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Distribution of *Dinophysis* species in the Bay of Biscay and possible transport pathways to Arcachon Bay

Francois Batifoulier [a,b], Pascal Lazure [a,*], Lourdes Velo-Suarez [a], Daniele Maurer [c], Philippe Bonneton [b], Guillaume Charria [a], Christine Dupuy [d], Patrick Gentien [a,1]

[a] IFREMER, Centre de Brest, B.P. 80, Plouzané, France
[b] UMR CNRS EPOC 5805, Université Bordeaux 1, 33405 Talence Cedex, France
[c] Laboratoire IFREMER DEL/AR, Quai du Commandant Silhouette, 33120 Arcachon, France
[d] Centre de Recherche sur les Environnements Littoraux et Anthropisés, CNRS-IFREMER-ULR UMR 6217, Université de La Rochelle, Pôle Sciences et Technologie, avenue Michel Crépeau, 17042 La Rochelle, France

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ABSTRACT

Dinophysis is the most harmful toxic phytoplankton on the French coast in terms of its impact on local economy and public health. In Arcachon Bay, *Dinophysis* spp. have periodically affected shellfish industry for the last ten years; the most important events are analysed in detail in this paper. Regular monitoring revealed that these events originated outside Arcachon Bay in the open ocean. Data from 14 surveys and two coastal networks showed that *Dinophysis* was primarily found in the vicinity of Capbreton, 100 km south of the mouth of Arcachon Bay. The *Dinophysis* distribution on the continental shelf was determined during two surveys in 2005 and 2008: the highest concentrations were located along the coast and reached 18 000 cells.L^{-1}. Analysis of available current data revealed that strong westerlies lead to northward currents of up to 19 cm.s^{-1}. These marine meteorological conditions were frequently observed just prior to *Dinophysis* events and lead us to suggest that northward currents transport *Dinophysis* from the Capbreton area to Arcachon Bay.

1. Introduction

Diarrhetic shellfish poisoning (DSP) is a gastrointestinal disease resulting from ingestion of shellfish contaminated with lipophilic shellfish toxins. Recurrent occurrence of toxin-producing *Dinophysis* spp. causes the accumulation of DSP toxins in shellfish above regulatory levels. These harmful events, during which even low *Dinophysis* levels can contaminate seafood, constitute the main threat for the Northeast Atlantic shellfish industry (Hallegraeff, 1993). Proliferation of *Dinophysis* spp. in Arcachon Bay (southwest France) has periodically affected commercial mussel and oyster harvest for the last 10 years.

Despite numerous studies over the past two decades, *Dinophysis* ecophysiology and mechanisms of bloom formation are not well known. Since the first successful cultivation of *Dinophysis acuminata* (Park et al., 2006), the understanding of *Dinophysis* biology and ecology has progressed considerably. However, although laboratory experiments constitute the first step in characterising *Dinophysis*, field studies are still needed to understand the complex coupling of biological and physical processes in natural environments.

Dinophysis spp. are known to be slow-growing (Stolte and Garcés, 2006; Velo-Suarez et al., 2009) and nutritionally versatile dinoflagellates (photosynthetic obligate mixotrophs and heterotrophs; Hansen, 1991; Jacobson and Andersen, 1994; Kim et al., 2008). Maximum cell concentrations of different species of *Dinophysis* have often been related to marked temperature and salinity gradients in the water column (Maestrini, 1998) and they have been observed to form thin, species-specific layers (Moita et al., 2006; Velo-Suarez et al., 2008).

Previous studies on the dynamics of harmful algal blooms have highlighted that water mass circulation can act as transport vectors for harmful populations (Anderson, 1997; Pitcher et al., 2010; Sellner et al., 2003; Trainer et al., 2002). Different transport pathways have been described to carry populations of harmful algae from offshore into coastal areas and bays. Among all the proposed mechanisms, alongshore transport of cells in major water masses and their episodic intrusion towards shore due to downwelling and favourable wind forcing has recently been suggested (Escalera et al., 2010) as the phenomenon that causes recurrent blooms of *Dinophysis acuta* inside Galician rias. *D. acuta* populations originating from Portuguese coasts have been shown to be transported to the rias by a narrow poleward current, over a distance of at least 170 km.

The interaction between harmful algal populations and hydrodynamics can play a key role in explaining the initiation, development and decline of harmful algal blooms (HABs).

* Corresponding author. Tel.: +33 298224341; fax: +33 298224864.
E-mail address: pascal.lazure@ifremer.fr (P. Lazure).
[1] Deceased.

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The present study focuses on the dynamics of *Dinophysis* spp. in the vicinity of Arcachon Bay. *Dinophysis* events were identified by the REPHY network (REseau de surveillance PHYtoplanctonique; a network of stations along French coasts that monitor toxic phytoplankton in seawater weekly or biweekly) as well as field surveys. The circulation on the Aquitaine shelf was studied and new current measurements are presented. Meteorological conditions during the *Dinophysis* spp. outbreaks were analysed and the circulation during these events was inferred. Clues to understanding the origin of toxic populations are discussed.

2. Materials and methods

2.1. The study area

Arcachon Bay is located halfway along the Aquitaine coast (44°40′N, 1°10′W) (Fig. 1). The Aquitaine shelf is located in the SE corner of the Bay of Biscay. It extends from the Adour estuary to the Gironde estuary. The Aquitaine shelf is 170 km wide off the Gironde estuary, tapering to only 30 km off the Basque Country coast. The French coast is oriented north–south, whereas the Spanish coast trends east–west. The shelf is interrupted by the Capbreton canyon whose head cuts into the Landes coast.

2.2. Dinophysis sampling and analysis

2.2.1. Network sampling

Annual concentrations of *Dinophysis* spp. used in this study were obtained from two different sources: (1) weekly and biweekly samples from the REPHY (IFREMER) monitoring programme (http://envlit.ifremer.fr/surveillance/phytoplancton_phycotoxines); and (2) monthly samples from the Water Framework Directive (WFD) monitoring programme (http://envlit.ifremer.fr/surveillance/directive_cadre_sur_l_eau_dce).

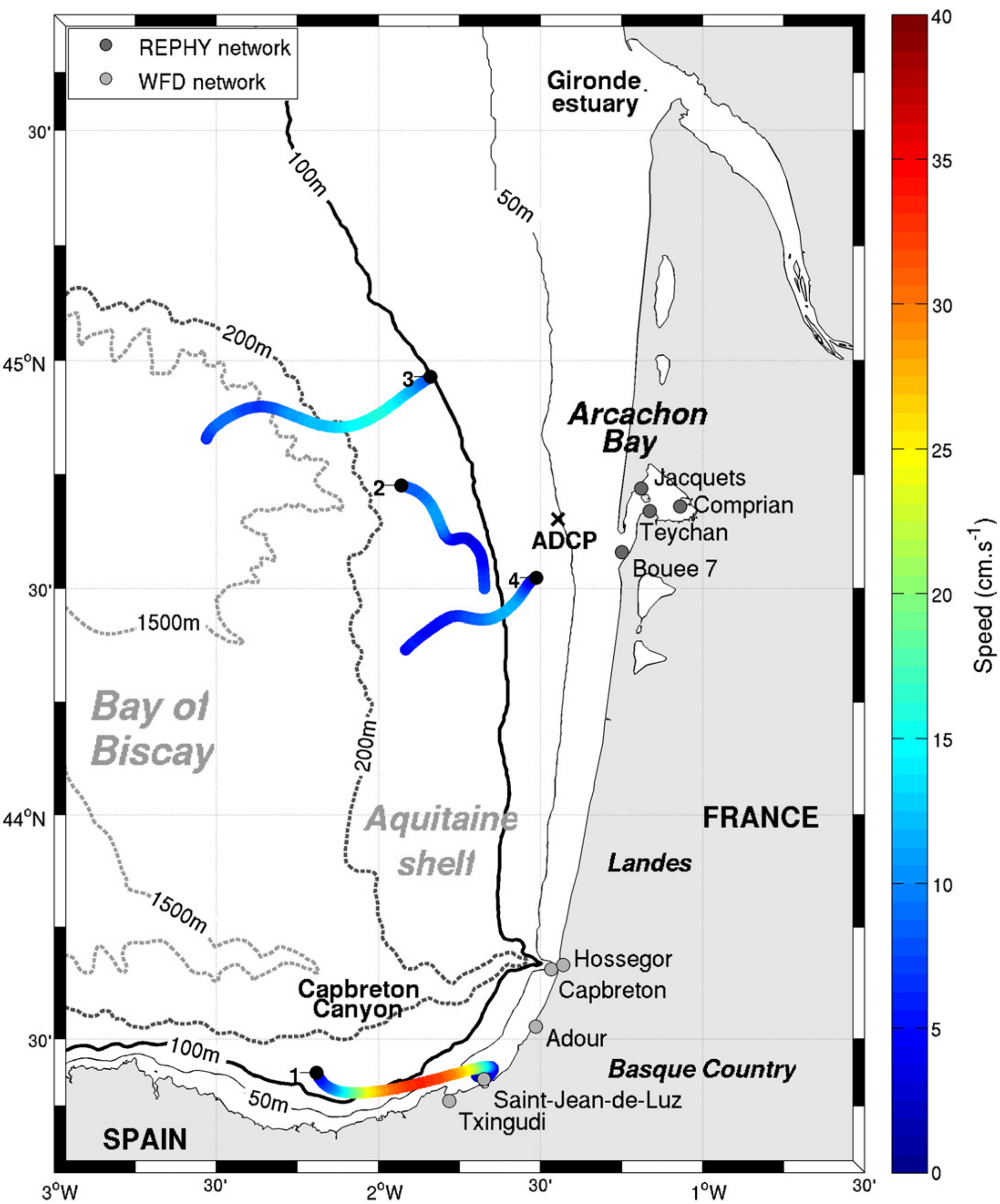

Fig. 1. Map of the Aquitaine shelf showing location of sampling points for REPHY and WFD and location of the ADCP. The four buoy tide filtered trajectories from the 16th July 2009 to the 23th July 2009 are presented. The colour of the trajectory represents the intensity of the current. Black dots show where the trajectories start.

REPHY water samples were collected 1 m below the surface with 4 L Niskin bottles and preserved with Lugol's iodine solution (1:1000). Four stations were sampled in Arcachon Bay: Teychan, Bouee7, Comprian, and Jacquets (Fig. 1). Water depth at the different stations was less than 15 m. Sampling frequencies and start dates vary with stations. Teychan has been sampled weekly since 1987; Bouee7 has been sampled biweekly since 1995; Comprian and Jacquets have been sampled biweekly since 2002. Data analysed in this study include those collected from the start date until 2009. Quantitative analyses of phytoplankton were carried out using the Utermöhl (1931) method: after sedimentation in 10 mL, 25 mL and 100 mL settling chambers, samples were counted under an inverted microscope (Olympus IMT2).

WFD water samples were collected with Niskin bottles 1 m below the surface along the French Basque Country and Landes coasts (Fig. 1). Water depth was about 25 m at the Capbreton station, 20 m at the Saint-Jean de Luz station and less that 5 m for the Adour, Hossegor and Txingudi stations. Samples were fixed with Lugol's solution and counted after sedimentation in 10 mL chambers. *Dinophysis* spp. cell concentrations were also estimated following the Utermöhl (1931) method.

2.2.2. Dinophysis spp. bloom initiation in Arcachon Bay

This study is based on Maurer et al. (2010) in which seven *Dinophysis* or okadaic acid events are defined. The characterisation of these events is based on various kinds of data: results from mouse tests, chemical analyses and abundance of *Dinophysis* in 1995, 2002 and 2003 when chemical analyses were not carried out.

Dinophysis bloom initiation is defined here as the first observation of *Dinophysis* concentrations of more than 100 cells.L^{-1} that precede toxic events (obtained from Maurer et al., 2010). If no concentrations greater than 100 cells.L^{-1} were observed before a toxic event, the beginning of the toxic event was used to mark the *Dinophysis* bloom onset. Dates of the beginning of the *Dinophysis* season in Arcachon Bay from 1995 to 2008 are shown in Fig. 2. They all occurred in the spring except the event in 2002, which occurred in late autumn.

2.2.3. PELGAS and ARCADINO field sampling

To estimate *Dinophysis* spp. distribution and spatio-temporal variability on the shelf outside Arcachon Bay, plankton samples were collected during the PELGAS and ARCADINO surveys from 2003 to 2009 (Table 1). Surveys took place in spring and summer, seasons during which *Dinophysis* is most frequently observed within Arcachon Bay (Maurer et al., 2010). Phytoplankton samples and CTD vertical profiles were taken simultaneously at several stations in the Bay of Biscay (at night during the PELGAS survey). Phytoplankton samples were taken with Niskin bottles at the surface, at the fluorescence maximum and on the bottom. For ARCADINO surveys, the 2 L sample of seawater was concentrated on board on a 20 μm mesh. The concentrated fraction was diluted in 40 mL of filtered seawater. Samples were not concentrated in the PELGAS survey. Samples were sedimented in 10 mL settling chambers. The detection limit was 2 cells.L^{-1} for ARCADINO surveys and 104 cells.L^{-1} for PELGAS surveys. Plankton samples fixed with Lugol's iodine from these surveys were used to estimate *Dinophysis* concentrations. Cell concentrations were estimated using the Utermöhl (1931) method. From 2007, *Dinophysis* cells were identified and counted to species level; before 2007, the total *Dinophysis* count was grouped and referred to as simply *Dinophysis* spp.

2.2.4. Percentile analysis

The large amount of data from the 14 surveys (PELGAS and ARCADINO) in spring (from 20 March to 21 June, period during which most of the surveys are done) was split into six geographical areas. The entire survey area stretched from longitude 2.5°W to the French coast and from latitude 46°N to the Spanish coast. The six areas were delimited by longitude 1.5°W and by latitude 44.2°N and 45°N (see Fig. 4). Values of the 75th, 50th and 25th percentiles of *Dinophysis* concentrations (maximum in the water column) were calculated for each area. Values for all three percentiles in spring were also calculated for the data from the two coastal networks (REPHY from 1995 to 2008 and WFD from 2007 to 2009).

2.3. Meteorological and oceanographic observations

Wind data were taken from the ARPEGE numerical model developed by Météo France. This model provides the wind field four times per day with a resolution of 0.5° in longitude and latitude, i.e. 55.6 km.

From 11 April to 12 July 2002, from 9 July to 25 August 2008 and from 18 May to 13 August 2009, coastal currents were measured. A bottom-mounted 300 kHz RDI acoustic Doppler current profiler (ADCP) was located offshore Arcachon Bay (44°39.118′N, 01°26.800′ W, see Fig. 1) at a depth of about 54 m. Current velocities were recorded at hourly intervals with a bin size of 2 m in 2002, at 5 min intervals with a bin size of 1.5 m in 2008 and at 10 min intervals with a bin size of 1 m in 2009. Data corresponding to the first 6 m below the surface (detected using the pressure sensor) was considered as noise due to water–air discontinuity and the presence of waves and air bubbles.

Four trajectories of satellite-tracked buoys available during ADCP measurements were also used. They were drogued at a depth of 15 m and are therefore representative of the currents at 15 m.

A Demerliac filter (Demerliac, 1974) was used to remove the tide signal from ADCP data and buoy trajectories.

2.4. Wavelet analysis

To study the link between wind and currents, a wavelet analysis was performed. This method enables an analysis of the links between two signals in time and in frequency, which, in turn, makes it possible to discern intermittent periodicities. In this study, the wavelet coherence toolbox developed by Grinsted et al. (2004) was used. It performs continuous wavelet transform (CWT) and computes wavelet coherence (WTC) between two CWTs. The WTC can be thought of as the local correlation between two CWTs: it can find significant coherence even when common power is low, and reveal the level of confidence. The level of significance of the WTC was determined using Monte Carlo methods. The Morlet wavelet was used in this study.

3. Results and discussion

Three scenarios were considered to explain the origin of *Dinophysis* found in Arcachon Bay: (1) development within Arcachon Bay, (2) development in the ocean at the mouth of Arcachon Bay, or (3) development at a remote source followed by advection to Arcachon Bay. The main difficulty encountered in this study was that periods with significant *Dinophysis* concentrations in Arcachon Bay and available physical observations did not coincide.

To support or reject each scenario, three types of data were considered. First, results of *Dinophysis* observations made by the REPHY network inside Arcachon Bay are presented. Then, the only two years with observations of *Dinophysis* both within and without Arcachon Bay during a bloom event are presented (years 2005 and 2008). Next, percentiles were used to summarise all the *Dinophysis* data from the surveys and the networks to identify the areas where *Dinophysis* was most often observed. Then, the hydrodynamics of the Aquitaine shelf was studied to check the possibility of links between the different areas. Finally, a plausible scenario was formulated for the origin of Arcachon Bay *Dinophysis* and compared to the actual events.

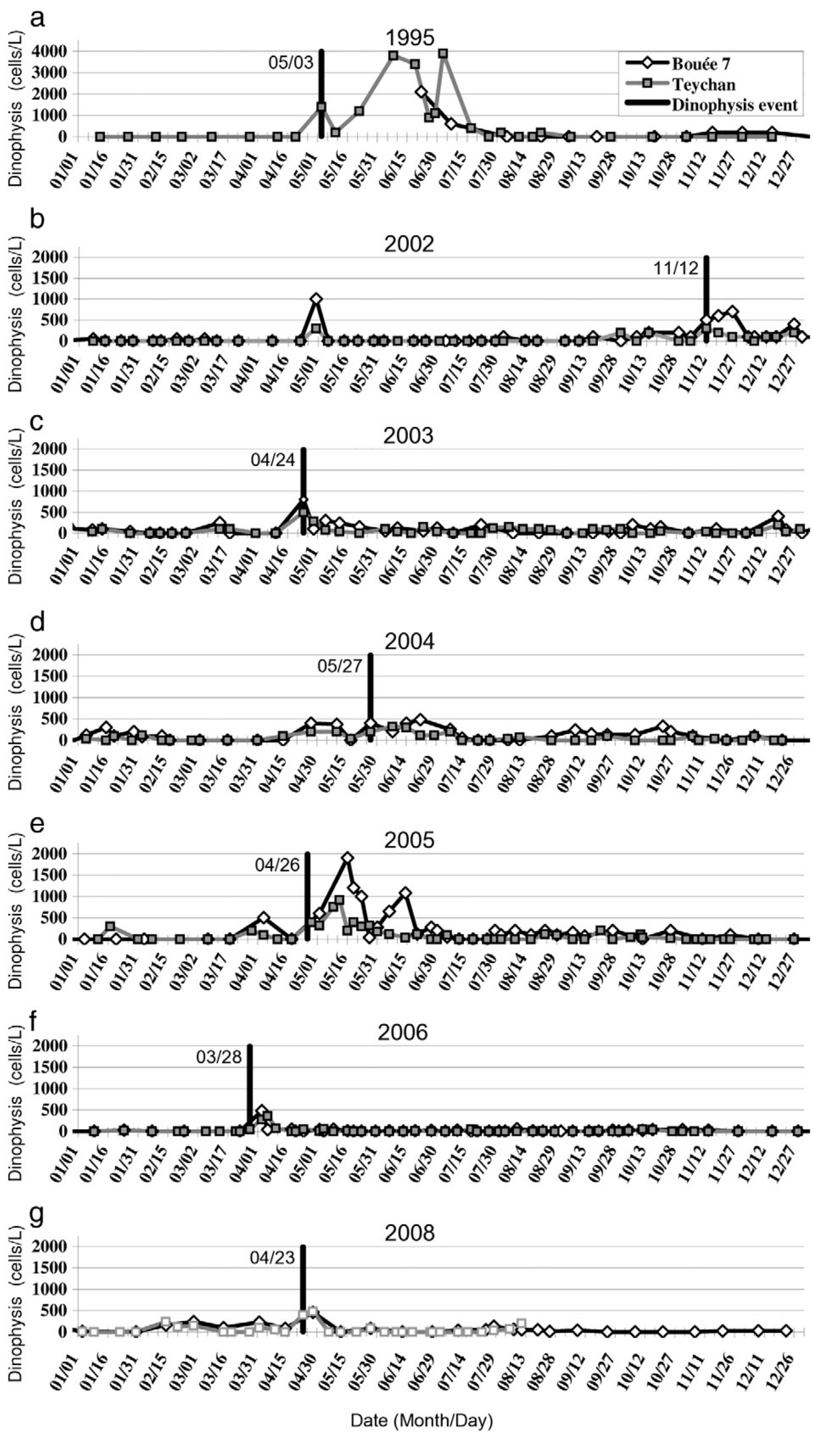

Fig. 2. *Dinophysis* concentrations at 'Bouee7' and 'Teychan' stations for the years in which *Dinophysis* events occurred. (a) 1995. (b) 2002. (c) 2003. (d) 2004. (e) 2005. (f) 2006. (g) 2008. Events are symbolised by a thick vertical bar, and the date of the event is indicated near the bar.

3.1. Dinophysis observations

3.1.1. Dinophysis spp. in Arcachon Bay

Dinophysis has been regularly observed all throughout the year in the Teychan Channel since 1987, with concentrations of around 10 cells.L^{-1} (Fig. 2). High abundances (above 100 cells.L^{-1}) generally occur in the spring (particularly in 1995 and 2005), but also during the summer (1989, 1990, 1995, 1996, 1997) and sometimes in the autumn (1992 and 2002) (Maurer et al., 2010). *Dinophysis* concentrations were generally higher at Bouee7 than at Teychan, with

Table 1
PELGAS and ARCADINO surveys since 2003.

Survey	Dates (MM/DD)
PELGAS 2003	05/30–06/10
PELGAS 2004	04/28–05/10
PELGAS 2005	05/05–05/16
PELGAS 2006	05/02–05/13
PELGAS 2007	04/27–05/02
PELGAS 2008	04/27–05/03
ARCADINO 2007	04/06–04/07
	06/09–06/10
	07/14–07/15
	08/25–08/26
ARCADINO 2008	04/11–04/13
	05/15–05/18
	06/09–06/14
	07/18–07/20
	08/21–08/23
ARCADINO 2009	03/14–03/17
	04/18–04/21
	05/18–05/22
	06/19–06/23
	07/09–07/13
	08/10–08/14

Bouee7's maxima usually occurring a few days before those of Teychan. Concentrations in the inner Arcachon Bay at Comprian and Jacquets were very low all year round. These observations suggest that *Dinophysis* does not develop within Arcachon Bay, and are consistent with the hypothesis that *Dinophysis* originates outside Arcachon Bay and is then advected into the bay from the open ocean. In some years, *Dinophysis* was not very abundant at all, particularly in 1991, 1993, 1998, 1999, 2000, 2006, 2007 and 2009. In 2006, an event was identified, but, compared to the concentrations observed in other years (see Fig. 2f), the event was minor and little background noise was detected, unlike the other years.

D. acuta, *D. acuminata*, *Dinophysis caudata*, *Dinophysis fortii*, *Dinophysis rotundata* (=*Phalacroma rotundatum*), *Dinophysis sacculus* and *Dinophysis tripos* were identified in Arcachon Bay. The most frequent and abundant species were *D. acuminata* and *D. caudata*. The first was dominant in the spring and the second in the summer and autumn. *D. acuminata* was likely responsible for the high concentrations of okadaic acid in oysters and mussels during the typical spring events, although other *Dinophysis* species may also have contributed (Maurer et al., 2010).

3.1.2. Dinophysis spp. on the Aquitaine shelf

Dinophysis spp. were frequently observed during the PELGAS and ARCADINO surveys, 16 of the 21 surveys showed abundances greater than 200 cells.L^{-1}. Concentrations greater than 10 000 cells.L^{-1} were rare. *Dinophysis* spp. cell densities in the water column (surface, bottom or at the depth of maximum fluorescence) were highly variable. In most surveys, *Dinophysis* was located either near the bottom or at the surface and more rarely at the depth of maximum fluorescence. The environmental conditions in which *Dinophysis* spp. were found were variable, i.e. high and low salinities and temperatures. However, the highest *Dinophysis* concentrations were always found when the water column was stratified. *Dinophysis* concentrations of over 1000 cells.L^{-1} were found in waters with salinities ranging from 31.2 to 35.4 and temperatures ranging from 12.3 to 15 °C.

PELGAS 2005 and 2008 were the only surveys that were carried out close (in space and time) to *Dinophysis* blooms observed within Arcachon Bay. Results from these surveys were used to analyse the distribution of *Dinophysis* spp. outside Arcachon Bay to better understand from where *Dinophysis* spp. populations might have originated.

PELGAS 2005 was carried out from 05 to 10 May. The distribution of maximum *Dinophysis* spp. concentrations with respect to depth in Fig. 3a shows that high concentrations were limited to a strip along the coast, with a visible north–south gradient. The highest concentrations observed on the bottom at latitude 44°N (Fig. 3b) were up to 11 000 cells.L^{-1}. North of latitude 45°N, concentrations were low, less than 200 cells.L^{-1} at all depths. During this survey, no measurements were made just outside Arcachon Bay or inside the bay itself. However, observations were made just after an event occurring on 26 April 2005 (Fig. 2e). According to the REPHY network, concentrations were about 760 cells.L^{-1} at Teychan (09 May 2005) and increased to 1900 cells.L^{-1} on 16 May 2005 at Bouee7.

The PELGAS 2008 survey lasted from 26 April to 05 May. Fig. 3c shows that the high *Dinophysis* concentrations were restricted to a strip along the coast as in the PELGAS 2005 survey. High *Dinophysis* spp. concentrations greater than 10 000 cells.L^{-1} were observed along the coast (Fig. 3d). To the north of Arcachon Bay, *Dinophysis* cells were located in the bottom layer at 25 m (18 000 cells.L^{-1}). Conversely, further south along the Landes coast, high *Dinophysis* spp. concentrations were located 1 m below the surface (13 000 cells.L^{-1}). Low *Dinophysis* spp. concentrations (200 cells.L^{-1}) were found at the station located just south of the mouth of Arcachon Bay.

On 28 April 2008, *Dinophysis* was observed at Bouee7 (460 cells.L^{-1}) and at Teychan (480 cells.L^{-1}) (Fig. 2g). The PELGAS 2008 survey and REPHY network data confirmed that *D. acuminata* was the only *Dinophysis* species present both outside and inside Arcachon Bay.

In 2005 and 2008, the *Dinophysis* events within Arcachon Bay were linked to the bloom along the Aquitaine shelf with high *Dinophysis* concentrations. The strip-like distribution suggests that a bloom occurring along the coast was being advected onto the shelf.

The presence of large *Dinophysis* populations (11 000 and 18 000 cells.L^{-1} in 2005 and 2008, respectively) near the sea bottom deserves special attention. Dense aggregations of *Dinophysis* spp. in bottom layers have only rarely been observed and their ecological importance in *Dinophysis* spp. life cycles is still unknown (Reguera et al., 2011). Recently, Velo-Suárez et al. (in review) proposed a conceptual model in which deep layers of *D. acuminata* play an important role as seed sources and in dispersal in the Galician rias. Our results suggest that deep layers of *Dinophysis* spp. are recurrent features on the French platform. Surface and bottom populations can be found together in areas close to the coast (Fig. 3). Nevertheless, these populations can move apart and travel different paths within surface and bottom currents. Cells fixed with Lugol's iodine looked morphological healthy and no empty thecae were included in our counts. Unfortunately, we do not have any information on the specific characteristics (ploidy, pigment composition, viability etc.) of these deep populations. Further research is needed to address their importance in the *Dinophysis* life cycle and their advection along French coasts.

3.1.3. Percentile results

Results of the 75th percentile from the surveys (Fig. 4) revealed high values on the south-east coasts of Arcachon Bay, with values of up to 5000 cells.L^{-1} in area 6, but not exceeding 200 cells.L^{-1} in the other areas. In the coastal networks, the maximum 75th percentile occurred at the Capbreton station (WFD network, Fig. 1), with 760 cells.L^{-1}. Values for the other stations of the WFD network were under 50 cells.L^{-1}. Values from the REPHY network were low: 200 cells.L^{-1} at Bouée 7 and 100 cells.L^{-1} at Teychan.

Values of the 50th percentile were less than 50 cells.L^{-1} except in the Landes coast (area 6) (240 cells.L^{-1}) and Capbreton station (480 cells.L^{-1}). Values for the 25th percentile were close to 0 cells.L^{-1}.

Values of percentiles from both the open ocean surveys and the coastal networks indicated the Landes coast as the area the most subject to *Dinophysis* blooms. The southern end of the Landes coast was thus considered as a source of *Dinophysis*.

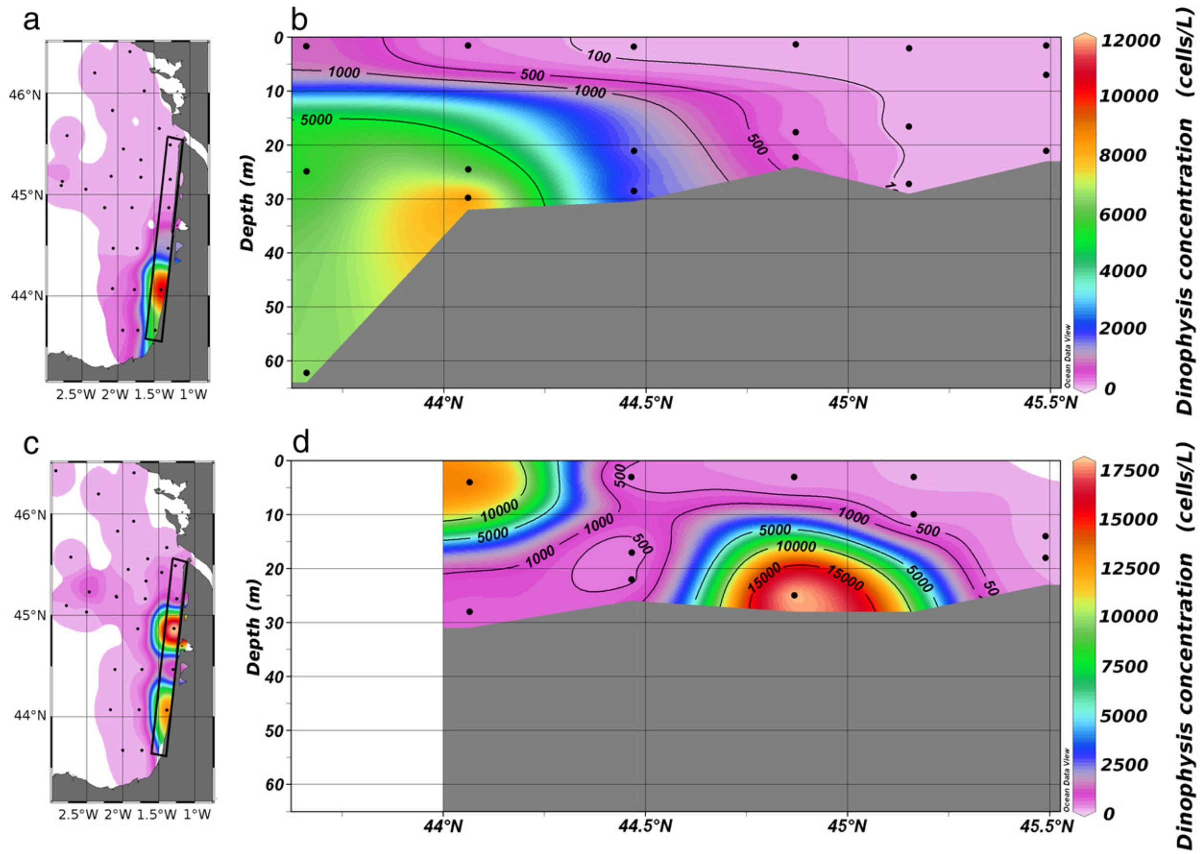

Fig. 3. Horizontal distribution of *Dinophysis* spp. cell maxima with respect to depth during the PELGAS surveys in (a) 2005 and (c) 2008. The black box represents the coastal transect of *Dinophysis* concentrations for (b) 2005 and (d) 2008. Locations of PELGAS 2005 and 2008 sampling stations are indicated by solid black circles.

3.2. Hydrodynamics

3.2.1. Eulerian current measurements

Fig. 5 shows the direction and the intensity of the depth-averaged current (tide-filtered using a Demerliac filter (Demerliac, 1974)) on the shelf just outside Arcachon Bay for the three ADCP data sets from 2002, 2008 and 2009. Overall, 30% of the currents flowed towards the south, 34% towards the north, and the rest were mainly weak currents flowing towards the west (i.e. offshore). Thus, the main circulation goes along the isobaths, i.e. along a north–south axis. The strongest currents are oriented north. The mean current can reach 0.30 m.s^{-1} northward, but did not exceed 0.15 m.s^{-1} southward.

The intensity of the tide-filtered current at mid-depth (27 m) and wind intensity (extracted from the ARPEGE model at the grid point closest to the ADCP location i.e. (44.5°N, 1.5°W)) are presented in Fig. 6a for the 2009 data set. Variation in the intensity of both signals were linked, and periods of weak wind and weak current were in phase, as were those of intense winds and currents. It can be inferred that circulation depends strongly on the wind regime and responds rapidly to changes in wind. Strong velocities were observed around 19 July 2009 after intense winds (Fig. 6a). Fig. 6b shows the components of the tide-filtered current at mid-depth (27 m). This current had a strong northward component (up to 0.19 m.s^{-1}) and a small westward component (up to 0.05 m.s^{-1}). Fig. 6c, which represents the wind components (sliding average on 3 days), shows that this strong current event was preceded by strong westerlies. Westerlies blew from 16 to 19 July with a maximum of 8.7 m.s^{-1} on 17 July along the westward component. To check the correlation between the burst of westerlies and the triggering of a poleward current, wavelet coherence between the northward component of the current and the eastward component of the wind was calculated (Fig. 7). Around this date, coherence was very high for periods of between 4 and 16 days. It was over 0.8 for a period of 6 days from 10 to 20 July and the maximum of 0.83 was reached on 16 July when strong winds started to blow. This shows that intense westerlies were very well correlated with intense northward circulation. The phase difference between the wind and the current on 16 July (during the maximum intensity of westerlies) was about 44 h.

Currents at mid-depth were chosen because they are representative of the currents in the water column since the implicated poleward currents occur throughout the water column (except at the surface where they are countered by the currents in the wind-induced Eckman layer). Using depth-averaged currents instead of mid-depth currents gave similar results.

The ADCP data sets from 2002 and 2008 gave similar events (not shown). In late May 2002, westerlies of up to 12.7 m.s^{-1} (daily averaged) resulted in poleward currents of 0.1 m.s^{-1} (depth-averaged). This event was then followed by two successive westerlies of up to 12.6 m.s^{-1} and 12.7 m.s^{-1} (daily averaged) in early June which led to poleward currents of 0.15 m.s^{-1} (depth-averaged). In August 2008, northwesterlies with a westward component (daily averaged) of 8.6 m.s^{-1} led to poleward currents of 0.26 m.s^{-1} (depth-averaged). ADCP data sets from 2002, 2008 and 2009 highlight a phenomenon that was not expected: strong westerlies generate strong barotropic northward currents at the mouth of Arcachon Bay. Westerlies are cross-shore winds on the Aquitaine coast, and cross-shore winds have little impact on alongshore circulation: they should just create southward currents in the Eckman surface layer (Tilburg 2003).

3.2.2. Lagrangian drifters

During the strong current events described above, four buoys (drogued at a depth of 15 m) were set out on the Aquitaine shelf. Their trajectories during the strong westerlies from 16 July to 20

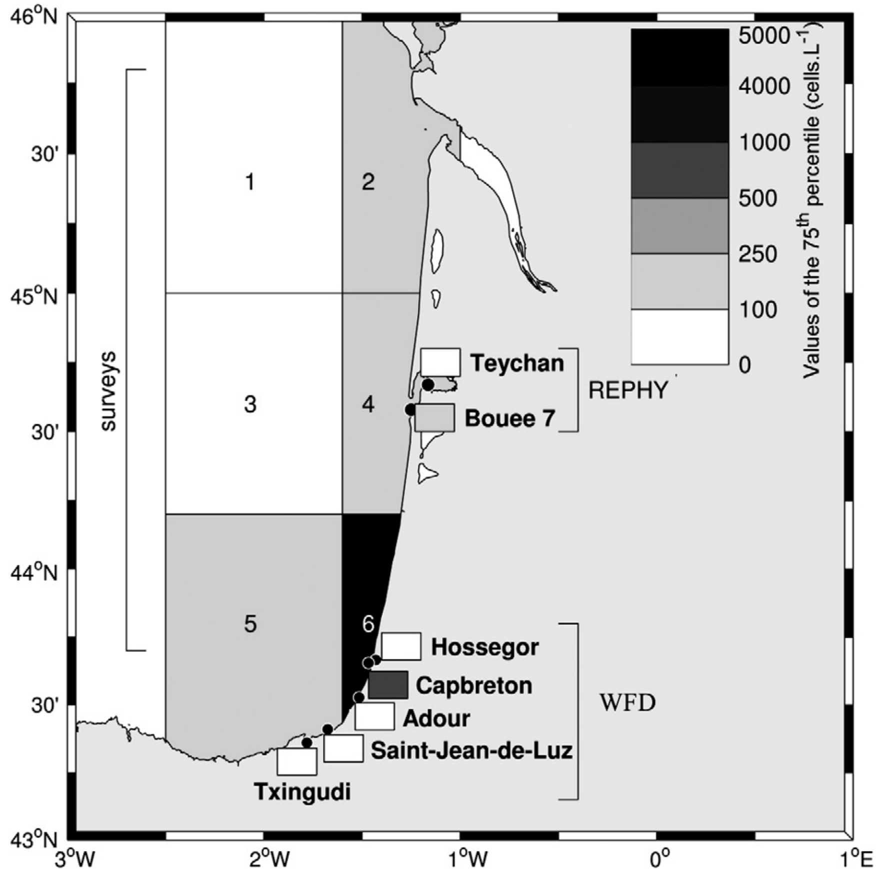

Fig. 4. Values of the 75th percentiles from the PELGAS and ARCADINO surveys and REPHY and WFD network data in spring (from 20 March to 21 June). Small rectangles on land along the coast correspond to the percentile values of network stations. The entire survey area stretched from longitude 2.5°W to the French coast and from latitude 46°N to the Spanish coast. Data from 14 PELGAS and ARCADINO surveys were split into six geographical areas delimited by longitude 1.5°W and by latitude 44.2°N and 45°N.

July 2009 are shown in Fig. 1 (trajectories are tide-filtered with a Demerliac filter (Demerliac, 1974)). After the strong westerlies, buoy 1 near the Basque Country coast revealed an intense current running along the Spanish coast. The strong current observed using ADCP measurements at the mouth of Arcachon Bay is thus suspected to be an extension of this current. However the three other buoys off

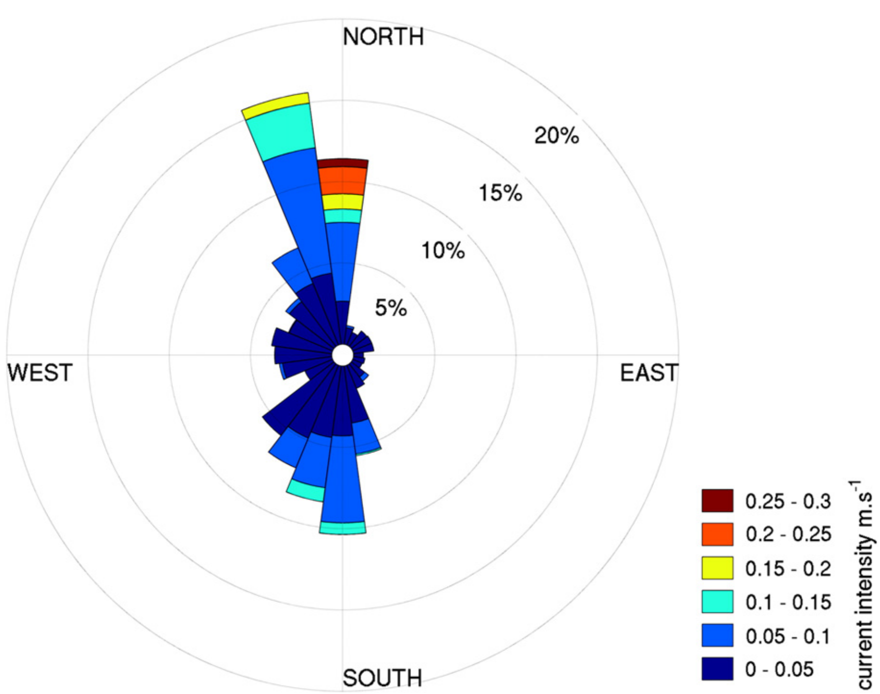

Fig. 5. Depth-averaged current rose showing current direction and intensity for the three ADCP data sets from 2002, 2008 and 2009. See Fig. 1 for the ADCP location.

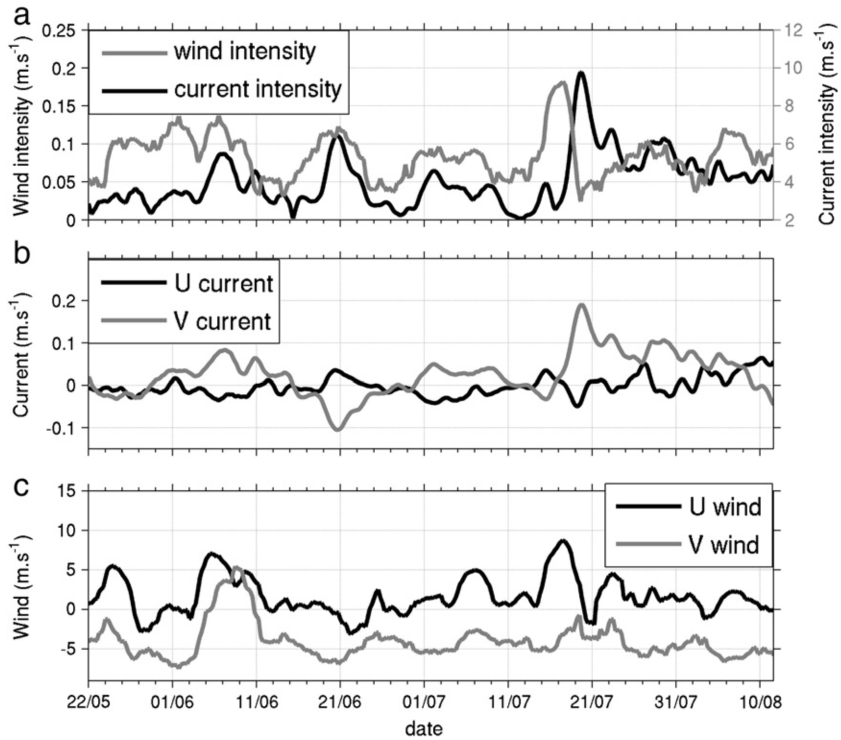

Fig. 6. (a) Wind intensity and current intensity at 27 m depth (b) eastern (U) and northern (V) current component at 27 m depth tide-filtered using a Demerliac filter (c) eastern (U) and northern (V) wind component smoothed over three days. See Fig. 1 for the ADCP location. Wind data is extracted from ARPEGE model at (44.5°N, 1.5°W).

Arcachon Bay did not show any effects of this current: two went offshore (buoys 3 and 4) and one went towards the south (buoy 2). Thus, the strong northward current seems to be very coastal. Buoy 1 in the coastal current reached 0.33 $m.s^{-1}$, with its maximum 14 h after the westerlies' intensity maximum. The northward current at 15 m below the surface (corresponding to the depth of the buoy drogue) measured by the ADCP reached its maximum 60 h after the buoy. The intensity of the current measured by the buoy on the southern part of the shelf was 0.08 $m.s^{-1}$ higher than the one measured more northward by the ADCP in front of Arcachon Bay.

Transport estimated from the ADCP data from 18 July to 23 July was towards the north. The distance of this transport ranged from

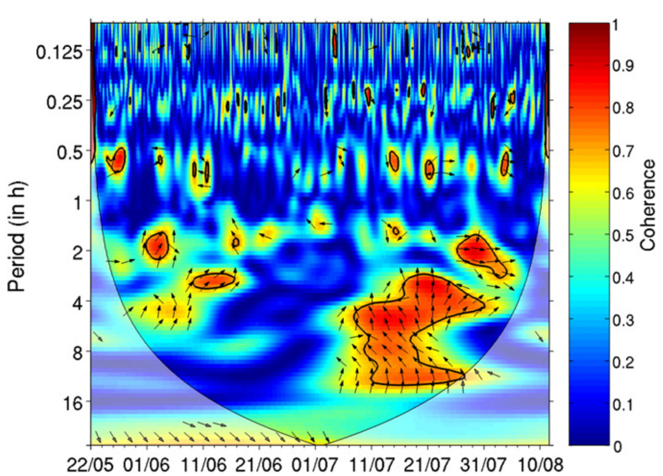

Fig. 7. Wavelet coherence of the eastern wind component and the northern current component at 27 m depth. The black lines represent the 95% confidence level of the wavelet coefficient (Chi^2 statistical test). Arrows represent the phase difference between the two variables. See Fig. 1 for the ADCP location. Wind data is extracted from ARPEGE model at (44.5°N, 1.5°W).

17 km to 84 km, depending on the depth of the measured current. The minimum was reached at the bottom and the maximum at 35 m above the bottom. The southern buoy measured currents 0.08 $m.s^{-1}$ higher; thus, currents were higher in the south of the shelf than in front of Arcachon Bay. The transport estimated from ADCP measurements is likely to have been underestimated and were probably higher.

ADCP results and the drifting buoys highlight the fact that each strong westerly wind event induces intense coastal transport from the Basque Country towards the north. ADCP measurements during southerlies were taken only in 2002 (not shown); moderate southerlies of 8 $m.s^{-1}$ during one day led to northward currents (mean in the water column) of 0.08 $m.s^{-1}$.

Contrary to the Armorican shelf, the hydrodynamics on the Aquitaine shelf are poorly known. Tidal currents are relatively weak, less than 0.15 $m.s^{-1}$ (Lecann, 1990). These weak tidal currents result in strong vertical stratification. Hydrodynamics are mainly governed by wind and density currents. From spring to autumn, prevailing northerly winds are able to induce transient upwellings along the Landes coast (Froidefond et al., 1996).

Barotropic simulations by Pingree and Lecann (1989) show that over the Armorican and the Aquitaine shelves, wind-driven currents are typically around 0.1 $m.s^{-1}$ and may locally rise to 0.2 $m.s^{-1}$. Northwesterly and westerly winds cause southward currents. The southwesterly and southerly wind reverses the circulation towards the northwest. The main characteristic is the relatively rapid response of the dynamics to a change in wind stress (less than 4 days).

However, these poleward currents due to westerlies such as those observed in this study have never been reported before. The fact that Pingree and Lecann (1989) did not reproduce these currents in their barotropic simulations leads us to believe that these currents may be due to some physical processes not taken into account in their studies. Their purpose was to study the 2D response of a homogeneous ocean to winds of different directions. Large-scale circulation was not considered in their study but is not likely to be involved since the observed currents were nearshore and did not extend over the entire shelf and the shelf break. Another type of circulation not reproduced in their simulations is geostrophic circulation (3D circulation) induced by density gradients over the shelf. This is the most plausible explanation; however, the mechanism that gives rise to the density gradients remains unknown.

The Adour River (120 km south of Arcachon Bay) has an annual mean runoff of 315 $m^3.s^{-1}$, with strong seasonal variability. The Adour plume has an influence on the salinity distribution over the shelf (Petus et al., 2010; Puillat et al., 2004). The dynamics of this plume is under the influence of wind regimes and shows high seasonal variability. The Adour plume could give rise to poleward density currents. However, the Adour flow was low during these events of intense poleward currents (100 $m^3.s^{-1}$ in July 2009).

Recent investigations of the southeast part of the Bay of Biscay provide a better description of seasonal patterns on the Spanish Basque Country coast (Valencia et al., 2004). During spring and summer, moderate northerly and easterly winds are associated with alternating southward and westward circulation and upwelling. These factors maintain stratification and the vertical stability of the water column. During autumn and winter, strong southerly and westerly winds prevail and induce eastward and northward currents. Moreover, the currents are downwelling and thus favour vertical mixing and homogeneity of the upper layers of the water column.

3.3. Possible advection of Dinophysis populations from the south

Fig. 8 shows daily winds during the 14 days before the seven indentified *Dinophysis* events in Arcachon Bay. Before the 26 April 2005 *Dinophysis* event that preceded the PELGAS 2005 survey, predominant westerlies of up to 11.3 m s^{-1} had blown for 11 days. Similarly, before the 23 April 2008 event which occurred before the PELGAS 2008 survey, westerlies of up to 12 m s^{-1} had occurred for 11 days with short periods of easterlies and southerlies. Therefore, strong westerlies blew before both *Dinophysis* events in 2005 and 2008 and they blew longer than the westerlies that triggered the strong poleward currents measured in 2009. With regard to the hydrodynamic response to strong westerlies described above, these two events were probably preceded by intense northward currents along the coast. These currents could have transported *Dinophysis* populations from the southern putative Capbreton source up to Arcachon Bay. The narrowness of the current may explain why the highest concentrations were found along the coast.

All the *Dinophysis* events recorded by REPHY in Arcachon Bay (Fig. 2) were preceded by 7 to 15 days of strong westerlies and southerlies except in 2004 (Fig. 8). Both strong southerlies (Pingree and Lecann, 1989) and strong westerlies generate intense northward currents. Consequently, before those events, northward circulation may have transported *Dinophysis* populations from the Landes coast up to Arcachon Bay as observed during the 2005 and 2008 PELGAS surveys.

In the case of the 2004 event, the scenario of transport along the coast could not be validated solely from the meteorological conditions. The exact onset of this event was not very clear, which may explain the lack of support for this scenario. If the high concentrations found from April to July are considered as a whole single event, the bloom would have begun on 27 April 2004 (Fig. 2d). One week prior, strong westerlies of up to 13 $m.s^{-1}$ had blown for 3 days.

Transport of harmful algal populations has already been analysed in several studies. Delmas et al. (1992) hypothesised that an offshore (isobath 50 m) *Dinophysis* bloom could have been advected inshore in the Pertuis d'Antioche by a flood tide. More recently, Sellner et al. (2003) review HABs, their causes, impacts and detection and indicate that circulation of water masses determines local and more distant impacts. For example, in the Gulf of Maine, *Alexandrium* spp. populations can be transported by southwesterly alongshore transport (induced by favourable downwelling wind conditions) from the Bay of Fundy along the New England coast in two separate coastal currents, the Eastern and Western Maine Coastal Currents, part of the Gulf of Maine circulation (Anderson, 1997). Pitcher et al. (2010) reviewed HABs in the Benguela, California and Iberian upwelling systems. Particular features of these systems are inner-shelf, poleward counter-currents, which may coexist with farther offshore, equatorward flow when upwelling winds relax or reverse to downwelling winds (Fawcett et al., 2008; Hickey, 1989; Sordo et al., 2001; Torres and Barton, 2007). These poleward flows have in some cases been associated with poleward transport of HABs (Pitcher and Calder, 1998; Pitcher and Weeks, 2006). Escalera et al. (2010) showed that blooms of *D. acuta* in Galician rias were due to longshore transport of populations located off Aveiro (Portugal) to the north under downwelling conditions. This corresponds to a

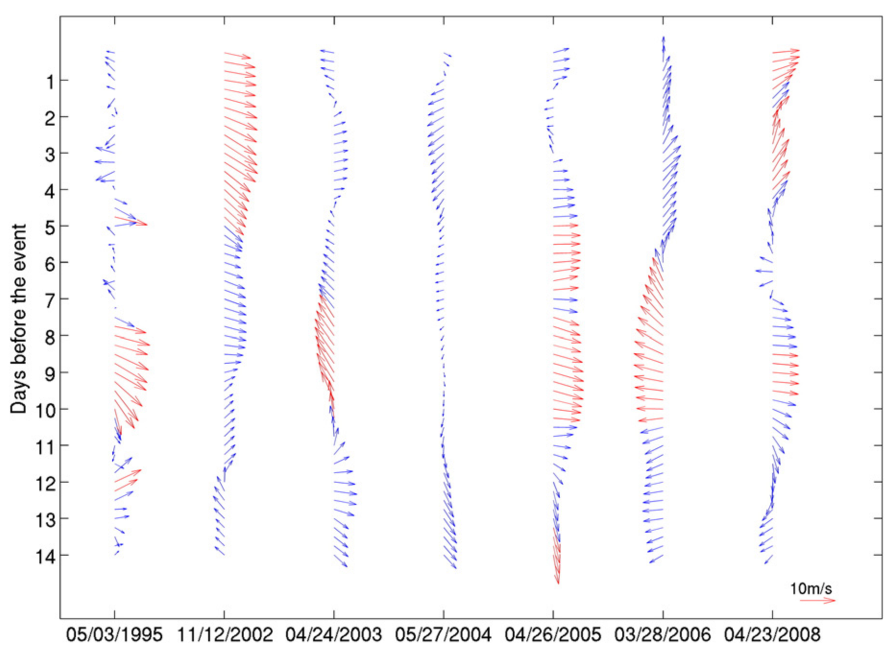

Fig. 8. Daily averaged winds over the two weeks before the seven *Dinophysis* events. Wind data is extracted from ARPEGE model at 44°N, 2.5°W. Red arrows correspond to winds with intensities over 7 $m.s^{-1}$.

journey of at least 170 km. The bloom was suspected to have been transported by a relatively narrow poleward current which exists during the autumn transition except under upwelling conditions. Haynes and Barton (1990) estimated the northerly component of the poleward flow from drifter data at up to 0.31 $m.s^{-1}$. The intensity of this flow is similar to the speed measured in our study. In our study, the distance between the suggested source and Arcachon Bay is less than that observed by other authors. Nevertheless, the current observed in this work also had a shorter lifetime.

This poleward current does not correspond to the counter-current mentioned in the above studies. Meteorological conditions do not correspond to upwelling or downwelling conditions, but to cross-shore winds on the Aquitaine coast. However, although these currents do not share the same climatological origin, they can help explain functional transport pathways of HAB populations.

4. Summary and conclusions

The REPHY network monitoring programme demonstrated that *Dinophysis* spp. cells that are frequently found in Arcachon Bay originate from the open shelf and that they do not develop within Arcachon Bay.

Two surveys on the Aquitaine shelf during *Dinophysis* events in Arcachon Bay show the distribution of *Dinophysis* on the Aquitaine shelf. *Dinophysis* cells are located along the Aquitaine coast in high concentrations (up to 11000 $cells.L^{-1}$ in 2005 and up to 18000 $cells.L^{-1}$ in 2008).

Compilation of *Dinophysis* observations from surveys demonstrate that *Dinophysis* spp. are found in high concentrations in the Capbreton area. This was confirmed by the value of the percentile from the WFD station in Capbreton. The reasons for the development of a *Dinophysis* population in this particular area are not yet understood, but various factors may be involved, such as weak tidal currents in this area, topographical effects induced by the Capbreton canyon and the proximity of the Adour River.

The *Dinophysis* found in Arcachon Bay during REPHY monitoring and all along the coast in observations made during PELGAS 2005 and 2008 surveys may have originated in the Capbreton area. This hypothesis is based on northward transport along the coast. Unfortunately, data taken during *Dinophysis* events are not available, and this hypothesis cannot be directly validated. However, the analysis of available current data shows that strong westerlies lead to intense northward currents. Meteorological conditions prior to most *Dinophysis* events involve strong westerlies or strong southerlies. Both lead to intense northward currents that are able to transport *Dinophysis* from the Capbreton area, where *Dinophysis* appears to initiate and develop, northward up to Arcachon Bay.

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