



Toward predicting *Dinophysis blooms* off NW Iberia: A decade of events



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ARTICLE INFO

Keywords:

Harmful algal blooms
Upwelling
Interannual variability
Meteorological anomalies
Shelf circulation

ABSTRACT

Dinophysis acuminata and *Dinophysis acuta* are recurrent species off NW Iberia but their outbreaks occur under different conditions. A decade (2004–2013) of weekly data for each species at two sentinel stations located at the entrance of Rias de Aveiro–AV (NW Portugal, 40°38.6' N) and Pontevedra–PO (Galicia, Spain, 42°21.5' N), were used to investigate the regional synchronism and mesoscale differences related to species detection, bloom (>200 cells L⁻¹) initiation and development. Results highlight the high interannual variability of bloom events and summarize the associated meteorological/oceanographic conditions. *D. acuta* blooms were observed in 2004–2008 and 2013, and the species highest maxima at AV occurred after the highest maxima of its prey *Mesodinium*, with a time-lag of 2–3 weeks. *D. acuminata* blooms were observed every year at both stations. The cell concentration time series shows that the blooms generally present a sequence starting in March with *D. acuminata* in PO and three weeks later in AV, followed by *D. acuta* that starts at AV and three months later in PO. Exceptionally, *D. acuminata* blooms occurred earlier at AV than PO, namely in high spring upwelling (2007) or river runoff (2010) years. A four-year gap (2009–2012) of *D. acuta* blooms occurred after an anomalous 2008 autumn with intense upwelling which is interpreted as the result of an equatorward displacement of the population core. Numerical model solutions are used to analyze monthly alongshore current anomalies and test transport hypotheses for selected events. The results show a strong interannual variability in the poleward/equatorward currents associated with changes in upwelling forcing winds, the advection of *D. acuta* blooms from AV to PO and the possibility that *D. acuminata* blooms at AV might result from inocula advected southward from PO. However, the sensitivity of the results to vertical position of the lagrangian tracers call for more studies on species distribution at the various bloom stages.

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1. Introduction

Harmful Algal Bloom (HAB) species are regular components of the phytoplankton in northwestern Iberian upwelling waters, a coast annually affected mainly during summer and autumn by blooms, sometimes in very high concentration of cells, of *Dinophysis* species. These dinoflagellates are diarrhetic shellfish poisoning (DSP) producers and are the main cause for long periods of shellfish harvesting closures with serious socio-economic

impacts in the region. *Dinophysis*, though tolerating upwelling turbulence, are favored by thermal and haline stratification and there is little evidence that blooms are induced by elevated nutrient concentrations (Delmas et al., 1992; Reguera et al., 1995; GEOHAB, 2008). They seem to be excellent survivors and can attain high growth rates (Reguera et al., 2012).

Dinophysis are obligate mixotrophic species that in cultures depend simultaneously on the availability of prey, e.g. the phototrophic ciliate *Mesodinium rubrum*, and on light intensity for photosynthesis (Kim et al., 2008). In nature, populations of the predator and prey still need to aggregate to enhance encounter rates. Despite these specificities, the development of *Dinophysis* blooms follow the general phases of population development (initiation, growth, maintenance and decay) that, together with their transport by currents, need to be studied in order to better

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predict the events and mitigate their effects (Reguera et al., 2012). Furthermore, Reguera et al. (2012) pointed out that the conditions for the initiation, or for the supply of inoculum populations, may hold the key to explain *Dinophysis* bloom interannual variability.

Twenty five years of HAB monitoring on NW Iberia waters show that blooms of the endemic dinoflagellates *Dinophysis acuta* and *Dinophysis acuminata* are recurrent although presenting a high interannual variability whose causes are still poorly understood. Both species coexist but their maxima never coincide in space or in time (Palma et al., 1998), and their peaks can alternate in late summer and early autumn associated with different stratification patterns (Reguera et al., 1993). In the west coast of Portugal (Fig. 1), the region between Figueira da Foz (F.Foz) and Aveiro (AV), i.e. between 40°10' N and 41° N, is the most problematic area, where the species maxima are normally reported (Palma et al., 1998; GEOHAB, 2005; Vale et al., 2008), and have been observed in thin subsurface layers within the pycnocline (Moita et al., 2006). This area is in general considered the epicenter for *D. acuta* blooms in northwestern Iberia where they often occur first and are more intense than in adjacent areas (Moita et al., 2006; Escalera et al., 2010). For similar reasons, Ría de Pontevedra, in Galicia, is thought to be a hot-spot for *D. acuminata* blooms in NW Iberia (Pazos et al., 2005). Exceptionally in some years, intense blooms of *D. acuta* were observed only in Galicia and not further south (e.g. 1989, Reguera et al., 1995) or the reverse with *D. acuminata* blooms in Portugal (e.g. 2007, this work).

The very sudden increase in *Dinophysis* cell numbers detected in some coastal monitoring sites cannot be fully explained by the species growth rates alone. There is evidence that populations of both species can be transported alongshore but relaxation/downwelling events may also cause their accumulation inshore (Reguera et al., 1995; Sordo et al., 2001; Crespo et al., 2006; Escalera et al., 2010). Upwelling, through pycnocline shallowing, can serve as a mechanism of concentrating populations that can be

advected by the inshore poleward currents when the winds weaken, a physical mechanism observed by Sordo et al. (2001) and Oliveira et al. (2009). Contrasting climatic conditions were also evoked to explain the selection in the Galician rias of *Dinophysis acuminata* and *Dinophysis acuta* blooms in 2002 and in 2003 respectively (Escalera et al., 2010): *D. acuminata* was associated with thermohaline stratification and persistent northerly winds while *D. acuta* was related to an exceptionally hot summer with the lowest upwelling index of the previous 50 years. Díaz et al. (2013) showed that the early initiation of *D. acuminata* blooms in the Galician Rías Baixas, observed in 2002 and 2012, were related to positive anomalies in SST and atypical predominance of upwelling winds during the immediately previous winters.

This work aims at investigating in detail the conditions related to *Dinophysis acuta* and *Dinophysis acuminata* bloom initiation and intensification in two sites off NW Iberia (Galician rias and NW coast of Portugal) separated by 200 km. Data include: (i) a decade (2004–2013) of *Dinophysis* weekly data samples from two monitoring stations where the species often present regional maxima; (ii) meteorological reanalysis data and (iii) daily sea surface maps to provide a synoptic view of the sea surface conditions prior to bloom development; (iv) hydrodynamic model solutions to investigate the advection of *Dinophysis* populations between the two regions.

2. Study area, data and methods

2.1. The study area

The area of study is located at the NW coast of Iberia (Fig. 1), in the northern limit of the upwelling system associated with the north Atlantic anticyclonic gyre. In this region, the upwelling occurs seasonally, from late spring to early Autumn with a



Fig. 1. Map of NW Iberia showing the position of the two HAB long term monitoring stations, PO located in front of Buéu in Ría de Pontevedra (Galicia, NW Spain) and AV at the entrance of Ria de Aveiro (Portugal).

maximum in July, under the influence of northerly winds, whose events normally last for 5–10 days (Wooster et al., 1976; Fiúza et al., 1982). As reported for other eastern boundary systems (Smith, 1981), the velocity and width of the coastal upwelling jet is dependent on the duration and strength of the northerly wind events. The upwelling front can expand over the slope, or contract toward the coast, under northerly or southerly winds respectively. Several studies have shown the existence of a poleward counter current carrying warm oceanic water northwards over the slope (Frouin et al., 1990; Haynes and Barton, 1990), and also an inner-shelf poleward current that advects warm water after the cessation of upwelling (Sordo et al., 2001). These authors also showed this current promoted the alongshore transport of HABs.

The local upwelling patterns of NW Iberia also depend on the coastal morphology, which is NW-SE oriented between cape Finisterre (Galicia) and 41° N latitude (~Porto, Portugal) and NE-SW from that latitude until cape Carvoeiro. In Galicia, the coastline is deeply indented by Rías Baixas allowing a dynamic exchange of water between the shelf and the Rías, leading to a local increase in phytoplankton productivity (Figueiras et al., 2002). The Rías also act as resonance boxes for HABs events (Escalera et al., 2010). To the south, the coastline is straight and the shelf becomes gradually wider and flatter until F.Foz (40.2° N), contributing to the thermal increase of water column stratification. This stratification is also enhanced by the discharges of several important rivers (e.g. Douro and Minho). The coast between 42 and 41° N has been described as the source for a recurrent upwelling filament that, depending on the wind conditions and its interaction with the offshore eddies, develops with different intensities (Relvas et al., 2007).

2.2. Data and methods

Dinophysis acuta and *Dinophysis acuminata* data from April 2004 until December 2013 were provided by the Galician (INTECMAR) and the Portuguese (IPMA) HABs Monitoring Programs and are from two selected sampling stations where, over the years, these species maxima often occurred. Data on *Mesodinium rubrum* counts at Aveiro, from May 2004 to December 2006 and from April 2008 until December 2010, are also presented. Additional data of *D. acuta* from all the HAB monitoring stations to the north of Lisbon were used to determine in each year the area of the coast where blooms initiated and the maxima were observed.

Station **PO**-Buéu (known as P2 in Galician monitoring program) is located at the southern side of ria de Pontevedra, Galicia (42°21'30.00" N; 8°46'20.00" W; 30 m depth) and station **AV**-Marégrafo is located at the entrance of ria de Aveiro (40°38'38.95" N; 8°44'55.18" W; 5 m depth), a site always sampled one hour before high tide to monitor shelf waters that enter the ria (Fig. 1). Water samples were collected with a hose-sampler to 15 m at PO and at the surface with a Niskin bottle at AV. In both cases, the samples are considered to represent the upper mixed layer of the water column, resulting from the tidal and wave mixing at the entrance of Ria de Aveiro, and the use of the integrated sampler in PO. All samples were immediately preserved with Lugol solution. Subsamples of 25–50 ml were allowed to settle before counting. The species were identified and counted by using the Utermöhl technique and inverted contrast microscopy.

Daily sea surface temperature (SST) maps were obtained from the Operational Sea Surface Temperature and Sea Ice Analysis – OSTIA (spatial resolution 0.05°, ~5 km) available from the MyOcean service. Meteorological parameters (surface wind components, photosynthetic active radiation – PAR) were obtained from the ECMWF ERA Interim re-analyses (spatial resolution 0.25° × 0.25°, ~25 km).

Bakun (1973) upwelling indices – UI ($\text{m}^3\text{s}^{-1}/100\text{ m}$) = τ_y/f – were calculated, based on the N-S wind component over the shelf (9° W) and a latitude between AV and PO (41.5° N). The wind stress was computed using the quadratic drag law $\tau_y = \rho_a CD|v|v$, where $|v|$ is the wind speed (m s^{-1}), v is the northward wind component (m s^{-1}), ρ_a is the air density (1.22 kg m^{-3}) and CD is the drag coefficient (0.0014). Using this formulation, the UI has the same signal as the NS wind component; therefore negative UI corresponds to offshore Ekman transport driven by the upwelling favorable equatorward winds, while positive UI corresponds to convergence/downwelling driven by poleward winds.

A Lagrangian model (Regional Ocean Modeling System-ROMS) was used to test several hypotheses of bloom initiation/detection after passive transport. Particle-tracking experiments used a 3D hydrodynamic model configured to reproduce NW Iberia shelf circulation. Monthly maps of current component anomalies, relative to the decade average (2004–2013), were computed from NEMO model solutions distributed as the MyOcean “Atlantic-Iberian Biscay Irish-Ocean Physics” products. The decade-long dataset for NW Iberia was constructed by merging the “reanalysis” product for the period 2004–2011 and the “analysis and forecast” product for 2012–2013.

An Empirical Orthogonal Function (EOF) analysis of OSTIA SST data for the period 2004–2013 was used to identify the main variability patterns. The EOFs were computed using the singular value decomposition routine implemented in the Ferret software (Hankin et al., 1996). Depending on the author, slightly different EOF terminologies are used. Here we use the term EOF for the eigenvectors $F_i(x)$ and EOF coefficients $a_i(t)$ such that $\text{SST}(x,t) = \text{SUM}[F_i(x)a_i(t)]$. To aid the visualization of the relative magnitude of the first three EOFs, that account for 98.9% of the temporal variance, the eigenvectors and corresponding coefficients were respectively scaled by factors k and $1/k$, so that all EOF coefficients $a_i(t)$ fall within similar ranges. The results presented below refer to the so-called “temporal EOFs” in the sense that diagonalization of the covariance matrix was obtained by removing the temporal mean. To reduce the computer memory requirements, the daily SST fields at ~5 km resolution were averaged to 5-day and 1/14° (~7 km) resolution prior to the EOF decomposition. To complement the EOF analysis, SST anomalies over the inner-shelf (depths up to 50 m) between 39.5° N and 43° N were computed by subtracting the daily maps from its 10 year mean.

The freshwater continental runoff was estimated based on the sum of daily discharges from dams of rivers Lima, Cávado and Douro made available by Serviço Nacional de Recursos Hídricos (SNIRH, Agência Portuguesa do Ambiente).

2.3. Time series analysis (2004–2013)

To study the conditions prior to *Dinophysis* bloom initiation, we define a bloom event as the time corresponding to *Dinophysis* cells concentration larger than 200 cells L^{-1} . This threshold, currently in use as the early warning level by the HAB monitoring program in Portugal, was chosen because above this limit the concentration of *Dinophysis* cells generally increases and lead to shellfish toxicity levels above regulatory limits. We also used the term epicenter for the area of the coast where blooms are first detected each year. In addition, a second threshold of 10³ cells L^{-1} was used to analyze the conditions related to the development of events with a high concentration of cells. The different subsets were generated and analyzed using the R statistical computing environment (R Development Core Team, 2011). Summary statistics of the *Dinophysis* occurrence dates, SST, UI and PAR were calculated for each area and for different species concentrations.

2.4. Lagrangian offline model

In order to simulate *Dinophysis* pathways, an Individual Based Model (IBM), similar to that used in the Nolasco et al. (2013a), was coupled to a ROMS configuration (Nolasco et al., 2013b) using ROFF (Carr et al., 2007). ROFF is a drifter-tracking code which simulates particle trajectories from stored ROMS velocity and hydrological fields.

The drifter-tracking code simulates *Dinophysis* trajectories from stored ROMS velocity and hydrological fields using a high order predictor-corrector scheme to integrate the motion equation $dX/dt = UROMS(X,t)$, with X being the position vector (x,y,z) , and $UROMS$ being the modeled 3D velocity vector over time, given an initial condition $X(t_0) = X_0$. This algorithm is run with a timestep, dt , of 300 s, which is also the timestep used to generate the ROMS fields, provided to ROFF as daily averages. In addition to the advection generated by the model velocities, the particle movements included random velocities in the vertical direction, which were used to parameterize unresolved turbulent processes.

3. Results

3.1. Mesoscale and interannual variability of the oceanographic conditions

The studied period was characterized by a high interannual variability of meteorological and oceanographic conditions. 2013 presented the weakest upwelling season of the studied decade, with upwelling almost absent from April to September (Fig. 2A, thick line, arrow 1). In contrast, 2007 showed an almost uninterrupted sequence of very strong upwelling events (Fig. 2A, gray line, arrow 3), from March until the end of August, with only a two week relaxation period in June (Fig. 2A, thick line, arrow 3). In 2004, the upwelling was also weak from mid May until the end of August, only with a two week event of strong northerlies in early July. The year 2006 was characterized by very low upwelling in April and May, followed by weak upwelling episodes until the end of August (Fig. 2A, thick line, arrow 2). The remaining years presented moderate upwelling during spring and summer. Autumn 2008 deserves particular attention since, contrarily to the

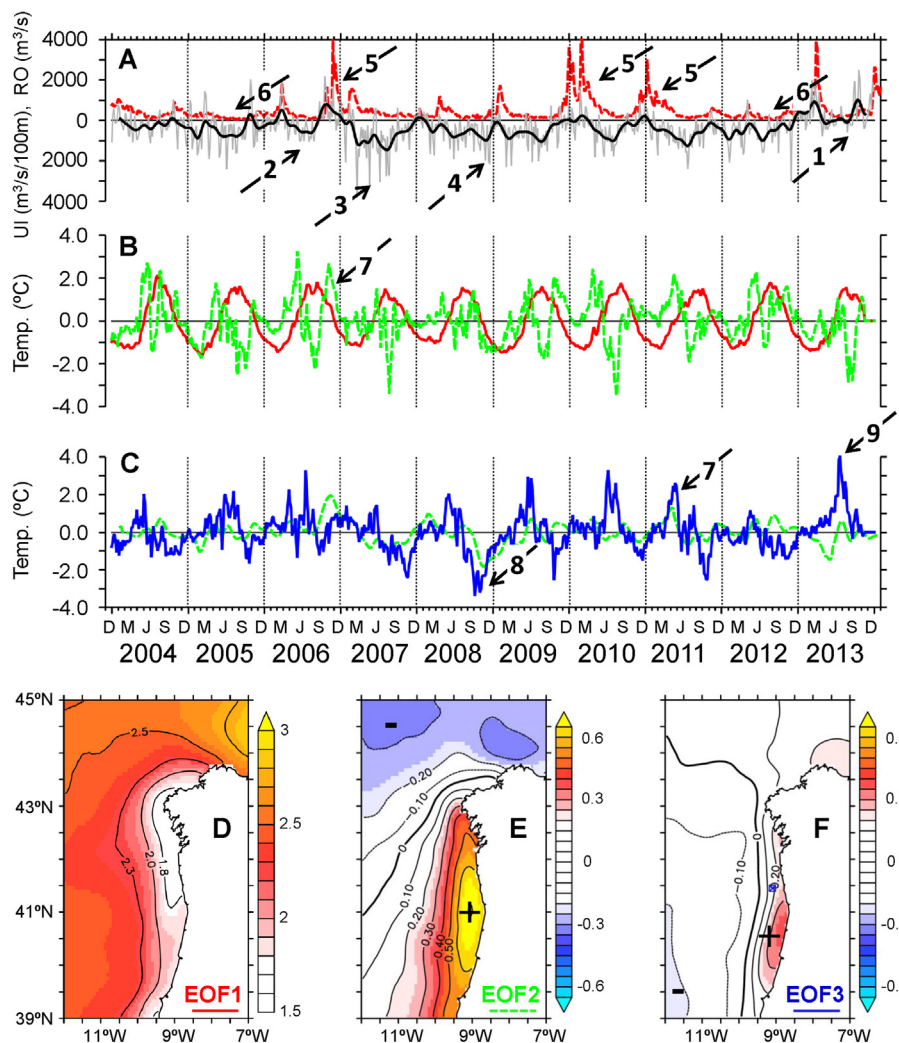


Fig. 2. (A) Daily upwelling index – UI – time series (gray line), 5-day running mean (thick line) and daily regional river runoff – RO (dashed line); (B and C) temporal EOF coefficients and (D–F) eigenvectors of the first three EOFs, explaining 98.9% of the SST variance. The temporal coefficients are represented according to the corresponding eigenvector: (B) solid line (EOF1), dashed line (EOF2); (C) solid line (EOF3). The dashed line in (C) represents the SST anomaly at the inner-shelf. Numbers in arrows indicate special events discussed in the text: 1 – no upwelling and positive SST anomaly off AV (EOF3); 2 – mild upwelling; 3 – strong spring and summer upwelling; 4 – strong autumn upwelling; 5 – high river runoff; 6 – dry year; 7 – strong positive SST anomaly (EOF2 area); 8 – strong negative SST anomaly (EOF3 areas); 9 – the highest positive SST anomaly (AV area).

downwelling episodes normally observed in this season, the period was characterized by very strong upwelling, from September to December (Fig. 2A, thick line, arrow 4).

Runoff data show that the 2009–2010 winter was particularly rainy (Fig. 2A, dashed line, arrow 5), with March 2010 being the wettest of the series. Autumn 2006, winter 2011 (January to March) and January to April 2013 also presented high river discharges. The driest years were 2005 and 2012 (Fig. 2A, dashed line, arrow 6).

The results of the EOF analyses, extracting the main SST variability patterns, are presented in Fig. 2B–F. The first mode, which accounts for 96.9% of the variance, is related to the seasonal cycle of the cross[along]-shore SST gradient off west[north] Iberia. The EOF1 temporal coefficient (Fig. 2B, solid line) has a clear annual periodicity and EOF1 has an alongshore distribution over W Iberia, contrasting with the northern coast (Fig. 2D). The lower values of this mode over the western shelf show that the amplitude of the seasonal cycle is lower along the coast, resulting from the cold coastal upwelling waters that occupy the shelf during summer. The minimum values are found in the northernmost tip of the region around cape Finisterre, defining the area of coldest summer temperatures. EOF2, accounting for 1.63% of the variance, shows maximum positive values over the shelf centered at 41° N, south of the Galician Rías (Fig. 2E). EOF3, which represents 0.35% of the variance, follows a similar pattern off W Iberia but with localized coastal maxima off Ria de Aveiro and the Galician Rías (Fig. 2F). Both EOFs present considerable interannual variability (Fig. 2B dashed line and Fig. 2C, solid line). The areas with higher EOF values are thus interpreted as the locations with stronger interannual

fluctuations of the coastal processes driving the sea surface temperature, namely the summer coastal divergence/convergence. The simultaneous analyses of EOF2 and EOF3 coefficients allows, for each date, to highlight the periods and events that presented mesoscale differences or similarities between the two sampling regions.

Some years present periods characterized by opposite signals of EOF2 and EOF3 coefficients, being EOF3 positive, meaning that the region off Aveiro was locally warmer than surrounding shelf waters in general, and consequently warmer than the Galician Rías further north. Examples of these events, focusing in the period from the end of spring until the end of summer, were: mid June–mid September 2005, May–mid August 2008, mid June–August 2010 and mid July–mid September 2013 (Fig. 2A, e.g. arrow 1). The opposite was observed during several autumn periods such as in 2008, when waters off Aveiro were much cooler (Fig. 2C, arrow 8) than October–November 2012, due to the abnormally intense autumn upwelling.

The comparison between EOF coefficients and the SST anomalies over the inner-shelf between 39.5° N and 43° N (Fig. 2C, dashed line) highlights the regional scope of the various events. The highest positive inner-shelf anomalies were recorded in autumn 2006, corresponding mostly to the EOF2 pattern which also presents high coefficient values. Conversely, the lowest values (negative) inner-shelf anomalies in autumn 2008 correspond to both EOF2 and EOF3, with a stronger contribution from the later revealing that the very intense upwelling has further affected the areas off Aveiro. On the other hand, the same comparison shows that EOF decomposition can uncover localized features that might not be captured by the analysis of broader inner-shelf SST

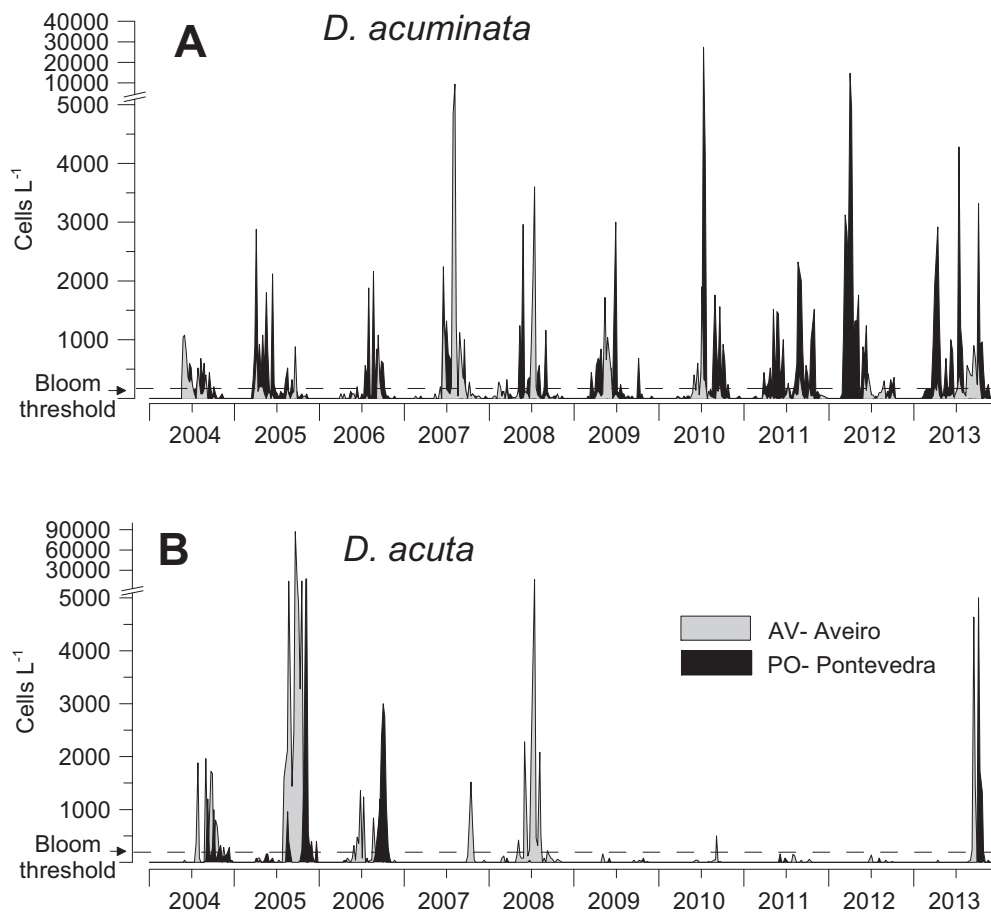


Fig. 3. Interannual variability of (A) *Dinophysis acuminata* and (B) *Dinophysis acuta* cell concentration at Aveiro (AV) and Pontevedra (PO) stations, from 18 May 2004 to 31 December 2013.

anomalies. This is the case of the highest EOF3 summer 2013 values, showing that the effect of the very weak upwelling season mostly affected the coastal areas between 40° N and 41° N.

3.2. Interannual variability of *Dinophysis* species

During the decade, *Dinophysis acuminata* blooms were more frequent although less intense than those of *Dinophysis acuta* in both stations (Fig. 3 and Annex 1). At AV *D. acuminata* blooms reached higher intensities and durations in 2007 and 2008 than in PO (e.g. 9.4×10^3 cells L⁻¹ in AV, 3×10^3 cells L⁻¹ in PO), decreasing in intensity during the following years. In PO, *D. acuminata* blooms were particularly intense from 2010 to 2012, reaching 27×10^3 cells L⁻¹ in July 2010. During 2004, *D. acuminata* outbreaks appear to be the weakest of the decade (up to 10^3 cells L⁻¹), but there is a lack of data before May.

At AV station, *Dinophysis acuta* bloomed annually from 2004 to 2008, 2005 being characterized by exceptional blooms that reached 87×10^3 cells L⁻¹ in September, when a historical maximum of the species in Portugal (14×10^4 cells L⁻¹) was observed at a site located 10 km to the south. A maximum (17.6×10^3 cells L⁻¹) for the decade was also observed in PO but detected later in November. *D. acuta* did not exceed the bloom threshold level in 2009 and from 2011 to 2012, while in PO the species did not bloom from 2007 until 2012 (Fig. 3, Annex 1). In 2010, only a short and weak peak (0.5×10^3 cells L⁻¹) was observed at AV, in September. In general, the blooms were more intense (slightly lower in 2013) and lengthy in AV than in PO, confirming AV as the epicenter of *D. acuta* blooms. Even in 2006, when a peak of 3×10^3 cells L⁻¹ was registered in PO, a cruise covering the Portuguese shelf between F. Foz and Aveiro registered 9×10^3 cells L⁻¹ of *D. acuta* at midshelf (Silva et al., in prep, data not shown). In 2007 and 2008 *D. acuta* blooms were only observed at AV. In 2007 they last during two weeks in October, while in 2008 the blooms initiated in May and persisted until mid August. After a decline in bloom events from 2009 to 2012, in 2013 *D. acuta* reached 4.6×10^3 cells L⁻¹ during a short two weeks episode in mid September. In PO the blooms suddenly occurred two weeks later, with a concentration of 5×10^3 cells L⁻¹ and lasted for one month.

3.2.1. Interannual distribution of *Dinophysis* and *Mesodinium*

All counts of *Mesodinium* cells used in the present work were identified as *Mesodinium cf. rubrum* regardless their size. However, considering the several *Mesodinium* species presented recently by Garcia-Cuetos et al. (2012), it is possible that our counts included at least two of them, a smaller form that must be *M. rubrum* and a

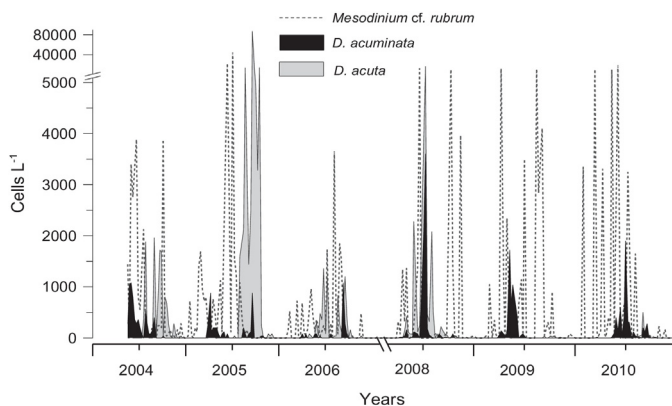


Fig. 4. Interannual distribution of *D. acuta* and *D. acuminata* cell concentration and of their potential prey, the ciliate *Mesodinium cf. rubrum*, at the AV station, for the indicated years.

larger form that probably is the new species *Mesodinium major*, both species are marine, pelagic and phototrophic, with a reddish-brown color.

The available *Mesodinium* data at AV (Fig. 4) show that the ciliate was present from spring to autumn during the periods 2004–2006 and 2008–2010. *Mesodinium* peaks often coincided with *Dinophysis acuminata* maxima and both species were very persistent, although *Mesodinium* normally remained after *D. acuminata* disappearance. The only exception was observed in 2005, coinciding with *Dinophysis acuta* highest peak. Concerning *D. acuta*, the maximum concentrations were not coincident but appeared related to the peaks of *Mesodinium*. The initiation of the intense blooms of *D. acuta* on the 1st August 2005, occurred three weeks after the highest maximum of *Mesodinium* registered in the present time-series (44×10^3 cells L⁻¹ on 4th July). A two week delay was also observed in 2008, when the initiation of *D. acuta* outbreaks occurred on 7 May (Annex 1), after a first moderate concentration peak of *Mesodinium* (1.3×10^3 cells L⁻¹) on 21 April. A subsequent *D. acuta* maximum, reaching 16×10^3 cells L⁻¹ on 14 July, was observed three weeks after the maximum of *Mesodinium* (12×10^3 cells L⁻¹) observed on 23 June. In 2004, despite the lack of data before May, the initiation of the first *D. acuta* bloom on 27 July also occurred two weeks after a maximum of *Mesodinium* that reached 8.2×10^3 cells L⁻¹ on 12 July.

3.2.2. Time of species first detection, bloom initiation and maintenance

The time of species detection and bloom initiation in both stations, as well as the periods of bloom occurrence (>200 cells L⁻¹ and $>10^3$ cells L⁻¹) for the decade, is summarized in Fig. 5. The date of the first detections within the years, for each species and sampling station, is presented in Annex 1. *Dinophysis acuminata* was normally detected earlier than *Dinophysis acuta*, between January and May, in some years first in AV, others in PO, but in both stations most detections occurred in a narrow window between the last week of February and the last week of March. In turn, the onset of *D. acuta* is marked by a large interannual variability. The first cells in the year can be detected from the end of February and

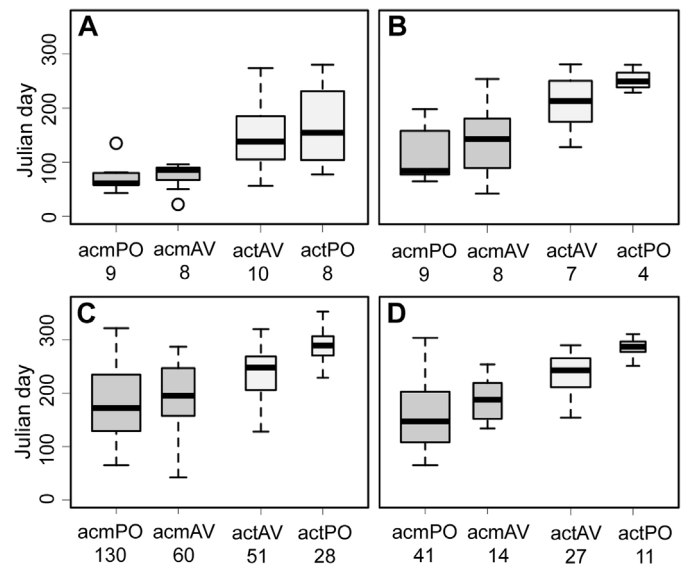


Fig. 5. Julian day boxplots of *D. acuminata* and *D. acuta* events at PO and AV during the 2004–2013 decade: (A) the first detection of the year, (B) first bloom of the year, (C) all blooms (>200 cells L⁻¹) and (D) all high concentrated blooms ($>10^3$ cells L⁻¹). The labels along the X axis indicate the species, “act” refers to *D. acuta* and “acm” to *D. acuminata*, observed in stations AV and PO. The numbers below the labels indicate the number of samples in each data subset.

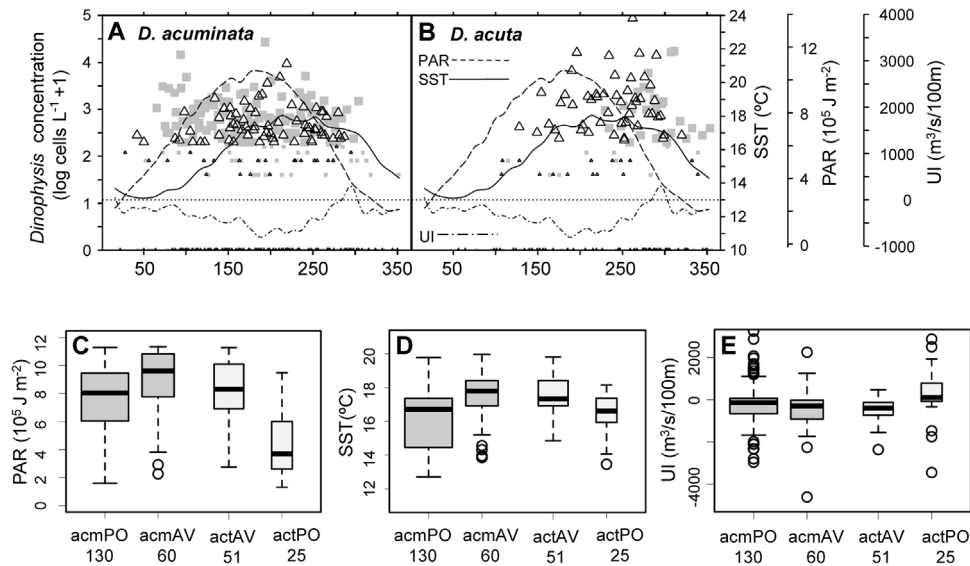


Fig. 6. Cell concentrations of (A) *D. acuminata* and (B) *D. acuta* at Aveiro-AV (Δ) and Pontevedra-PO (\square) superimposed on low-pass 10-year (2004–2013) daily mean SST ($^{\circ}\text{C}$, solid line)/PAR (Jm^{-2} , dashed line) and UI ($\text{m}^3/\text{s}/100\text{m}$, dash-dotted line) annual cycle (right axis). Large symbols indicate cell concentrations above 200 cells L^{-1} . Negative UI values represent upwelling (horizontal dotted line indicates $\text{UI} = 0$). Boxplots showing the median, percentile 25% and 75% and outliers of the bloom conditions ($>200\text{ cells L}^{-1}$) for each of the species: (C) PAR, (D) SST and (E) UI. The labels along the X axis indicate the species, “act” refers to *D. acuta* and “acm” to *D. acuminata* observed in stations AV and PO. The numbers below the labels indicate the number of samples in each data subset.

mid March, at AV and PO respectively, until the beginning of October in both stations (Annex 1, Fig. 5A). In 2007 and 2010 no cells of *D. acuta* were observed in PO. With the exception of 2011, *D. acuta* was normally observed earlier in AV than in PO and twice, in 2005 and 2006, the species was detected almost simultaneously on both stations.

Fig. 5B–D highlights the sequence of bloom events throughout the year. Excluding 2008, the 1st events each year (Fig. 5B) began with *Dinophysis acuminata* in PO (1st week of March) and afterwards in AV, followed by *Dinophysis acuta* blooms in AV (1st week of May) and afterwards in PO. Regarding *D. acuminata* (Fig. 5C), the inter-quartile (25–75%ile) of all events in PO occurred from the 1st week of May until the 3rd week of August ($123 < \text{Jday} < 235$, median: 173, where Jday means Julian day). In AV, the events were in general observed two weeks to one month later and lasted from mid June until mid September ($168 < \text{Jday} < 254$, median: 202). In PO, 50% of the high concentrated blooms of *D. acuminata* were observed earlier than the 25%ile, from the 3rd week of April until the end of July ($108 < \text{Jday} < 203$, median: 147). In AV, the period is reduced, in 50% of the events, about one month ($173 < \text{Jday} < 222$, median: 193).

In AV, the inter-quartile of *Dinophysis acuta* events ($>200\text{ cells L}^{-1}$) shows they occurred from the 3rd week of July until the end of September ($206 < \text{Jday} < 269$, median: 206). Highly concentrated blooms occurred during the same period with a slight reduction in length ($211 < \text{Jday} < 266$) with the median in the first week of September (Jday: 245). In PO, most events lasted from late September until the 1st week of November ($271 < \text{Jday} < 307$, median: 290) and the period of blooms with an elevated number of cells was shorter ($278 < \text{Jday} < 297$, median: 287).

3.3. *Dinophysis* distribution and physical conditions

In Fig. 6A and B all the occurrences in AV and PO of each species together with the averaged variations of SST, PAR and UI are represented. *Dinophysis acuminata* blooms, occurring earlier in the

year than *Dinophysis acuta*, appear to be more related to the annual cycle of PAR than the blooms of *D. acuta* which are more associated with the average annual SST cycle. Fig. 6C shows that most (25–75%ile) *D. acuminata* blooms occur in the PAR range of $6.0\text{--}9.4 \times 10^5\text{ Jm}^{-2}$ in PO and $7.8\text{--}10.8 \times 10^5\text{ Jm}^{-2}$ in AV, although the different medians observed for AV and PO indicate that PAR is closely related to the time of the year the blooms occur in each of the sites. In turn, *D. acuta* blooms occur within distinct PAR ranges at AV ($9.6 \times 10^5\text{ Jm}^{-2}$) and PO ($8.0 \times 10^5\text{ Jm}^{-2}$) and are therefore not related to PAR.

In relation to temperature (Fig. 6D) *Dinophysis acuta* events in AV, and the first high intensity events in PO (Fig. 7C) were found around the same SST median (17°C), although subsequent blooms in PO occur under lower temperatures (Fig. 6D, median around 16°C) because they occur later in autumn. Most *Dinophysis*

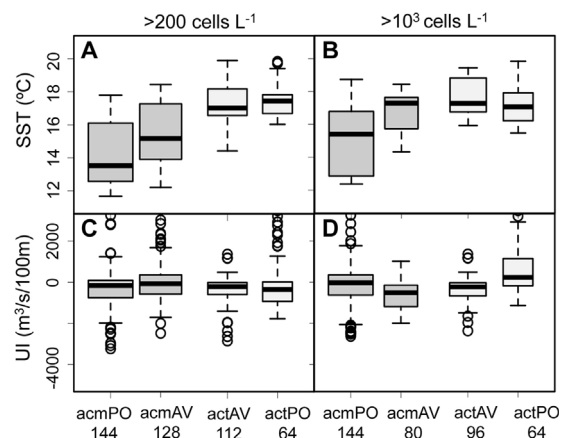


Fig. 7. *D. acuminata* (acm) and *D. acuta* (act) conditions boxplots at AV and PO stations showing 25 and 75%ile, median and outliers of: (A and B) SST ($^{\circ}\text{C}$) and (C and D) UI ($\text{m}^3/\text{s}/100\text{m}$), on the 15 days preceding blooms. Left column refers to conditions before the 1st bloom ($>200\text{ cells L}^{-1}$) in the year and the right column to conditions before the first event with a high concentration of cells ($>10^3\text{ cells L}^{-1}$). The numbers below the labels indicate the number of samples in each data subset.

Table 1

Selected initial (ini) and final (fin) conditions for the prediction exercise of the first *D. acuminata* and *D. acuta* bloom of the year in AV and PO. Conditions: JDay (julian day), SST (°C) and upwelling index – UI (m³/s/100 m).

Sp/site	JDay_ini	JDay_fin	SST_ini	SST_fin	UI_ini	UI_fin
<i>D. acum</i> /PO	69	198	12.6	16.1	–753	87
<i>D. acum</i> /AV	82	254	13.9	17.3	–575	336
<i>D. acut</i> /AV	146	281	16.6	18.1	–601	–16
<i>D. acut</i> /PO	232	280	16.7	17.8	–929	–6

acuminata blooms in PO occur in a different temperature range than in AV. The number of *D. acuminata* blooms with elevated concentrations seem to decrease during the maximum intensity of upwelling (i.e. Fig. 6A, around Jday 190–230), while blooms of *D. acuta* typically occur at the end of the upwelling season when the frequency and intensity of the convergence episodes increase. Fig. 6E highlights that most blooms of *D. acuminata* in both stations and *D. acuta* in AV develop under mild upwelling conditions although in PO they are favored by downwelling conditions.

3.3.1. Conditions for first bloom initiation and intensification

The first annual blooms of *Dinophysis acuminata* initiate within a wide SST range (13°–17°), mostly below 13 °C at PO and 15 °C at AV (see median in Fig. 7A). However an increase of 2 °C is apparently needed before the development of events with a high concentration of cells, which indicates the temperature conditions favoring the species growth or an accumulation of nearshore cells due to coastal convergence conditions. On the contrary, both the initiation of blooms or the development of elevated concentration of *Dinophysis acuta* cells occur between 16 °C and 18 °C with the median of all events in AV or PO around 17 °C.

Regarding the upwelling conditions (Fig. 7B and D), each year outbreaks of both species initiated after mild upwelling conditions, although the first intense events of *Dinophysis acuminata* in AV require stronger upwelling winds while those events of *Dinophysis acuta* in PO occurred after downwelling conditions (Fig. 7D), as mentioned above.

3.3.2. Oceanographic conditions for the 1st bloom of the year

The results presented in the previous sections show that the first blooms (>200 cells L⁻¹) of the year occur under a relatively wide range of oceanographic and meteorological conditions. In addition, the disappearance of *Dinophysis acuta* blooms for several years suggest that abnormal conditions lead to major changes in the geographical location of the population cores. To further explore the sources of interannual bloom initiation variability, an elementary exercise to predict the 1st bloom event, for each species/station, was carried out using the above results. It also allows identification of possible routes to establish capacities for forecasting *Dinophysis* events off NW Iberia. The prediction exercise was performed by identifying the simultaneous occurrence of the following conditions, whose data are presented in Table 1:

- Jday between 25%ile and maximum;
- SST and UI between 25 and 75%ile;
- existence of *Dinophysis* cells in water samples during the two previous weeks.

Table 2 shows that in a total of 37 cases, the simple use of the overlapping conditions predicted in 16 cases (43%) the appearance/lack of blooms in the week before or the same week of their actual detection/absence (i.e. $-14 < n^{\circ} \text{ days} < 5$ and prediction of no blooms), a time lag considered effective for early warning of an eventual shellfish ban. The analysis also predicted 3 false positives of *Dinophysis acuta* in AV.

One half of the *Dinophysis acuminata* blooms in PO could also be anticipated with a delay of one to two weeks. The results of the exercise also showed that *D. acuminata* outbreaks are the less predictable using a simple parameter range intersection, especially in AV and in particular years such as 2006, 2010 (both at AV and PO) and in 2011. These results underpin the hypothesis that advective effects, not taken into account in this exercise, are at least equally important as the local conditions to predict *Dinophysis* outbreaks.

Table 2

Prediction of *Dinophysis* events at PO and AV, with indication of the n° of days before (-) or after (+) the observed date of bloom initiation. Bloom or prediction dates are respectively preceded by “B:” or “P:”. The code “no pred” marks that the exercise successfully predicts the absence of blooms, and “pred no” marks that the exercise predicted the absence of blooms that in reality occurred at the indicated dates.

Sp/site	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
<i>D. acum</i> /PO	no data	10	-55	B:18Jun pred no	-8	-5	-69	2	4	11
<i>D. acum</i> /AV	no data	2	-157	-26	46	-15	-66	-103	no data	13
<i>D. acut</i> /AV	-46	27	-2	-5	26	no bloom P:19Sep	-90	no bloom P:03Aug	no bloom P:7Jul	-3
<i>D. acut</i> /PO	-4	10	-5	no bloom no pred	no bloom no pred	no bloom no pred	no bloom no pred	no bloom no pred	no bloom no pred	B:7Oct pred no

successful prediction
 2 weeks before or the next week
 too early or late prediction
 bloom not predicted

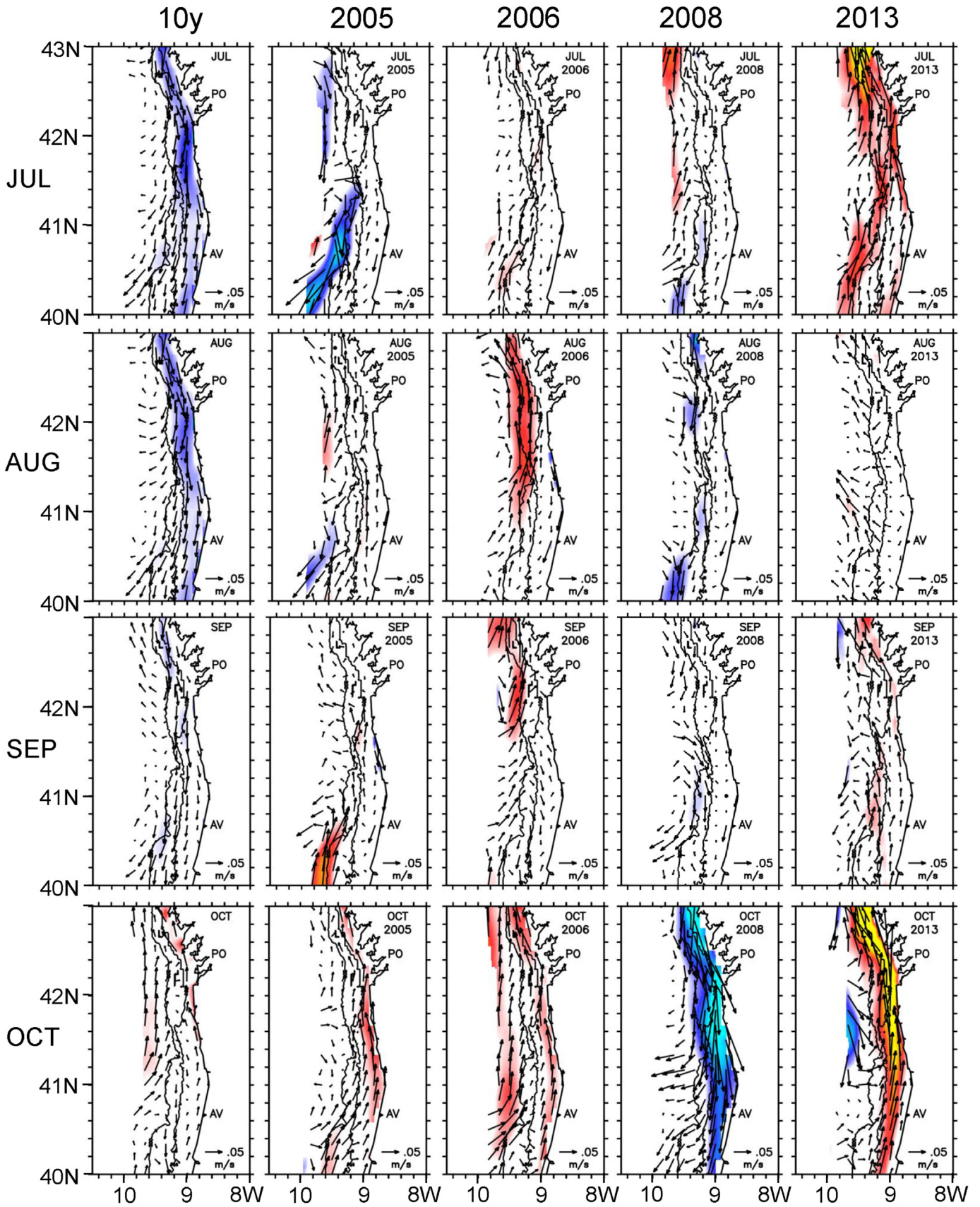


Fig. 8. Ten-year monthly mean surface currents (0–30 m) off NW Iberia (left column, July-top to October-bottom) and monthly surface current anomalies for selected years relative to the 10-year mean. Shaded areas correspond to absolute NS currents/anomalies higher than 0.05 m s^{-1} . Poleward and equatorward NS currents/anomalies are indicated by vector directions.

3.4. Modeling simulations for species transport between the two sampling sites

To explore the role of the oceanic circulation on bloom dynamics and the species advection between the two monitoring sites, two approaches were developed based on different time scales. Firstly, monthly anomalies of surface (0–30 m) currents relative to the 10-year mean were computed to investigate if the circulation structures were favorable to the alongshore or cross-shore transport and to highlight the role of particular features, such as counterflows, inshore currents or upwelling filaments. Secondly, event-scale numerical experiments were carried out using a

Lagrangian transport model to test if the time lag between the bloom detection at the two monitoring sites can be explained by advective processes.

The monthly anomalies for selected years (2005, 2006, 2008, 2013) and months (July–October) are presented in Fig. 8, together with the 10-year mean of monthly currents, to draw attention to years/months when the greatest *Dinophysis acuta* blooms occurred and when the circulation features appeared to exert a significant impact on those blooms. The decadal monthly means (Fig. 8, left) clearly illustrate that circulation in the upper 30 m is more intense over the shelf in July and August, with a strong equatorward jet over the narrower shelf north of 41.2° N, becoming less intense and

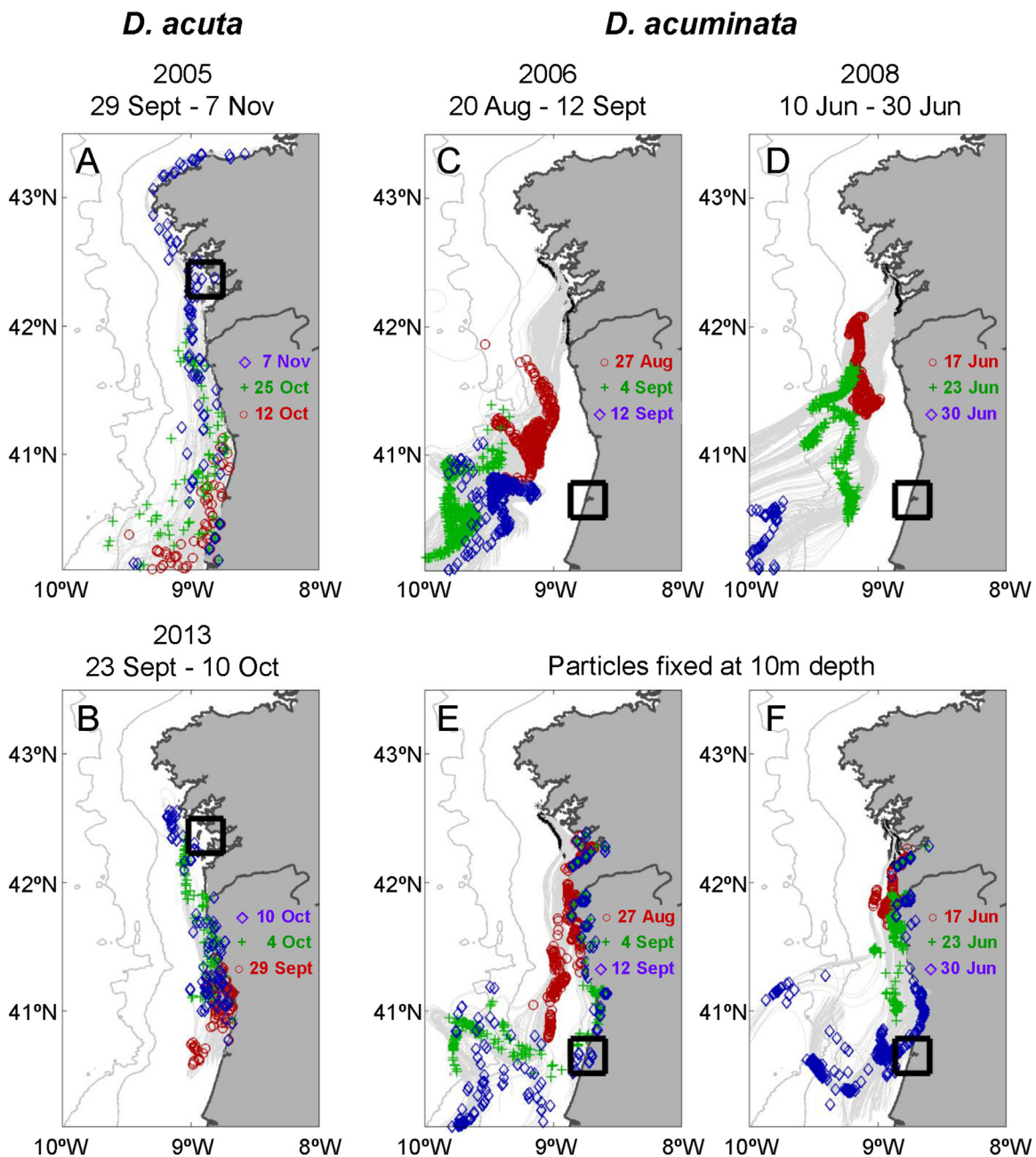


Fig. 9. Lagrangian model results for 4 bloom events showing (A and B) two poleward (deployment at AV) and (C–F) two equatorward (deployment at PO) particle transport experiments with different vertical advection constraints: (A–D) the vertical movement is unconstrained and the particles are advected according to the 3D circulation field; (E and F) the vertical movement is constrained so that the particles are maintained within the initial (7.5–12.5 m) depth range. Squares at PO (A and B) and AV (C–F) indicate target area.

more spatially variable in September and October when a mean poleward current establishes over the slope and the inner-shelf. It is also worth noting the flow branching at the Aveiro canyon (40.6° N) where the shelf widens, creating a relatively small area south of the canyon (40.4–40.6° N) where the currents are high over the slope and the inner shelf, with a relative minimum at mid-shelf.

The monthly anomalies show the strong interannual variability of the surface currents. This is particularly noticeable in October when the generally weak inner-shelf poleward current was much more intense and covered the whole shelf in 2013, being also strong in 2006 but restricted to depths shallower than 100 m. This pattern is totally reversed in 2008 when the out-of-season strong upwelling winds drove intense equatorward currents over the entire shelf. The results also show the frequent occurrence of opposite current anomalies in the outer-shelf south of the Porto Canyon at 41.6° N, specially in July–August 2005, September 2006 and July 2008.

Lagrangian particle model experiments are presented in Fig. 9. The events were selected based on the observation of a clear time lag between the bloom occurrence at AV and PO monitoring sites. Two events correspond to the poleward advection of *Dinophysis acuta* blooms as inferred from the observation of high cell concentrations, first at AV and ~3 weeks later at PO (2005, 2013), and two cases correspond to the equatorward advection of *Dinophysis acuminata* blooms that were first recorded at PO and ~3 weeks later at AV (2006, 2008). Several experiments were carried out using different initial particle locations and vertical positions. In general, a higher sensitivity of model solutions was observed with respect to the vertical particle distribution during southward/active upwelling (northerly wind) periods. To illustrate this effect, two solutions for the 2006 and 2008 *D. acuminata*

bloom advection patterns are shown in Fig. 9. In the first case the particles are deployed at depths between 7.5 m and 12.5 m and are advected according the 3D circulation field (Fig. 9C and E). In the second case the particles were deployed at the same initial locations and depths but their vertical movement is constrained so that they are maintained within the same (7.5–12.5 m) depth range (Fig. 9D and F).

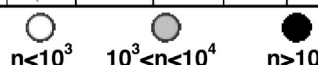
As expected in a region where the circulation is mainly driven by coastal upwelling, the trajectory patterns are very distinct during contrasting wind forcing phases. In the two downwelling/poleward events, the *Dinophysis acuta* cells are transported mainly over the inner-shelf and the particles tend to have similar trajectories and converge to shallower depths (Fig. 9A and B). On the contrary, during the active upwelling phase the trajectories are more disparate and divergent while the particles are advected equatorward and offshore (Fig. 9C and D). The results with no vertical distribution constraint show that it is very unlikely that *Dinophysis acuminata* blooms at AV might result from inocula advected from PO. However, when the vertical particle movement is constrained so that they are maintained within a 5 m layer centered at 10 m, some particles follow trajectories close to the coast and arrive at AV with a travel time that is compatible with the observed time lag between the bloom detection at PO and AV (Fig. 9E and F).

3.5. Interannual change of *Dinophysis acuta* epicenter and maxima at the NW coast of Portugal

As described above, *Dinophysis acuta* blooms were not observed in PO from 2007 to 2012, and almost disappeared in AV from 2009 to 2012, where only a single peak of one week was observed in 2010. Despite a possible lack of the necessary conditions for

Table 3
Annual location of *D. acuta* blooms epicenter (Epic) and maximum (Max) at NW Portugal.

Latitude (°N)	41°50' - 41°20'		41°20' - 40°50'		40°50' - 40°20'		40°20' - 39°40'		39°40' - 39°		39° - 39°40'		
	Coast designation		Viana C.		Porto		Aveiro		F.Foz		Peniche		Lisboa
	Epic	Max	Epic	Max	Epic	Max	Epic	Max	Epic	Max	Epic	Max	
2003						●							
2004					☼	●							
2005					☼	●							
2006							☼	●					
2007					☼	●							
2008					☼	●							
2009											☼	●	
2010			☼	○									
2011									☼	○			
2012											☼	●	
2013											☼	●	
2014					☼	●							

Maxima (cells L⁻¹):


 ○ $n < 10^3$ ● $10^3 < n < 10^4$ ● $n > 10^4$

growth in AV, we hypothesized that the species could have changed its center of distribution to a location further south in the Portuguese coast. In Table 3 it is confirmed that, with the exception of 2010 when only a short event on the 1st week of September occurred in AV area, *D. acuta* bloom initiation and maxima moved southwards until 2013, with substantial blooms reaching 6×10^3 cells L^{-1} in Lisbon Bay in August 2012. In 2014, *D. acuta* bloom initiation and maxima occurred again in AV.

4. Discussion and conclusions

4.1. *Dinophysis* distribution in the water column and relationship with *Mesodinium*

Although *Dinophysis* populations off Iberia and elsewhere are related to stratification conditions (GEOHAB, 2008), stratification itself depends on different factors. Also, each of the species shows preferences on their position in the stratified water column that have consequences on their transport cross-shelf and alongshore as discussed below in Section 4.4.

On the NW Iberian shelf *Dinophysis acuminata* and *Dinophysis acuta* are distributed on the wind driven layer and reflect the oscillations of its base (Moita and Silva, 2001). However, *D. acuminata* appears to depend more on light availability since the maxima are generally observed closer to the surface than those of *D. acuta* normally found in the top of the pycnocline (Reguera et al., 1993; Palma et al., 1998; Velo-Suárez et al., 2009). Both species were found to concentrate in thin layers, *D. acuminata* in surface warm water patches at 0–4 m depth in Ría de Pontevedra (Velo-Suárez et al., 2008) and *D. acuta* at 18–20 m in the coast off F.Foz (Moita et al., 2006). There is also evidence that in Ría de Vigo *D. acuminata* undertake diel migrations between the surface and 10 m depth (Villariño et al., 1995), actively exploiting high levels of irradiance during the day and having access to higher nutrients concentration during the night. Curiously *Mesodinium rubrum*, not known at the time to be prey for *Dinophysis*, was part of the same assemblage and characterized by a similar vertical migration behavior.

Velo-Suárez et al. (2014) highlighted, for the first time in Iberian waters, the relationship between *Dinophysis acuminata* bloom initiation and maintenance with the presence of *Mesodinium rubrum* in Ría de Pontevedra, although they also reported that there is no single mechanism that accounts for all the stages of a bloom. Our results show that, in Aveiro waters, *D. acuminata* and *Mesodinium* almost always co-occurred during six years of study but the initiation of *D. acuminata* blooms are not immediately related to the prey occurrence since the ciliate generally occurs much earlier every year (e.g. 2010, Fig. 4). However, that dependency may occur further north in PO, as observed in 2007 by Velo-Suárez et al. (2014), when the blooms initiate earlier than in AV and before their possible advection southwards. Regarding *Dinophysis acuta*, the higher peaks occurred 2–3 weeks after those of *Mesodinium* adding further evidence of a relationship between the species at AV, but also that their growth is favored by similar environmental conditions. Nevertheless, the lack of *D. acuta* blooms in 2009 and 2010 did not correspond to the absence of the ciliate.

Previous field studies on the time-lagged correlations between *Mesodinium* and *Dinophysis* show quite variable results, 7 days in the case of *Mesodinium rubrum* and *Dinophysis acuminata* in Korean waters (Yih et al., 2013). Lags from 0 to 60 days between *Mesodinium* and *Dinophysis ovum* and evidence that in some years no predator-prey relationship existed between the two organisms were also reported in the Gulf of Mexico, under conditions similar to temperate waters and cultures (Harred and Campbell, 2014). Future studies off Iberia should include the separation of the

different *Mesodinium* species in monitoring counts as well as a more detailed study of prey-predator relationships, including the delay in bloom initiation at different latitudes.

4.2. Interannual variability of *Dinophysis* blooms and development of anomalous conditions

As observed in previous decades off Iberia (Reguera et al., 1995; Palma et al., 1998; Pazos et al., 1995), in this study (2004–2013) *Dinophysis* species exhibited a great interannual variability, characterized by years dominated by one of the species, or years when both species occurred simultaneously. The present study showed how meteorological anomalies are important in determining each year's dynamics of Iberian *Dinophysis* events.

Contrasting climatological conditions were highlighted by Escalera et al. (2006) for the selection of *Dinophysis acuta* and *Dinophysis acuminata* in Ría de Vigo in previous years, namely thermohaline stratification combined with persistent upwelling conditions favored *D. acuminata* in 2002, while a very hot summer with the lowest UI of the past 50 years favored *D. acuta* in late summer 2003. The present work shows that these findings become more complex when we join several years. In 2005, for example, when *D. acuta* showed an historical maximum in 30 years of monitoring at the Aveiro coast, despite this being a very dry year (Fig. 2A, dashed line) with high air temperature anomalies over the mainland (see <http://www.ipma.pt/pt/oclima/monitorizacao/index.jsp?selTipo=m&selVar=tx&selAna=an&selAno=2005>), SST only showed small positive anomalies on that coast during summer, as highlighted by EOF3 (Fig. 2C). In fact, there was a persistency of upwelling favorable winds, higher than in other years with lower blooms, for example 2004 and 2006 (Fig. 2A, thick line). The *D. acuta* bloom season of 2005 in NW Iberia was discussed by Escalera et al. (2010) who suggested that the sudden occurrence of outbreaks in Ría de Vigo was due to an alongshore transport of southern populations. Fig. 8 also shows that, in that year, the outer-shelf off AV was occupied by a poleward flow bounded by two southward upwelled water branches: one occupying the inner-shelf and another over the slope. The recirculation between the coastal flow and the mid-shelf may have acted as a pool for *D. acuta* growth during August and September in Aveiro. It is likely that *D. acuta* blooms were concentrated and distributed in the pycnocline in that pool as observed in 2003 (Moita et al., 2006), and were introduced inshorewards in AV station by the upwelled waters.

The atypical predominance of upwelling winds during winter and positive SST anomalies were suggested by Díaz et al. (2013) to favor the early detection of cells and initiation of *Dinophysis acuminata* blooms in PO, in 2002 and 2012. Our results confirm these findings but indicate that very high river discharges before the winter upwelling events, as observed in 2010 and 2011, remove the species from the coastal area and delay the initiation of blooms, despite their early detection. This proposed impact of anomalous runoff does not contradict several works that showed the importance of haline stratification associated with river plumes in the dynamics of *D. acuminata* blooms (Díaz et al., 2013; Peperzak et al., 1996; Velo-Suárez et al., 2010), a relationship also detected in southern Portugal when *D. acuminata* intense blooms (7×10^4 cells L^{-1}) appeared related to the Guadiana river plume in January 1998 (unpublished monitoring data from IPMA).

The most severe meteorological anomalies observed during the decade were, however, associated with the intensification of upwelling favorable winds in 2007 and 2008 that have disturbed the normal onset and development of *Dinophysis* blooms in the two areas. The very intense upwelling conditions observed in 2007 during the whole spring and summer (Fig. 2A, thick line) seem to have had important consequences on the availability of sufficient

innocula for the initiation of *Dinophysis acuta* blooms during the following seven years in PO, conditions which only re-appeared in 2013. That anomaly also delayed the 1st bloom of *D. acuta* in AV until October 2007, and there were no conditions for its growth or advection into PO. In 2008, similar consequences occurred in AV after the whole autumn 2008 characterized by anomalous intense upwelling winds and southward currents (Figs. 2 and 8) instead of the typical downwelling events. The strong equatorward and offshore currents seemed to have swept *D. acuta* blooms from the AV system until 2013, despite a small one-week outbreak observed in 2010 (Table 3). In those years, *D. acuta* populations were present in the system but were not able to reach a threshold concentration for bloom initiation. The blooms reappeared in 2013, after an anomalous year without upwelling during all summer, and with the highest positive SST anomaly in the AV area (Fig. 2C, arrow 9). In October there were conditions for their poleward transport from AV into the Galician Rías (Fig. 9B).

4.3. Bloom initiation and prediction

Dinophysis outbreaks were observed from mid February (*Dinophysis acuminata* in 2008, AV) until mid December (*Dinophysis acuta* in 2005, PO), a time window slightly wider than that observed in previous decades off the NW Iberian, French and Irish coasts (Pazos et al., 2005; Xie et al., 2007; Raine, 2014). Unexpectedly, the temporal window of each of the two species was more similar with their distribution in Flødevigen Bay, on the Skagerrak coast of Norway (Cembella et al., 2005), with *D. acuminata* blooms extended in time, and *D. acuta* events that mainly developed during the second half of the year.

The different behavior of the NW Iberia populations of *Dinophysis acuminata* and *Dinophysis acuta*, both in space and time, strongly suggests that the development of predictive tools must consider the species independently, so the approach followed by Singh et al. (2014), where all *Dinophysis* species are considered together, is not appropriate for NW Iberia. We also were not yet able to determine temporal relationships with the presence of its prey, *Mesodinium rubrum*.

In this work, we used a combination of simple overlapping conditions of readily accessible variables, like SST and UI, together with the knowledge of the periods most favorable for bloom initiation, to learn how far such an elementary approach could be used to predict the first bloom events each year. Reasonable results (Table 2) were obtained in anticipating the first *Dinophysis acuminata* events in PO and with *Dinophysis acuta* in AV, curiously the areas considered to be the distribution centers of the species. From 2007 until 2012, the nonexistence of *D. acuta* blooms in PO was also predicted just because we imposed the condition that the presence of cells is required before bloom initiation. The blooms were not anticipated in two cases, 2007 (*Dinophysis acuminata* in PO) and 2013, (*Dinophysis acuta* in PO) apparently for the same reason. The blooms initiated too rapidly suggesting the populations could have grown elsewhere and were advected to the area. This hypothesis is consistent with lagrangian model results for 2013 when *D. acuta* blooms were most likely transported from AV into PO. In 2007, the first outbreak of *D. acuminata* in the Ría de Pontevedra (only in mid June, during an upwelling-relaxation event) was well discussed by Velo-Suárez et al. (2014) and appeared to be triggered by heterotrophic feeding concomitant with the first peak in the season of *Mesodinium cf. rubrum*. Our results further suggest that the reported delay on the development of *Mesodinium* in 2007 was due to the observed anomaly related to high persistent and intense upwelling winds.

Bloom initiation of both species was predicted too early in 2010. In that year river runoff was the highest of the series during the interquartile period of bloom initiation and we can conclude there

were no conditions for the species growth. A similar reason can be evoked for the delay in *Dinophysis acuminata* initiation at AV in 2011. Salinity is therefore a variable that should be introduced in future exercises. In the case of the early prediction of *D. acuminata* in 2006, we were not able to have an explanation based on the available data, including the presence of *Mesodinium* cells in station AV.

4.4. Bloom connectivity between PO and AV

Previous studies have presented evidence of a northward transport of HABs in the NW shelf (Sordo et al., 2001; Escalera et al., 2010; Pitcher et al., 2010). However it can also be argued that this apparent transport reflects poleward changes in the conditions favoring these species rather than an effective poleward cell advection (Pitcher et al., 2010), or that downwelling is the oceanographic process that triggers a positive selection and sudden dominance of autochthonous populations of dinoflagellates in the Galician Rías Baixas in autumn (Crespo et al., 2006). The model solutions shown here for *Dinophysis acuta* transport from AV to PO, in late October 2005, support Escalera et al. (2010) suggestions that the cell increase in Ría de Vigo, in the absence of cellular division, was due to an alongshore transport from the coast of Portugal. In the same way, in October 2013, the sudden outbreak of *D. acuta* in PO, after a complete absence of cells during the whole year, can be explained by the bloom transport from the AV region as demonstrated by the model. These events, which originated sudden bans in Galician mussels harvesting showed how important will be to keep weekly exchange of information and early warning between monitoring programs of neighboring countries.

The connectivity between AV and PO in respect of the poleward transport of *Dinophysis acuta* is more complex when dealing with the southward transport of *Dinophysis acuminata* from PO to AV. The selected examples were developed during active upwelling periods, when transport is offshore and southwards. The first studies on coast-wide connectivity patterns off W Iberia were carried out to investigate the common shore crab *Carcinus maenas* recruitment on western Iberia coast (Nolasco et al., 2013a,b, following Carr et al., 2007), and that expertise was applied in the present work. The connectivity between PO and AV was demonstrated to be possible if tracking particles were forced to stay in a 5 m layer at 10 m depth (± 2.5 m). This way some particles remain close to the coast and travel southward reaching AV. This result can be applied to *D. acuminata* if the species has an active behavior in the water column maintaining its vertical distribution at a given depth. Its trophic relationship with *Mesodinium rubrum*, an active phototrophic swimmer well known as capable to have diel vertical migrations (Crawford and Lindholm, 1997), reinforces that possibility. The evidence of *D. acuminata* and *M. rubrum* diel migrations between 10 m and the surface was already observed in Ría de Vigo (Villariño et al., 1995) and encourage further studies on the *Dinophysis* position in the water column along the Diel cycle and on the different transport pathways according to different vertical migration scenarios.

4.5. Latitudinal changes in *Dinophysis acuta* epicenter

The observed changes of the upwelling patterns that occurred in spring/summer 2007 (persistence of very intense upwelling) and in autumn 2008 (intense autumn upwelling instead of downwelling) resulted in important latitudinal shifts of the *Dinophysis* epicenters off NW Iberia. Those abnormal upwelling conditions changed the *Dinophysis acuminata* bloom pattern in 2007 and 2008 by moving from PO into AV the bloom initiation and maxima. The bloom epicenter was re-established in PO only in

2009. They also strongly affected the epicenter of *Dinophysis acuta*. Firstly, the changes in the upwelling patterns interrupted for seven years the blooms or even the species detection (e.g. 2007 and 2010) in PO. They also shifted the species epicenter, located until 2008 on the coast of Aveiro-F.Foz, to more than 200 km southwards, leading to unexpected intense blooms that initiated and spread from Lisbon Bay in 2012 and 2013. In 2013, an year characterized by the lack of upwelling and, consequently, by the intensification of poleward coastal currents, the blooms initiated in Lisbon in July, reaching AV in September and PO in October. After this exceptional year, *D. acuta* outbreaks anchored again in AV where the initiation and maxima were observed in 2014. Changes in the epicenter of *Dinophysis* species were also reported in the North sea associated with a change in wind patterns in a larger temporal scale than our study. Edwards et al. (2006) used CPR data to describe that, over the last four decades, the *Dinophysis* epicenter (referred to as center of distribution) in the North Sea has moved eastwards toward the coast of Norway in association with the establishment of predominant southerly winds. In the W coasts of Ireland, Shetland islands, and France changes in wind patterns, in particular periods dominated by westerly winds instead of the usual southerlies, gave rise to rapid *Dinophysis* increases inside the bays or in other areas of the coast (Raine, 2014; Whyte et al., 2014; Batifoulier et al., 2012; Díaz et al., 2013), although changes in the distribution centers of *Dinophysis* were not discussed.

The present work used 10 years of two toxic *Dinophysis* species observations in two selected stations of NW Iberia and was able to highlight not only their seasonal variability but also the interannual variability of the upwelling intensity, runoff and SST patterns with emphasis on particular meteorological and oceanographic anomalies that were related with pronounced changes on the location and timing of bloom initiation and intensity. Future works should focus on improving the knowledge of the origin of the inoculum populations on the shelf and if they are related to *Dinophysis* populations that develop during winter in semi-enclosed coastal lagoons along the Portuguese coast, namely the Lagoa de Óbidos (Pereira et al., 2012) and Lagoa de Albufeira in Lisbon bay (Coutinho, pers. comm.).

Further studies on the relationship of the two *Dinophysis* species with their prey *Mesodinium rubrum* are also needed. Despite the observations that *Dinophysis* blooms usually occur after the *Mesodinium* blooms, it was still not possible to establish a direct link, partly due to the insufficient identification of the *Mesodinium* species (and possibly other ciliates) in Iberia waters. Such studies will help to clarify if they can be used as a predictors of *Dinophysis* blooms off Iberia. A better knowledge of the vertical position of both prey and predator vertical and diel migration in the water column will also be indispensable to appropriate simulations of the alongshore transport of blooms and connectivity between adjacent regions.

The changes in the *Dinophysis acuta* epicenter reported here could be identified because they were mainly observed along the Portuguese coast. Similar studies focused on *Dinophysis acuminata* will need a joint effort to combine the results from the HAB monitoring programs of Portugal and Galicia in order to cover the whole NW Iberian coasts.

Acknowledgments

Thanks are due to projects EU FP7 “ASIMUTH” (7FP SPACE-261860), FCT “HAB-SPOT” (PTDC/MAR/100348/2008) and to INTECMAR (Galicia, Spain) and IPMA (Portugal) HAB monitoring programs. Thanks to Vitor Bettencourt for his long and continuous help on the weekly sampling at Aveiro, and to the colleagues who collaborated on phytoplankton counts.

This study has been conducted using MyOcean, now Copernicus – Marine environment monitoring service, Products available at <http://www.myocean.eu/>. ECMWF ERA-Interim data have been obtained from the ECMWF data server. The authors acknowledge the use of the Ferret program, a product of NOAA's Pacific Marine Environmental Laboratory (information is available at <http://ferret.pmel.noaa.gov/Ferret/>).

This is a contribution to the SCOR and IOC GEOHAB program, Core Research Projects on “HABs in Upwelling Systems” and “HABs and Stratification”. [SS]

Annex 1. Interannual variability of dates of the first, last occurrence and bloom initiation of *Dinophysis acuminata* and *Dinophysis acuta*, and of dates and concentration of each species maxima

Years	<i>Dinophysis acuminata</i>										<i>Dinophysis acuta</i>									
	Aveiro – AV					Pontevedra – PO					Aveiro – AV					Pontevedra – PO				
	1st occur.	Date of bloom initiation >200 cells/L	Date of maxima	Maxima cells/L	Last occur.	1st occur.	Date of bloom initiation >200 cells/L	Date of maxima	Maxima cells/L	Last occur.	1st occur.	Date of bloom initiation >200 cells/L	Date of maxima	Maxima cells/L	Last occur.	1st occur.	Date of bloom initiation >200 cells/L	Date of maxima	Maxima cells/L	Last occur.
2004	1st sampling on 18 May 2004										1st sampling on 18 May 2004									
	N/A	N/A	31-May	1080	04-Oct	N/A	N/A	9-Aug	680	08-Nov	31-May	19-Jul	27-Jul	1880	13-Dec	30-Aug	07-Sep	7-Sep	0	20-Dec
							PO with several peaks of 600 cells					30-Aug	30-Aug	1960						
2005	28-Mar	28-Mar 19-Sep	8-Apr 19-Sep	880 880	31-Oct	21-Mar	21-Mar 13-Jun	4-Apr 13-Jun	2880 2120	07-Nov	08-Apr	1-Aug 5-Sep ^a	22-Aug 19-Sep 17-Oct	13920 87160 14160	05-Dec	04-Apr	17-Aug 17-Oct	17-Aug 7-Nov	960 17560	19-Dec
2006	03-April	– 11-Sep	25-Jul 11-Sep	80 1080	26-Sep	15-May	17-Jul 21-Aug	01-Aug 21-Aug	1880 2160	20-Nov	17-Apr	29-May 21-Aug	26-Jun 18-Sep	1360 1200	20-Nov	24-Apr	– 05-Sep	– 02-Oct	0 3000	30-Oct
2007	19-Feb	05-Jun 23-Jul	18-Jun 07-Aug	1480 9360	20-Nov	13-Mar	18-Jun 17-Sep	18-Jun 17-Sep	2240 1000	17-Dec	01-Oct	08-Oct	15-Oct	1520	11-Dec	–	–	–	0	–
2008	22-Jan	11-Feb 30-Jun	11-Feb 14-Jul	280 3600	21-Oct	27-Feb	12-May 01-Sep	26-May 01-Sep	2960 1160	10-Nov	26-Feb	07-May 28-Jul	14-Jul 06-Aug	16240 2080	28-Oct	17-Mar	–	17-Mar	80	23-Jun
2009	06-Apr	14-May	14-May	1720	06-Jul	02-Mar	16-Mar	29-Jun	3000	30-Nov	04-May	– –	04-May 08-Oct	160 40	12-Nov	01-Jun	–	01-Jun 26-Oct	80 80	26-Oct
2010	26-Mar	01-Jun 06-Sep	05-Jul 21-Sep	1900 280	20-Oct	22-Mar	07-Jun 23-Aug	12-Jul 30-Aug	27440 1760	13-Dec	01-Jun	06-Sep	06-Sep	500	21-Sep	–	–	–	0	–
2011	28-Mar	11-Jul	11-Jul 29-Aug	260 460	28-Nov	21-Feb	29-Mar 08-Aug 17-Oct	09-May 29-Aug 31-Oct	1520 5200 1520	21-Nov	01-Aug	–	01-Aug	150	17-Oct	06-Jun	–	06-Jun	160	04-Jul
2012	1st sampling on 30 May										1st sampling on 30 May									
	N/A	N/A	04-June	480	09-Oct	28-Feb	05-Mar 21-May	02-Apr 11-June	14640 1240	09-Oct	03-Jul	–	03-Jul	140	01-Oct	06-Aug	–	06-Aug	80	06-Aug
2013	25-Mar	02-Apr 16-Jul	15-Apr 17-Sep	340 900	16-Dec	12-Feb	25-Mar 08-Jul 7-Oct	09-Apr 15-Jul 7-Oct	5880 4280 3320	16-Dec	15-Apr	09-Sep	17-Sep	4640	16-Dec	07-Oct	07-Oct	07-Oct	5000	16-Dec

N/A – not applicable since sampling was considered to late for the species.

^a Date of a minimum (>200 cells/L) before another peak.

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