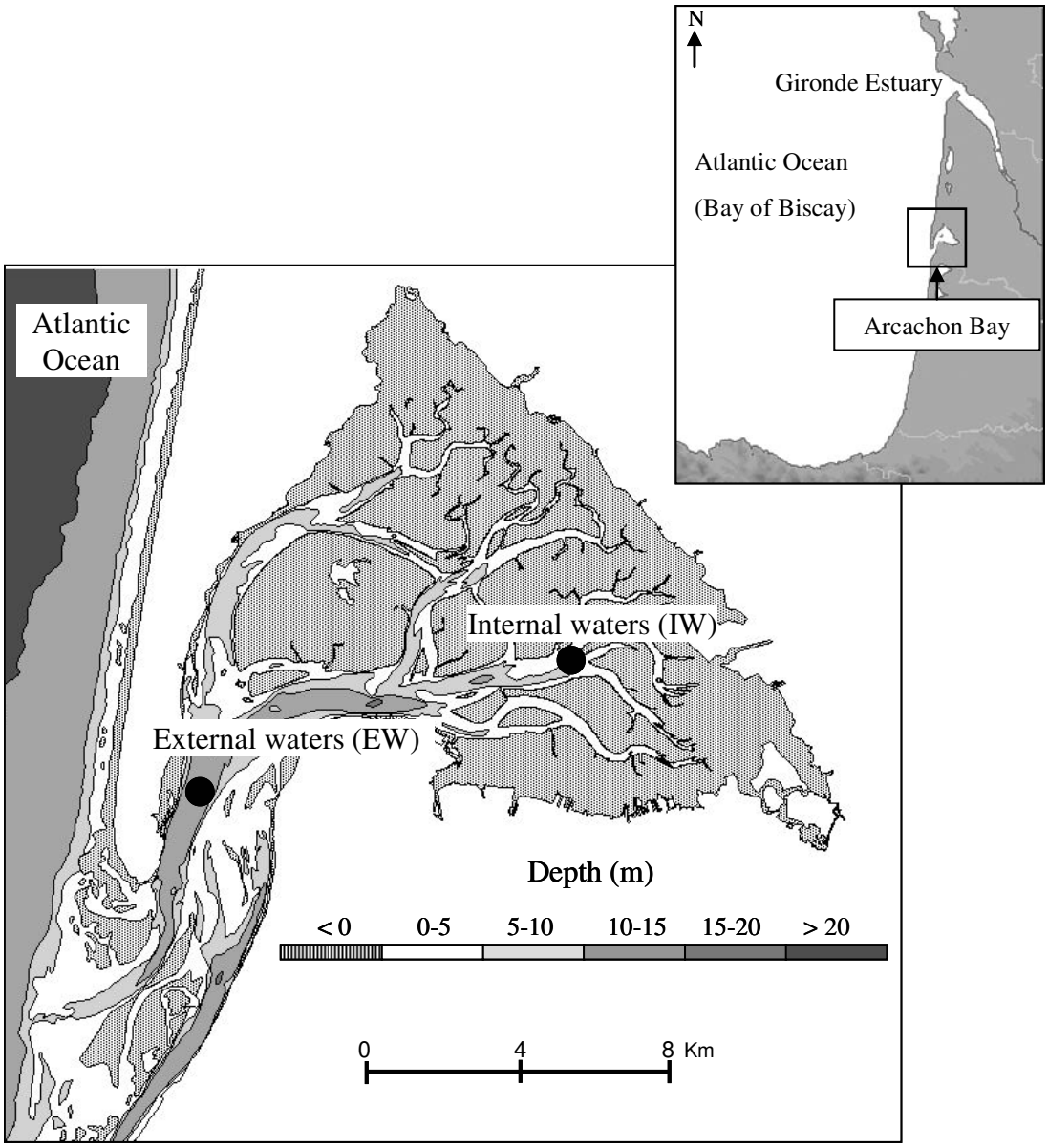
N
Gironde Estuary
Atlantic Ocean
(Bay of Biscay)
Arcachon Bay
Atlantic
Ocean
Internal waters (IW)
External waters (EW)
Depth (m)
< 0
0-5
5-10
10-15
15-20
> 20
0
4
8 Km

Fig. 1

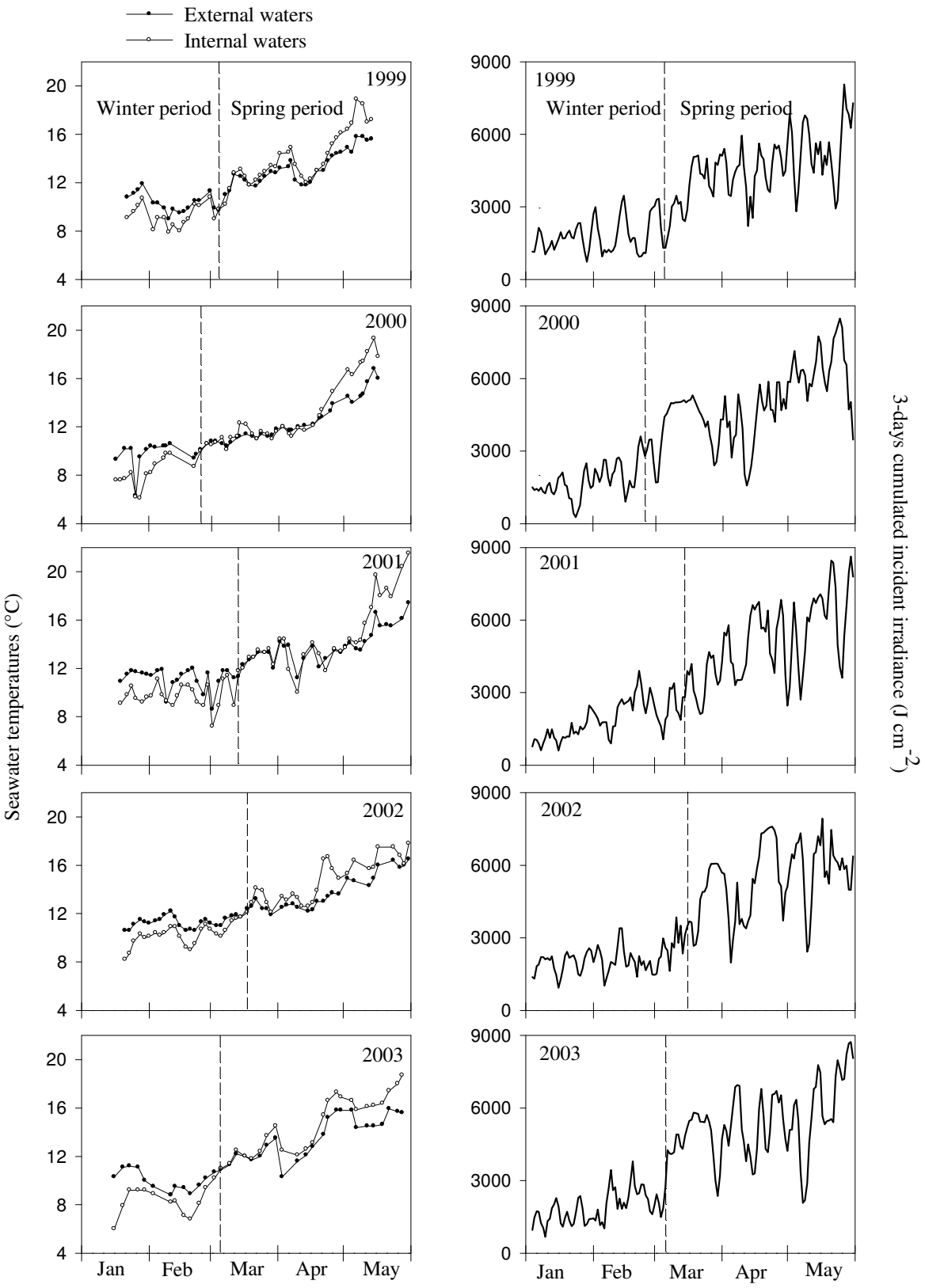
External waters
Internal waters
1999
Winter period
Spring period
2000
2001
2002
2003
Seawater temperatures (°C)
3-days cumulated incident irradiance (J cm-2)
Jan
Feb
Mar
Apr
May

Fig. 2

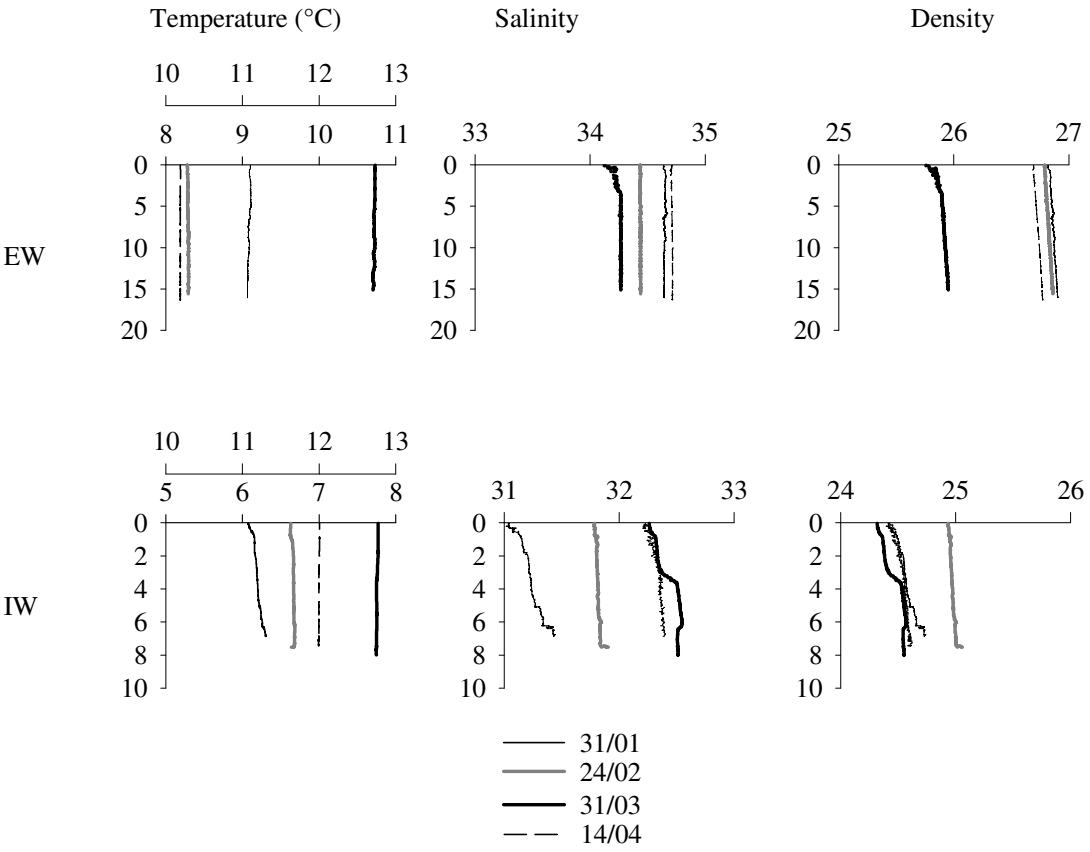
Temperature (°C)
Salinity
Density
EW
IW
10 11 12 13
8 9 10 11
33 34 35
25 26 27
10 11 12 13
5 6 7 8
31 32 33
24 25 26
0 5 10 15 20
0 2 4 6 8 10
31/01
24/02
31/03
14/04

Fig. 3

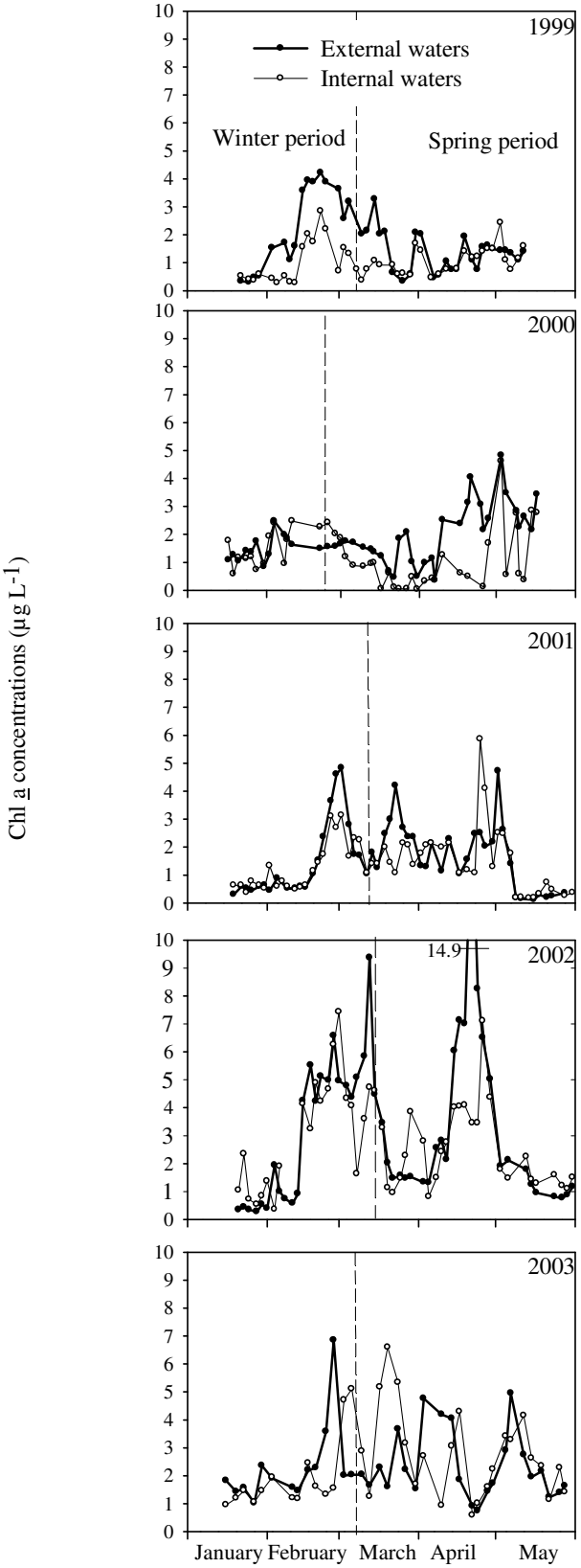
1999
External waters
Internal waters
Winter period
Spring period
2000
2001
14.9
2002
2003
January
February
March
April
May
Chl a concentrations (µg L-1)

Fig. 4

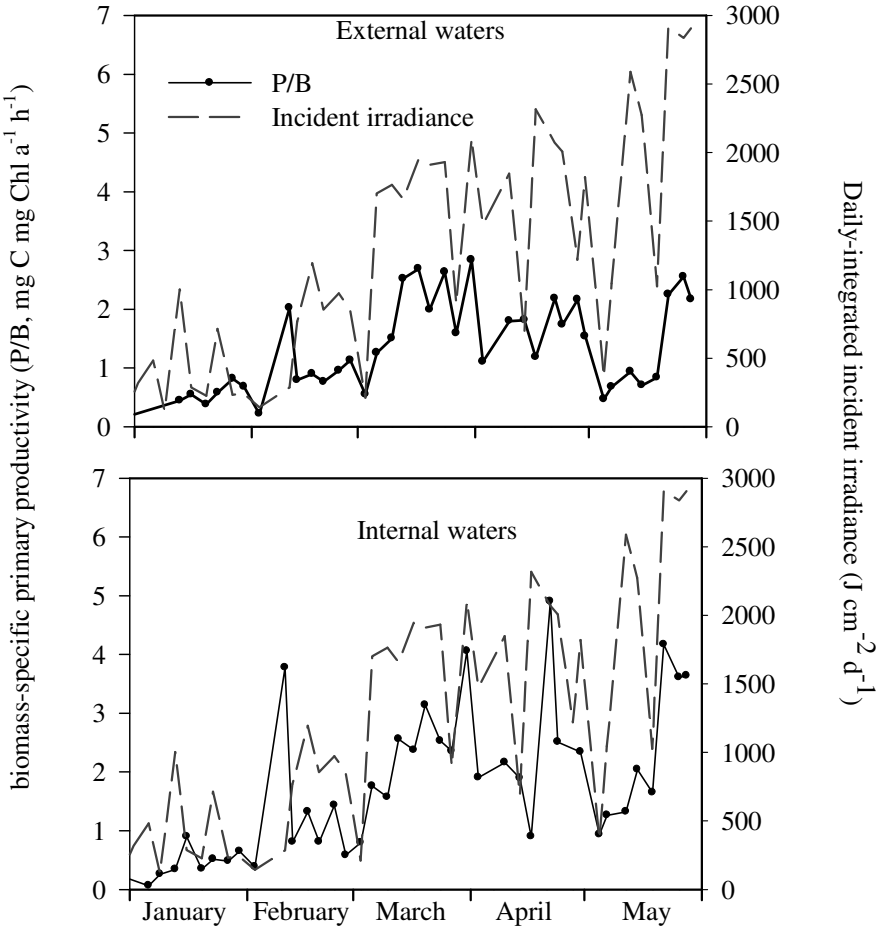
External waters
P/B
Incident irradiance
Internal waters
January
February
March
April
May
biomass-specific primary productivity (P/B, mg C mg Chl a$^{-1}$ h$^{-1}$)
Daily-integrated incident irradiance (J cm$^{-2}$ d$^{-1}$)

Fig. 5

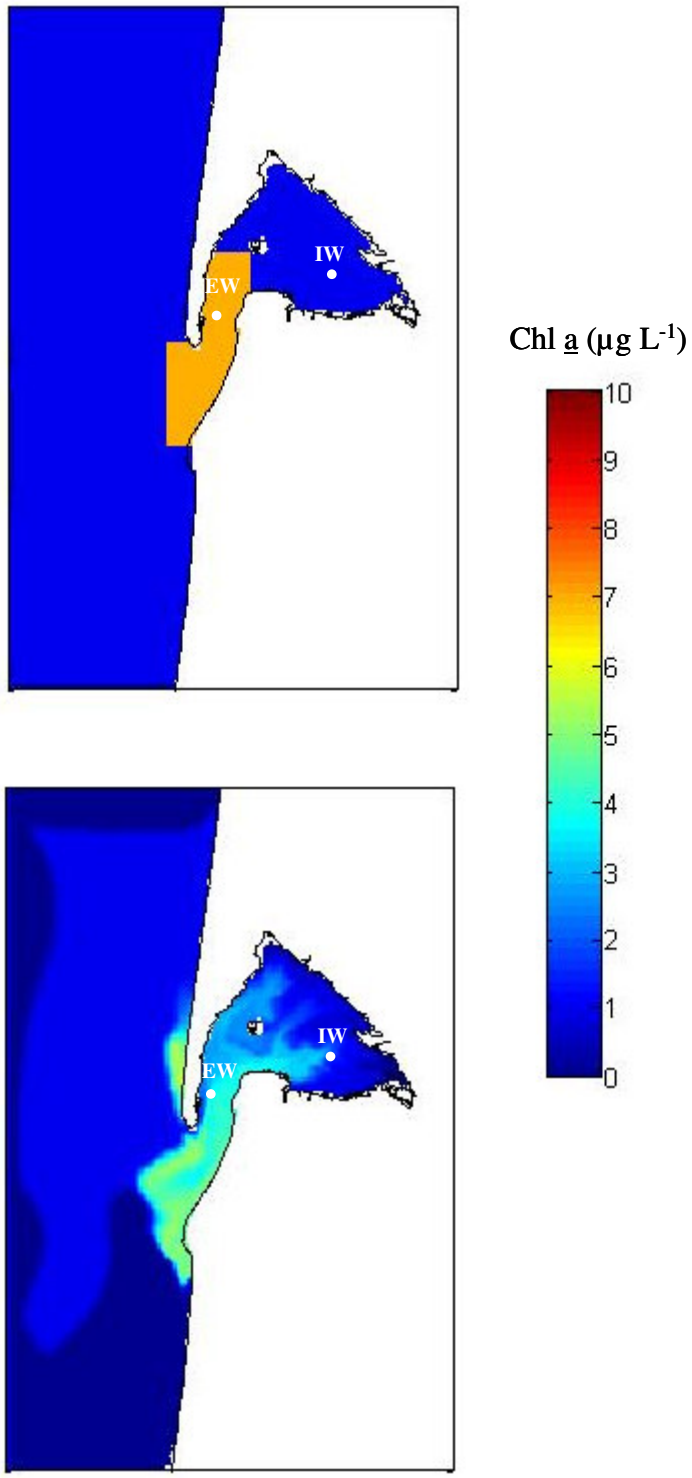


Fig. 6

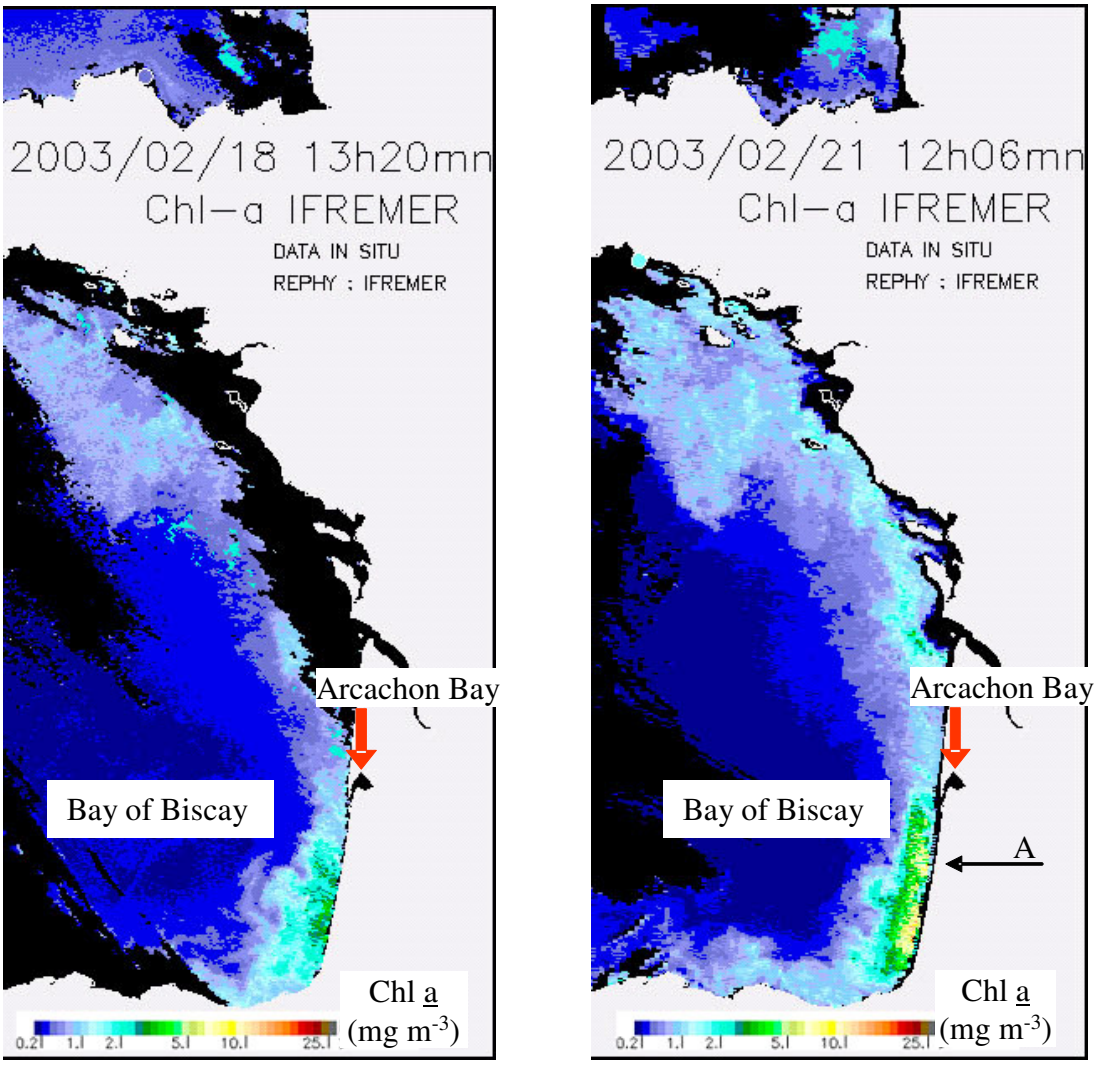
2003/02/18 13h20mn
Chl–a IFREMER
DATA IN SITU
REPHY : IFREMER
Arcachon Bay
Bay of Biscay
Chl a
(mg m-3)
0.2 1.1 2.1 5.1 10.1 25.1
2003/02/21 12h06mn
Chl–a IFREMER
DATA IN SITU
REPHY : IFREMER
Arcachon Bay
Bay of Biscay
A
Chl a
(mg m-3)
0.2 1.1 2.1 5.1 10.1 25.1

Fig. 7