

Climate variability and *Dinophysis acuta* blooms in an upwelling system



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ABSTRACT

Dinophysis acuta is a frequent seasonal lipophilic toxin producer in European Atlantic coastal waters associated with thermal stratification. In the Galician Rías, populations of *D. acuta* with their epicentre located off Aveiro (northern Portugal), typically co-occur with and follow those of *Dinophysis acuminata* during the upwelling transition (early autumn) as a result of longshore transport. During hotter than average summers, *D. acuta* blooms also occur in August in the Rías, when they replace *D. acuminata*. Here we examined a 30-year (1985–2014) time series of *D. acuta* from samples collected by the same method in the Galician Rías. Our main objective was to identify patterns of distribution and their relation with climate variability, and to explain the exceptional summer blooms of *D. acuta* in 1989–1990. A dome-shaped relationship was found between summer upwelling intensity and *D. acuta* blooms; cell maxima were associated with conditions where the balance between upwelling intensity and heating, leading to deepened thermoclines, combined with tidal phase (3 days after neap tides) created windows of opportunity for this species. The application of a generalized additive model based on biological (*D. acuta* inoculum) and environmental predictors (Cumulative June–August upwelling CUI_{JJA} , average June–August SST_{JJA} and tidal range) explained more than 70% of the deviance for the exceptional summer blooms of *D. acuta*, through a combination of moderate ($35,000\text{--}50,000\text{ m}^3\text{ s}^{-1}\text{ km}^{-1}$) summer upwelling (CUI_{JJA}), thermal stratification ($SST_{JJA} > 17^\circ\text{C}$) and moderate tidal range ($\sim 2.5\text{ m}$), provided *D. acuta* cells (*inoculum*) were present in July. There was no evidence of increasing trends in *D. acuta* bloom frequency/intensity nor a clear relationship with NAO or other long-term climatic cycles. Instead, the exceptional summer blooms of 1989–1990 appeared linked to extreme hydroclimatic anomalies (high positive anomalies in SST and NAO index), which affected most of the European Atlantic coast.

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1. Introduction

Several species of the genus *Dinophysis* produce lipophilic toxins (okadaic acid, its congeners and pectenotoxins) and cause lengthy shellfish harvesting bans in Europe (Van Egmond et al., 1993). Shellfish closures are especially damaging in the Galician Rías Baixas (NW Spain), the site of intense Mediterranean mussel

(*Mytilus galloprovincialis*) aquaculture with an annual production of up to 300,000 t (Blanco et al., 2013). These Rías (Fig. 1), are at the northern limit of the Canary Current Upwelling System, and subject to seasonal (spring to early autumn) upwelling pulses. Upwelling has been identified as the main factor controlling phytoplankton dominance in the Rías (Figueiras and Ríos, 1993; Pazos et al., 1995; Nogueira et al., 2000) and changes in upwelling patterns are expected to have species-specific effects on harmful algal events.

Dinophysis acuminata (Claperède & Lachmann) and *Dinophysis acuta* (Ehrenberg) are the main agents of Diarrhetic Shellfish Poisoning (DSP) outbreaks in temperate waters on the Atlantic coasts of Europe (Reguera et al., 2014). In Western Iberia the two

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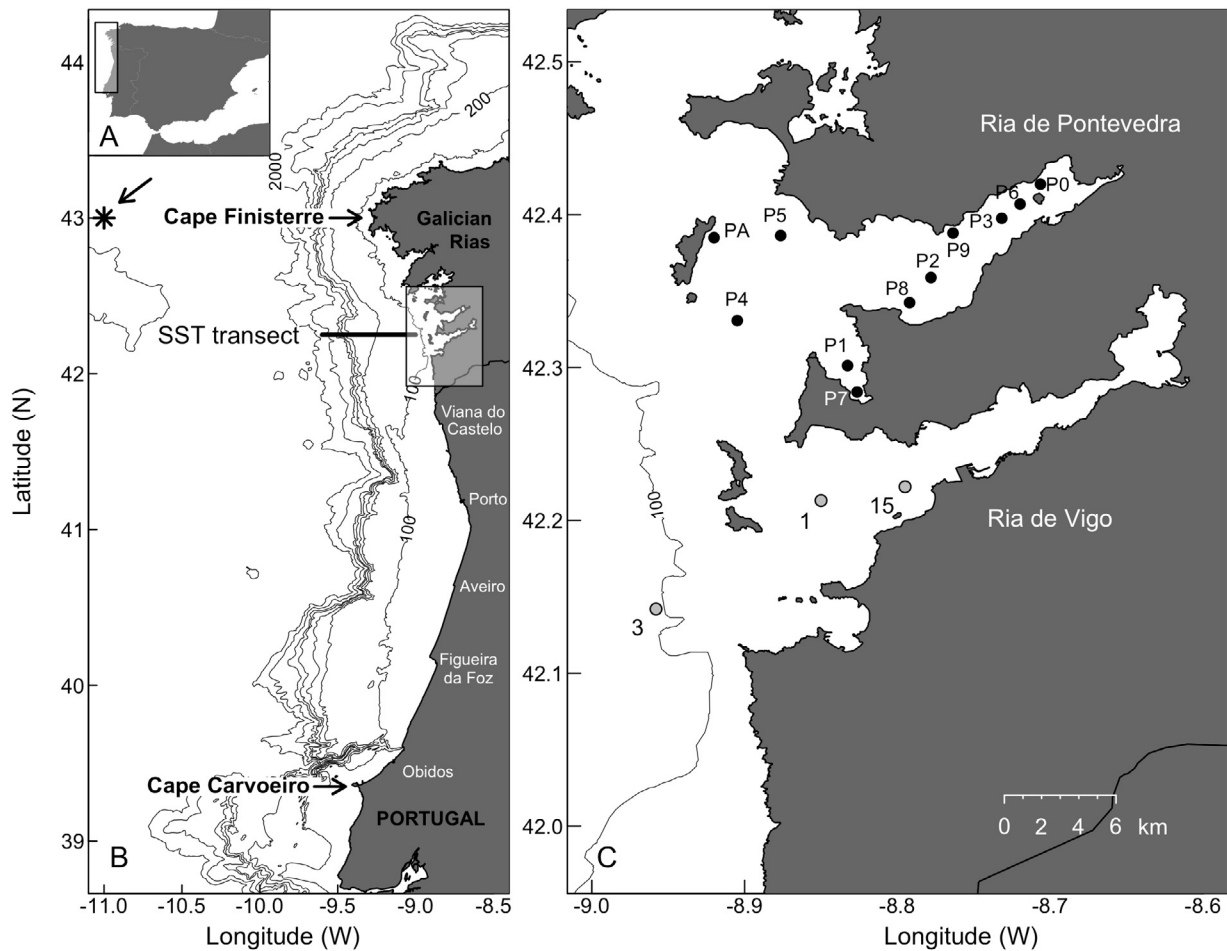


Fig. 1. Maps of the study area. (A) Iberian Peninsula; (B) Northwest Iberia and location of the transect used for cross-shelf SST and the location (asterisk) for upwelling index estimates; (C) Location of the 11 INTECMAR sampling stations (black circles) in Ría de Pontevedra and the three stations (grey circles) of the Ría de Vigo and adjacent shelf transect (Radiales-IEO).

species show marked differences in their spatial and seasonal distributions (Reguera et al., 1993; Palma et al., 1998; Escalera et al., 2006). *D. acuminata* occurs every year throughout the upwelling season (spring to early autumn), with the first maximum ($>10^3$ cells L^{-1}) around early June (Pazos and Moróño, 2008). In contrast, blooms of *D. acuta* are very seasonal and do not occur every year. These develop in Northern Portugal during upwelling conditions and thermal stratification in late summer. Blooms of *D. acuta* in the Galician Rías Baixas are associated with longshore transport at the end of the upwelling season (Escalera et al., 2010). Only exceptionally, late summer development of *D. acuta* has been observed during the upwelling season in the Rías Baixas. Years of persistent blooms of *D. acuminata* followed by those of *D. acuta* may keep harvesting bans on mussel production areas for up to nine months and constitute the worst scenario for the shellfish industry (Escalera et al., 2010; Blanco et al., 2013).

The potential impacts of climate variability on interannual fluctuations on the composition and abundance of different functional groups and trophic levels of plankton have received great attention in recent decades (Fromentin and Planque, 1996; Planque and Taylor, 1998; Edwards and Richardson, 2004). On the basis of a 40-year (1960–2000) time series from the Continuous Plankton Recorder (CPR) surveys, Edwards et al. (2002) suggested that long-term variations in several North Sea plankton species were closely linked with anomalous oceanographic events occurring episodically over a timescale of decades. The intensity of the response varied considerably amongst different phytoplankton groups. Long-term variations in phytoplankton composition

were identified over the last decade, in the same region, by Hinder et al. (2012) who suggested that a fundamental shift in the relative abundance of diatoms (e.g. *Pseudo-nitzschia* spp.) versus dinoflagellates, with a marked decline in dinoflagellates (e.g. *Prorocentrum* spp.), was driven by the combination of increasing sea surface temperature (SST) and windy conditions in summer. Changes in phytoplankton community succession, sometimes characterized by a relative increase of potentially toxic species, have been interpreted as a consequence of intensified water column stability favouring taxa of larger cell size and/or swimming capabilities (Smayda and Reynolds, 2001).

Although considerable knowledge has been gained about the seasonality and short-term responses of *Dinophysis* spp. to environmental conditions, the lack of long-term time series data has hindered progress in understanding the factors controlling their interannual variability. Multidecadal climate oscillations have been proposed to explain long-term variations in *Dinophysis* blooms in the Skagerrak, in western Swedish (Belgrano et al., 1999) and southern Norwegian coastal waters (Edwards et al., 2006; Naustvoll et al., 2012). These authors suggested that long-term changes of *Dinophysis* blooms in these areas were related to phase changes of the North Atlantic Oscillation (NAO), the most important mode of low-frequency variability of atmospheric circulation in the northern hemisphere (Hurrell, 1995). Nevertheless, *Dinophysis acuminata* and *Dinophysis acuta* respond in different ways to meteorological forcing (Escalera et al., 2006), and detailed description of the physical niche of each species is needed.

While large-scale atmospheric and oceanographic processes affect interannual variability, the short-term response may be determined by optimal local conditions (wind, tides, etc.), leading to formation of exceptional blooms. For example, exceptional blooms of *Dinophysis* spp. in the Shetland Islands, Scotland have been linked to anomalous summer wind patterns favouring transport of shelf populations into the lochs (Whyte et al., 2014). Recently, Díaz et al. (2013) associated exceptionally early blooms of *Dinophysis acuminata* in northwest Spain and southwest France with mesoscale anomalies of winter wind circulation patterns.

The relationship between tidal cycles and phytoplankton blooms, where the semi-diurnal component (tidal mixing promoter) is one of the most important sources of variability, is well known (Cloern, 1991; Lauria et al., 1999; Blauw et al., 2012). Díaz et al. (2014) found that short-term variability of *Pseudo-nitzschia* populations was modulated by semidiurnal and spring–neap tidal signals. Nevertheless, lunar fortnightly components are also important promoters of turbulence (Balch, 1986) and their relationship with *Dinophysis acuta* blooms have been poorly explored.

A good understanding of the different scales of variability is a key aspect for the development of operational models and improved risk assessment of shellfish poisoning in a region (GEOHAB, 2011). A main objective of the European project ASIMUTH was “the identification of key past events which would be re-analysed and used for training the modelling system”.

Here our priority was to identify conditions that promoted the exceptional summer blooms of *Dinophysis acuta* during 1989 and 1990. The interannual variability of *D. acuta* blooms was compared with local hydroclimatic conditions based on a 30-year time series of *D. acuta*, meteorological factors, upwelling patterns, stratification and lunar cycles. Statistical analysis, based on cumulative summer upwelling, monthly average sea surface temperature and the tidal cycle and range, accounted for 77% of the deviance provided *D. acuta* cells (*inoculum*) are present in July in Galician shelf waters.

2. Materials and methods

2.1. Study area

The Galician Rías Baixas, on the western Iberian margin, are at the northern limit of the Canary Current Upwelling system. Wind is the main driving force in upwelling systems, which can exhibit large variability on a variety of temporal scales related to atmospheric oscillations. On an annual basis, variability in the Galician Rías Baixas, under the influence of the North Atlantic weather system, results from the displacement of the Azores high-Icelandic low pressure dipoles (Wooster et al., 1976; Bakun and Nelson, 1991). During spring-summer, the displacement to the north of the Azores high and predominance of north-easterly winds promote upwelling of cold, salty and nutrient-rich Eastern North Atlantic Central Water (ENACW) on the shelf and a surface southward flow near the shelf break (Fiuza et al., 1998). In contrast, the southward shift of the Icelandic low and predominance of south-westerly winds during autumn–winter promote downwelling events and strengthen the general circulation of the region, which is characterised by the presence of a surface poleward current on the slope (Haynes and Barton, 1990). Transition periods occur in spring and autumn. However, variations in the wind regime due to changes in the position and/or strength of the high-low pressure systems cause short-term variability in upwelling-downwelling cycles within each season (Álvarez-Salgado et al., 2003) and lead to rapid changes in the hydrodynamics of the Rías and significant changes in plankton distribution and ecology

(Tilstone et al., 1994; Tilstone et al., 2000). Water column responses to these upwelling-downwelling cycles during the upwelling season are modulated by the degree of thermal stratification, which evolves from the weakest stratification in spring to the strongest in late summer–early autumn. HAB events are common in the Galician Rías Baixas between spring and early autumn, and have been described to result from both *in situ* growth and advection of shelf populations into the Rías. The latter process is especially intense during the autumn transition from upwelling to downwelling (Sordo et al., 2001). The Rías of Vigo and Pontevedra are more frequently affected by toxic outbreaks, than the more northerly Rías of Arousa and Muros (Blanco et al., 2013).

2.2. Meteorology and hydrography

2.2.1. Solar irradiance and NAO

Sunspot numbers, the most important proxy for solar irradiance (Lean, 2010), were obtained from the US National Oceanic and Atmospheric Administration (NOAA) (<http://solarscience.msfc.nasa.gov/SunspotCycle.shtml>). Winter (December–March) North Atlantic Oscillation (NAO) indices were obtained from the Climatic Research Unit, University of East Anglia (<http://www.cru.uea.ac.uk/cru/data/nao.htm>).

2.2.2. Rainfall, air and seawater temperature and salinity

Rainfall and air temperature (monthly mean) data from a meteorological station at Vigo airport (Peinador) (42°13.89' N, 8°37.29' W) were provided by the Spanish Meteorological Agency (www.aemet.es).

Monthly averages of SST (4-km resolution) from the Advanced Very High Resolution Radiometry (AVHRR), Pathfinder Version 5.0 (PFV5.0) as described by Casey et al. (2010), from January 1985 to December 2009, were obtained from the US National Oceanographic Data Centre and GHRSSST (<http://pathfinder.nodc.noaa.gov>). In addition, monthly averages of SST (4-km resolution) from the Moderate Resolution Imaging Spectroradiometer (MODIS) from January 2010 to December 2014 (available from 2002 to present) were obtained from the Giovanni online data system (<http://disc.sci.gsfc.nasa.gov/giovanni/>), developed and maintained by the NASA Goddard Earth Sciences Data and Information Services Centre (GES DISC). The good correlation ($r^2 = 0.97$) between AVHRR and MODIS images from 2002 to 2014 indicates that MODIS data can be used as a complementary source of AVHRR data. Although both day and night AVHRR and MODIS SST data were available, we used only night time data, because these are not affected by reflected solar radiation and geographically varying diurnal warming (Rayner et al., 2003). It is important to note that remote sensors measure radiance emitted only over the upper optical depth, typically at a depth of ~1 m in coastal waters (Gordon and McCluney, 1975). Therefore, SST distributions on a 50-km cross-shelf transect off Ría de Pontevedra, and over the entire northwestern Iberian shelf, were interpreted as a proxy for stratification and used to estimate monthly SST anomalies for July and August from 1985 to 2014.

Vertical profiles of temperature and salinity in the Rías were obtained from bathythermograph (1985–1991, only temperature) and Sea-Bird 25 CTD casts (1992–2014) of the Galician HAB monitoring programme. Additionally, CTD profiles at three stations on a perpendicular transect from Ría de Vigo to the adjacent shelf (Fig. 1C, stations 15, 1 and 3), were obtained from monthly monitoring of the IEO-RADIALES programme between 1990 and 2014.

2.2.3. Winds and Ekman transport

Time series of six-hourly Ekman transport data over the last 48 years (1967–2014), were estimated using model data from the

US Navy's Fleet Numerical Meteorology and Oceanography Centre (FNMOC) derived from sea level pressure (www.indicedeafloramiento.ieo.es) on a grid of approximately $1^\circ \times 1^\circ$ centred at $43^\circ \text{ N } 11^\circ \text{ W}$ (Fig. 1B), a representative location for the study area (González-Nuevo et al., 2014). Description of the timing, variability, intensity and duration of coastal upwelling in the Galician Rías Baixas was made following the model proposed by Bograd et al. (2009). In this model, the Total Upwelling Magnitude Index (TUMI) is estimated as:

$$\text{TUMI} = \sum_{\text{END}}^{\text{STI}} \text{CUI}(t_e - t_s)$$

where CUI, the Cumulative Upwelling Index, is the sum of the daily mean upwelling index during the whole year; STI, the Spring Transition Index, is the date on which CUI reaches its minimum value and END is the date of the annual maximum of CUI which marks the end of the upwelling season. TUMI is the summation of daily upwelling values (CUI) from the spring transition date (t_s) to the end of the upwelling season (t_e). The use of CUI as a potential predictor of *Dinophysis acuta* summer blooms was tested with the values observed between June, the beginning of the *D. acuta* growth season (Escalera et al., 2010), and August (CUI_{JA}).

2.3. Tidal range and lunar phases

To evaluate the relationship between the lunar cycle and *Dinophysis acuta* bloom intensity, the lunar phase and maximum tidal range associated with the occurrence of *D. acuta* blooms were calculated using the statistical and programming software R 2.1.12 (R Development Core Team, 2012), package “phenology” (Girondot, 2014), available through the CRAN repository (www.r-project.org). The new moon was set as day 29 and the following day, as day 1 following Balch (1986). A probability density function was fitted to describe the distribution of *D. acuta* bloom occurrence with respect to tidal range and lunar phases.

2.4. Phytoplankton data

Weekly reports of phytoplankton distribution in the Ría de Pontevedra from 1985 to 2014 were obtained from the IEO-Vigo HAB monitoring (1985–1992, data from three stations) and from the Galician Monitoring Program at INTECMAR (1992–2014, data from 11 stations, all year round). Plankton samples for quantitative analyses have been collected in the same way since 1986, with a dividable (0–5 m, 5–10 m, 10–15 m) hose sampler (Lindahl, 1986), a method recommended by the ICES group of experts as the most suitable for monitoring HAB species with patchy distributions (ICES, 1986). Samples were immediately fixed on board with acidic Lugol's iodine solution. Quantitative analyses of potentially toxic phytoplankton species were carried out according to the Utermöhl (1958) method. For *Dinophysis* and other large and less abundant microplanktonic species, the whole surface of a 25-mL sedimentation chamber was scanned, so the detection level was >40 cells L^{-1} . Weekly reports of phytoplankton distributions in 1989 and 2005 at different stations along the northern Portuguese coast (Fig. 1B) were obtained from the Portuguese HAB Monitoring Programme. Water samples were collected with Nansen bottles at the surface and preserved with buffered formalin. Subsamples of 50–100 mL were analysed according to the Utermöhl (1958) method, so the detection level was 10–20 cells L^{-1} .

2.5. The statistical modelling approach

A generalized additive model (GAM) with identity-link function for Gaussian distribution (McCullagh and Nelder, 1989) was

implemented to quantify the influence of different environmental and biological factors, identified in the descriptive analyses, on *Dinophysis acuta* summer blooms. The Cumulative Upwelling Index (CUI) from June to August (CUI_{JA}), the monthly average SST from June to August (SST_{JA}), tidal range during the day of the bloom and *D. acuta* cell densities in July (acting as *inoculum*) were used as predictor variables (fixed effects terms). Fixed effects influence only the mean of y (response variable), while random effects influence only the variance of y . Thus, a factor is modelled as a fixed effect when it contains all levels of the variable about which we want to make an inference. Data (cell densities) were first normalized using a logarithmic transformation [$\text{LN}(x + 1)$]. GAMs are a flexible extension of generalized linear models that allow the specification of the linear predictor (response) as a generalized linear or smooth function of covariates (Hastie and Tibshirani, 1986). The measure of discrepancy in a GAM to assess the goodness of fit of the model to the data is called deviance. Interaction terms were not used because they can obscure the effects of the individual predictor variables (Gotelli and Ellison, 2004). The variable providing the best fit was chosen according to Akaike's information criterion (AIC) (Akaike, 1974) and Generalized Cross Validation (GCV), where the selected model is the one that has lower values of AIC and GCV. Model assumptions—homoscedasticity, normality, and linearity of effects—were checked using diagnostic plots: QQ-plot, residual versus linear predictor, histogram of the residuals and plot of the response versus fitted values (Wood, 2006). The analyses were performed using the statistical and programming software R 2.1.12 (R Development Core Team, 2012), package “mgcv” (Wood, 2006) available through the CRAN repository (www.r-project.org/).

3. Results

3.1. Meteorological and hydrographic conditions

3.1.1. Solar activity and NAO

Solar activity since 1985 showed the classic 11-year irradiance cycle (sunspot cycle), with maximal values at the end of the 1980s (Fig. 2A), represented by high (~ 300) sunspot numbers. These maxima coincided with the two highest positive anomalies ($>+2.3$) of the winter NAO index within the last 30 years, in 1989 and 1990 (Fig. 2B). Nevertheless, there were also high positive NAO values in years, such as 2007 and 2008, when solar activity was minimal and blooms of *Dinophysis acuta* were not detected.

3.1.2. Rainfall and air temperature

Summers 1989 and 1990 in Northwest Spain were extremely hot and dry. Values of rainfall anomalies for July–August (JA) were -62 and -53 mm in 1989 and 1990 respectively (Fig. 2C), i.e. total rainfall was less than half the value of the historic (1961–2014) JA mean (82 mm). Nevertheless, there were other years, e.g. 1993, 2006, 2010 and 2012, with similar or even stronger negative rainfall anomalies, not associated with summer blooms. Positive air temperature anomalies for JA in 1989 and 1990 were $+3.78$ and $+3.33$ °C respectively (Fig. 2D), reaching values >36 °C in 1989; 2010 showed similar strong positive anomalies ($+3.48$ °C) in these two months. Other years, such as 1995, 1998, 2003, had strong positive anomalies but only in August. In contrast, years such as 2007, 2008 and 2012 had strong negative air temperature anomalies and no blooms of *Dinophysis acuta*.

3.1.3. Sea surface temperature (SST)

SST distributions on a 50-km cross-shelf transect off Ría de Pontevedra showed values above 18 °C and positive SST anomalies ($+1.2$ and $+1.6$ °C) for JA 1989 and 1990 (Fig. 2E), but also in 1999

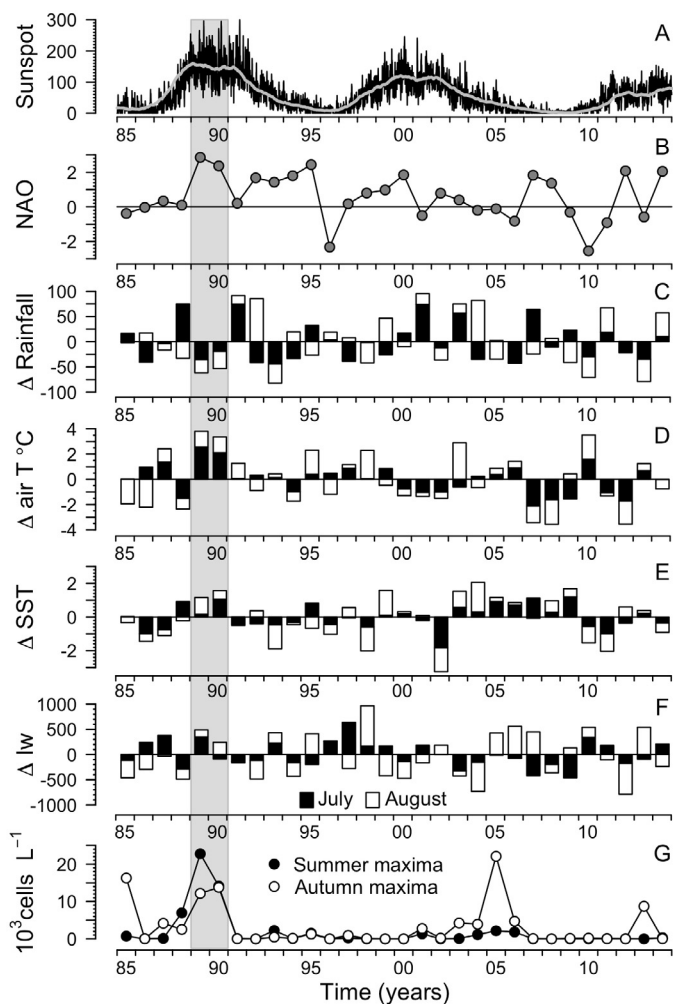


Fig. 2. Interannual variability of (A) Daily sunspot numbers; (B) Winter North Atlantic Oscillation (NAO); (C–F) Total rainfall (mm) (C), monthly average air temperature anomalies (D), Sea Surface Temperature (SST) anomalies along a cross-shelf transect perpendicular to Ría de Pontevedra (E) and monthly upwelling index anomalies (F) for July August (JA) and *Dinophysis acuta* cell maxima in summer (black circles) and autumn (grey circles) in Ría de Pontevedra obtained from the 11 monitoring stations (G), from 1985 to 2014.

(+1.6 °C, mainly in July) and between 2003 and 2009 (+0.9 ± 2.0 °C). Extreme negative SST anomalies (>−1.8 °C) for JA were observed in 1993, 1996, 1998, 2002, 2010 and 2011, years when *Dinophysis acuta* blooms did not occur, for the same transect (Fig. 2E).

At the mesoscale, positive SST anomalies during both months, July and August, were observed in western Iberian coastal waters, with extreme values (~+2 °C) during 1989, 1990, 2003 and 2004 (Figs. 3 and S1). These positive SST anomalies were highest in August 2004 reaching values close to +3 °C (Fig. 3J). In contrast, during years such as 1993, 1998 and 2002, SST anomalies in JA exhibited high negative values (~−2 °C) and *Dinophysis acuta* was hardly detected.

3.1.4. Thermal stratification

Changes in thermal structure at a shelf station (st. 3) (Fig. 4A) and in a transect of Ría de Vigo and the adjacent shelf (Fig. 1C) from 1990 to 2014 (based on IEO-RADIALES monthly sampling) showed a clear seasonal signal with maximal thermal stratification during July–August (only transects for years mentioned in the next paragraph are shown) (Fig. 4B–J).

Maximal thermal stratification during July was observed in 1990, with isotherms shoaling towards the coast as expected at

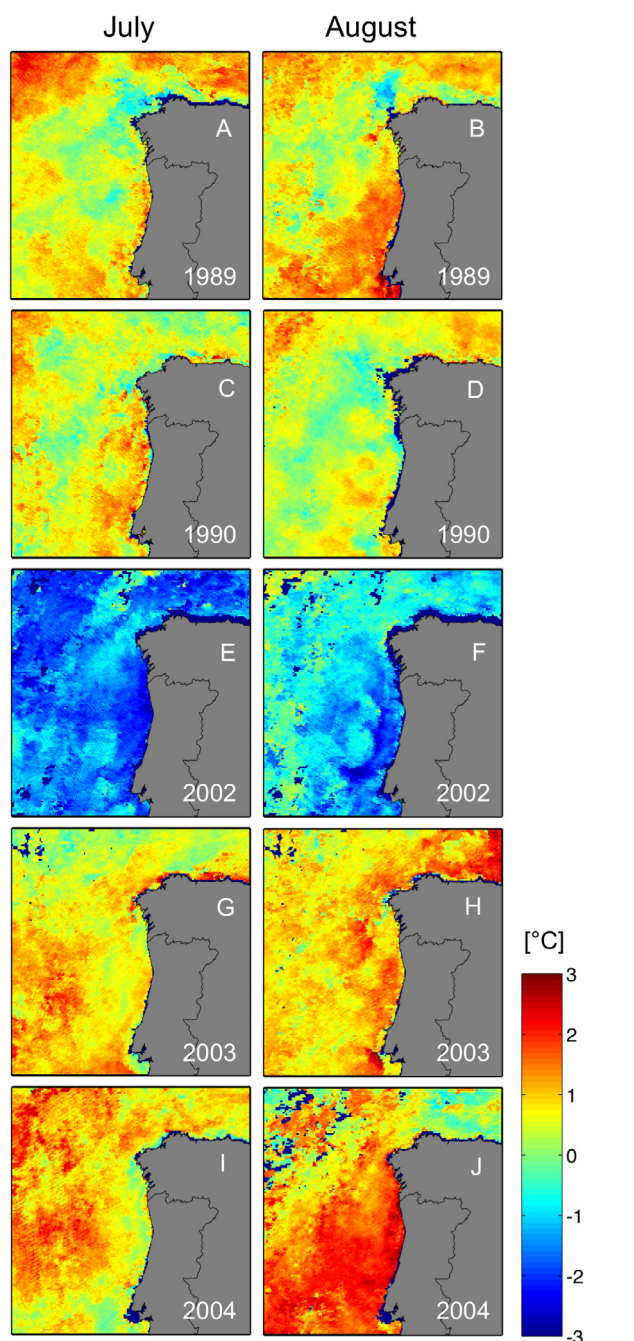


Fig. 3. Sea Surface Temperature (SST) anomalies for July (left panels) and August (right panels) from AVHRR images observed in NW Iberia in years (1989–1990) of exceptional summer blooms and in other selected years.

this time of the year due to upwelling events (Fig. 4B). There was a marked thermal gradient between 0 and 20 m (2.2 °C) with deeper thermoclines (~18–20 m) at the shelf station (st. 3) where SST reached values >19 °C, and the 17 °C isotherm was located at 20 m depth (Fig. 4B). Stable stratified conditions through July–August were observed also in 2003, but the position of the 17 °C isotherm was much closer to the surface (~3 m) at the shelf station (Fig. 4D,H). During July 2013, SST at the same station was also close to 19 °C, and the thermal gradient between 0 and 20 m was ~4.3 °C (Fig. 4F), but again the 17 °C isotherm and the thermocline were much closer to the surface (10 m), with values of 15.5 °C at the depth of maximum density gradient (14 m) and stratification in August was very poor (Fig. 4J). Concerning 2004, strong upwelling

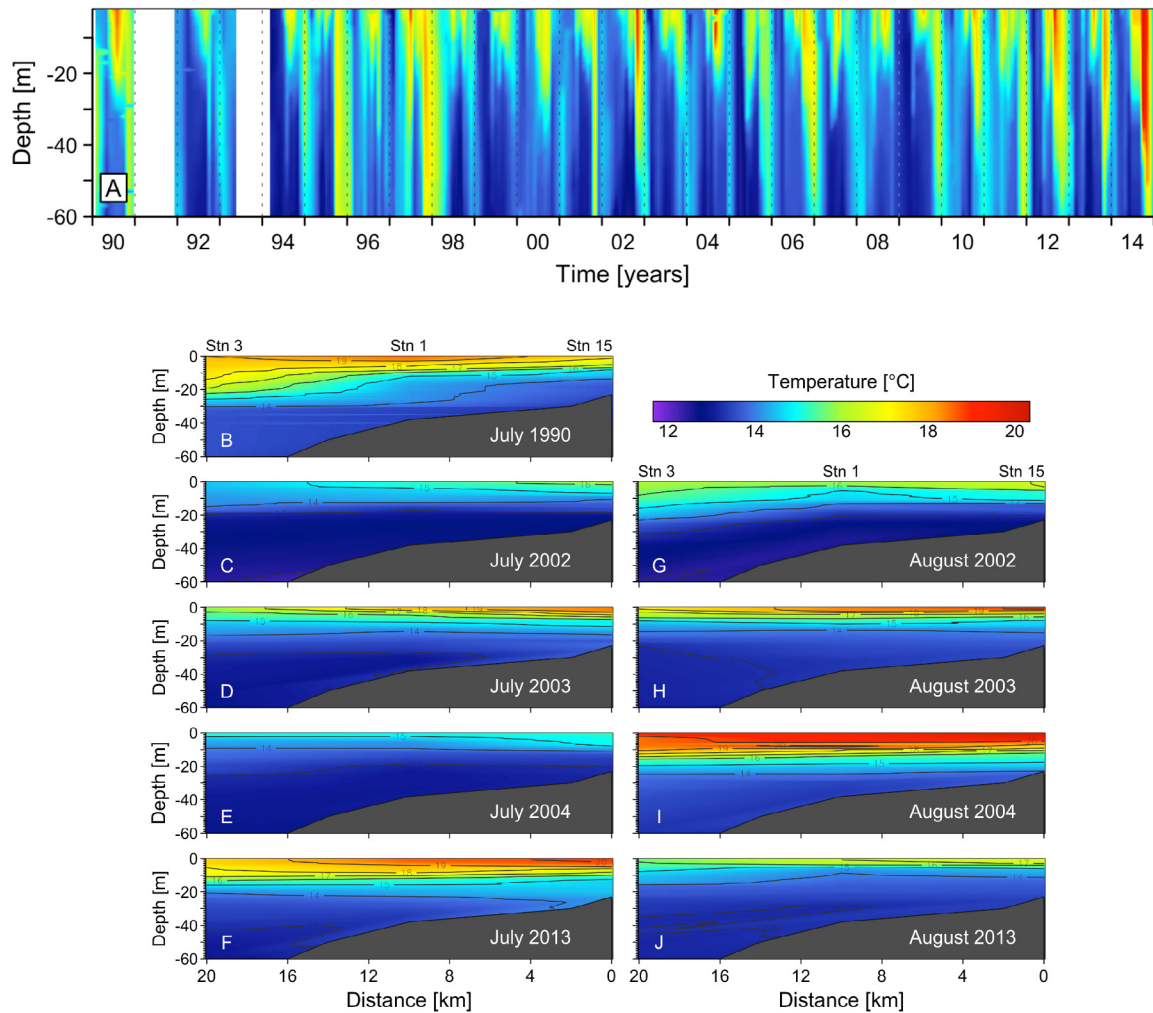


Fig. 4. (A) Changes in thermal structure at a shelf station (st. 3) between 1994 to 2014 (based on monthly sampling) and vertical distribution of temperature in July (B–F) and August (G–J) in representative years, in Ría de Vigo and along adjacent shelf transect. White band in the upper panel indicates data gap.

events in July led to an almost isothermal water column and a SST of around 15 °C (Fig. 4E), although in August the water column had reached a maximum SST of 20.3 °C with strong thermal stratification (5.44 °C between 0 and 20 m), and the 17 °C isotherm was at 14 m depth at the shelf station (Fig. 4I). During July and August 2002 (a year with no *Dinophysis acuta*) the water column appeared almost isothermal, with maximum SST values of 14.5 and 16.4 °C respectively at the shelf station (Fig. 4C and G).

3.1.5. Interannual variability of upwelling

The climatological upwelling season described with the Cumulative Upwelling Index (CUI) over the period 1967–2014 showed that the mean duration of the upwelling favourable season is 200 ± 48 days, from Julian day 80 ± 33 (21 March) to 280 ± 27 (7 October) (Fig. 5). The Total Upwelling Magnitude Index (TUMI) ranged from $21,600 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ to $109,350 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ with a mean of $69,650 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$.

The estimates of CUI from June (beginning of *Dinophysis acuta* growth season) to August, or summer upwelling (CUI_{JJA}), used as a potential prediction tool for *D. acuta* summer blooms, showed (Fig. 6A) maximum values in 1995 ($64,800 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$), 2010 ($67,300 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$) and 2013 ($60,350 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$), while minimum CUI_{JJA} estimates were found for 2012 ($-7500 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$). In 1989 and 1990, the years of exceptional *D. acuta* summer blooms, the CUI_{JJA} from June to August were

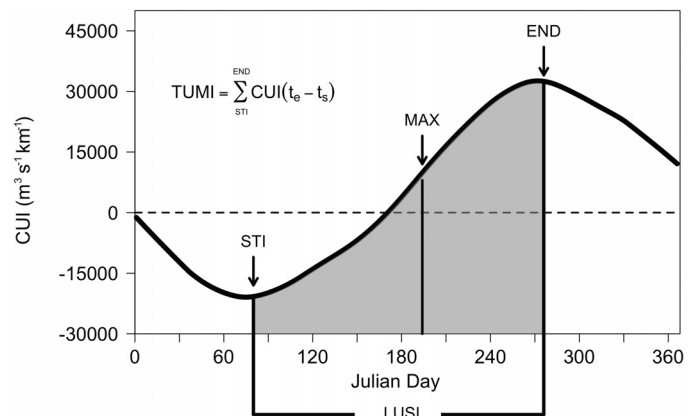


Fig. 5. Climatological annual cycle of cumulative upwelling index (CUI) over the last 48 years (1967–2014) at 43° N in the Canary Current upwelling system. Upwelling indices are shown schematically: STI (spring transition index), LUSI (length of upwelling season index), and TUMI (total upwelling magnitude index). MAX (maximum slope of CUI curve) and END (annual maximum of CUI) give the dates of the upwelling peak and the end of the upwelling season (autumn transition) respectively.

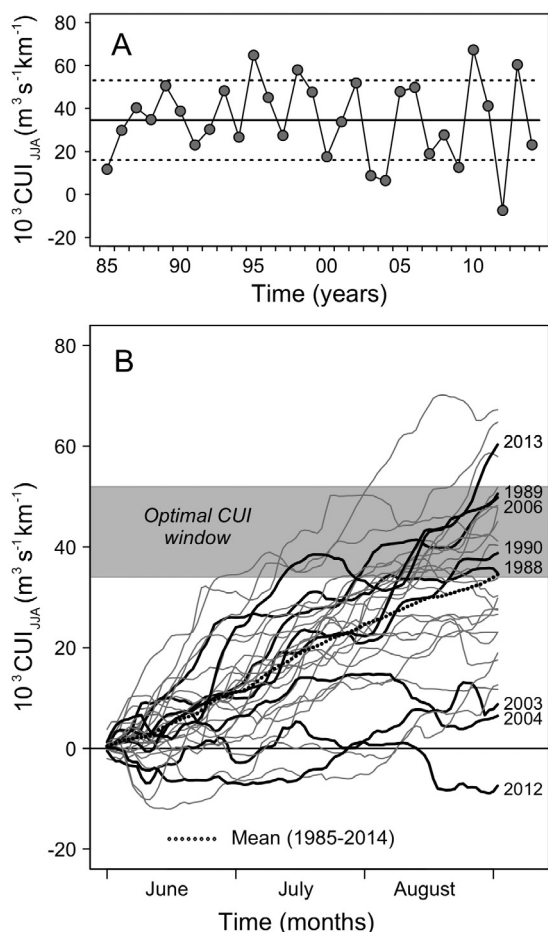


Fig. 6. (A) Time series of the cumulative upwelling index (CUI_{JJA}) and (B) Evolution of CUI_{JJA} observed at 43° N in the Canary Current upwelling system, during the *D. acuta* growth season (June–August) from 1985 to 2014. The optimal CUI_{JJA} window for *D. acuta* summer growth is shaded in grey.

$50,600 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ (1989) and $38,700 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ (1990) (Fig. 6B), i.e. 30% higher or close to the long-term mean ($34,950 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$). In contrast, during 2003 and 2004, years when stable thermal stratification lasted throughout July and August but *D. acuta* densities were extremely low, summer upwelling CUI_{JJA} (8750 and $6500 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ respectively) had record low values (4–5 times lower) in relation to the long-term mean. During 2002, the CUI_{JJA} ($51,850 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$) was similar to that of 1989 (Fig. 6B), but a quasi-isothermal structure was observed throughout July–August and the SST was close to 15°C .

3.2. Long-term changes in *D. acuta* abundance and phenology

The long-term data set shows a similar trend in Ria de Pontevedra, i.e. intensification of *Dinophysis acuta* blooms in 1988–1990 and 2003–2006, when plotting either the monthly average from all stations in Ria de Pontevedra or the yearly cell maxima (Fig. S2). Conspicuous autumn maxima of *D. acuta* ($>8 \times 10^3 \text{ cells L}^{-1}$ in integrated samples) were recorded in 1985, 1989, 1990, 2005, and 2013 and to a lesser extent ($>10^3 \text{ cells L}^{-1}$) in 1987, 1988, 1995, 2001, 2003, 2004 and 2006, i.e. in 12 years out of the 30-year time series (Figs. 2G and S2). Exceptional summer peaks only occurred in 1989 and 1990; but moderate populations ($<1 \times 10^3 \text{ cells L}^{-1}$) were detected in August 1988, 1993, and 2003–2006 (Figs. 2G and S2A). In contrast, very low numbers ($<1 \times 10^2 \text{ cells L}^{-1}$), close to detection levels in

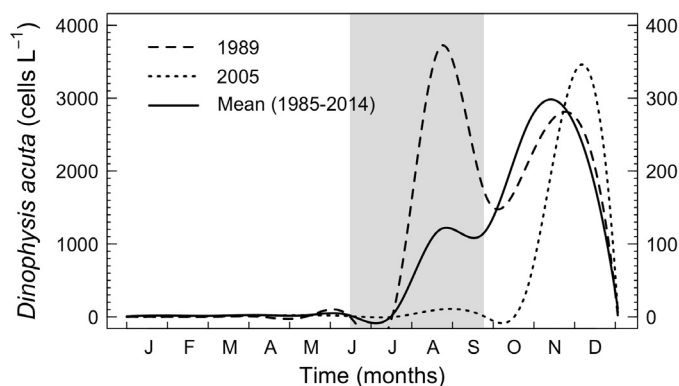


Fig. 7. Mean (1985–2014) seasonal cycle of *D. acuta* in Ria de Pontevedra (average from 11 stations) (solid line) and seasonal cycle in 1989 and 2005. Note the early development in 1989. Y-axis on the right represents the scale for the mean values (1985–2014).

the monitoring, were observed from 1996 to 2000 and from 2007 to 2012 (Figs. 2G and S2B).

The seasonal distribution of *D. acuta* in Galician coastal waters, in the years of occurrence of this species, exhibited two different patterns: a unimodal distribution, with a maximum in autumn in isothermal conditions at the end of the upwelling season (October), or a bimodal distribution (in particular during 1989 and 1990), with an additional maximum in late summer during stratified conditions (Fig. 7).

3.3. Mesoscale spatial distribution of *D. acuta*

The monthly evolution of *Dinophysis acuta* cell densities at the mesoscale, observed at monitoring sites in both Galicia and northern Portugal from June to November, showed quite different distribution patterns in 1989 and 2005, two years with contrasting dynamics of this species in the Galician Rías (Fig. 8). In 1989, *D. acuta* was detected (net samples) in the Rías from early June (Fig. 8A); numbers increased through July, reaching $1.8 \times 10^3 \text{ cells L}^{-1}$ on 26 July in Ria de Vigo and $1.2 \times 10^4 \text{ cells L}^{-1}$ in Aveiro and Figueira da Foz (off Portugal) (Fig. 8B). During August a *D. acuta* record (for integrated samples in the region) of $2.2 \times 10^4 \text{ cells L}^{-1}$ was observed in the Galician Rías (mainly in Ria de Pontevedra), coinciding with lower values in the Portuguese sites (Fig. 8C). A similar situation was observed in September (Fig. 8D) and October (Fig. 8E). Finally, high cell densities (up to $10^4 \text{ cells L}^{-1}$) were observed again during November in the whole region (Fig. 8F).

In 2005, *D. acuta* was present above detection levels in the Rías Baixas in March, but the population did not build up during summer (Fig. 8G–J). High cells densities ($>1 \times 10^4 \text{ cells L}^{-1}$) were observed at the same time in Portuguese waters, with a record value of $1.4 \times 10^5 \text{ cells L}^{-1}$ in Aveiro in early September (Fig. 8J). Later, very high *D. acuta* cell densities ($2.2 \times 10^4 \text{ cells L}^{-1}$) were found in early November in the Galician Rías, during the upwelling transition, coinciding with the practical disappearance of the species on the Portuguese coast (Fig. 8L). Thus in 1989, good conditions for *D. acuta* bloom development seemed to appear along the whole Iberian shelf from Cape Carvoeiro to Cape Finisterre. In contrast, in 2005 (a “normal” year), *D. acuta* was detected in summer but did not reach bloom levels ($>10^3 \text{ cells L}^{-1}$) until the end of the upwelling season (October).

3.4. Small-scale distribution of *D. acuta*

The largest anomalies in *Dinophysis acuta* distribution, in terms of seasonal timing and bloom density were observed in 1989. A

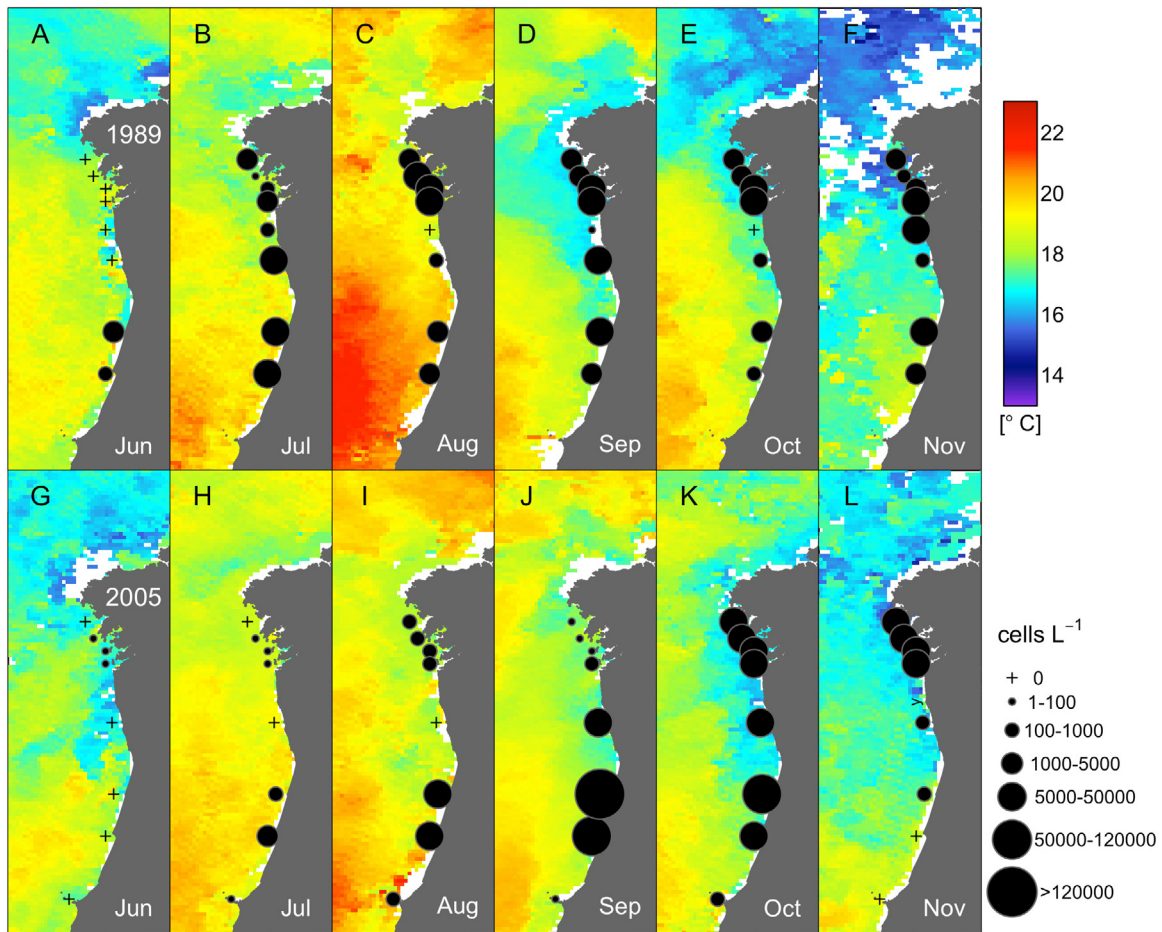


Fig. 8. Monthly evolution, from June to November, of *D. acuta* cell maxima at monitoring sites in Galicia and northern Portugal overlaid on satellite-derived SST (AVHRR monthly average) in 1989 (A–F) and 2005 (G–L).

maximum of 2.2×10^4 cells L⁻¹ in samples collected by integrated (5–10 m) hose samples was observed at station P2 in Ría de Pontevedra in the last week of August (Fig. 9A). To a lesser extent, atypical summer blooms of *D. acuta* also took place in 1990 in the

Rías Baixas, with a maximum of 1.4×10^4 cells L⁻¹ in integrated (10–15 m) hose samples at station P2 in mid-August (Fig. 9B). In both cases, a stable thermal gradient at station P2 was recorded during the six previous weeks. The strongest thermal stratification

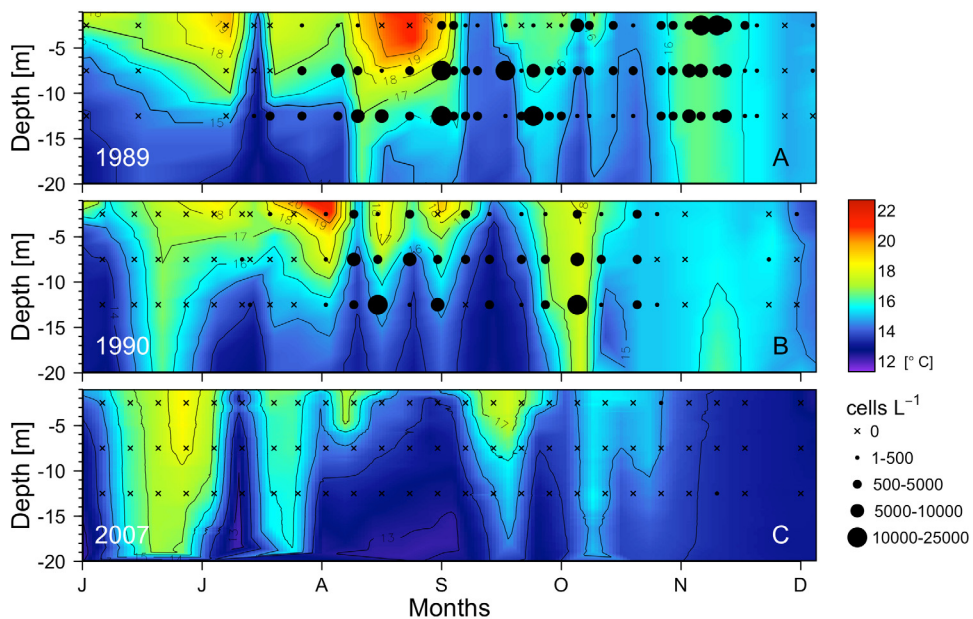


Fig. 9. Vertical distribution of temperature and *D. acuta* cell densities (cells L⁻¹) on integrated samples at three depth intervals (0–5, 5–10 and 10–15 m) at station P2 in Ría de Pontevedra from June to December during (A) 1989, (B) 1990 and (C) 2007. The contour lines represent isotherms at 2 °C intervals.

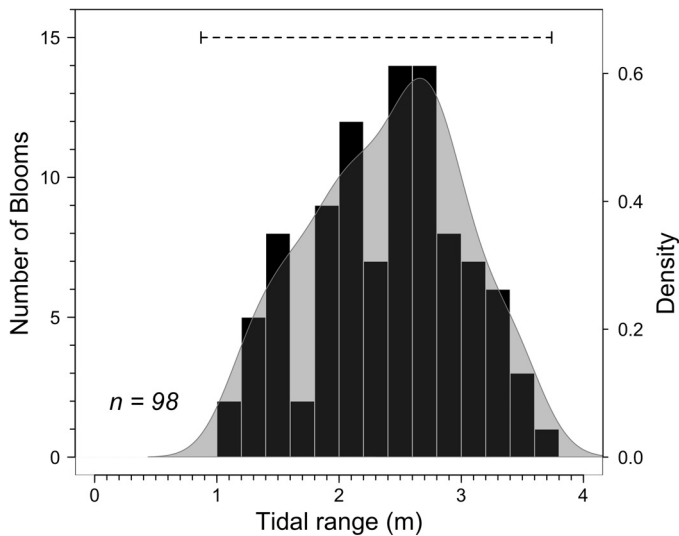


Fig. 10. Histogram of number of blooms of *D. acuta* (>500 cells L⁻¹) recorded versus maximum tidal range observed on the day of a reported bloom in Ría de Pontevedra. The probability density function of the tidal range is also represented (grey polygon). Dashed line on the top shows the difference between minimum and maximum tidal range.

was observed from mid-June to late August in 1989 and 1990, with exceptionally high surface temperatures reaching values >21 °C in August and a thermal gradient of 6 °C between 0 and 20 m (Fig. 9A,B). In contrast, in 2007, an isothermal structure and SST close to 15 °C was observed during most of the summer, and *D. acuta* was not detected (Fig. 9C).

3.5. Lunar cycle and tidal range

Moderate to dense populations of *Dinophysis acuta* (>500 cells L⁻¹, n = 98) occurred within tidal range values from 1.0 to 3.8 m at station P2 in Ría de Pontevedra; 27% of them were observed with values between 2.4 and 2.8 m, showing a unimodal distribution with a mode at 2.6 m (Fig. 10).

The relationship between the distribution of intense *Dinophysis acuta* blooms (>3000 cells L⁻¹, n = 60) and the lunar cycle at the same station (P2 station, Ría de Pontevedra) show that most of the blooms (39%) occurred between days 2 and 5 of the tidal cycle (Fig. 11). This provides evidence of a signal modulated by tidal

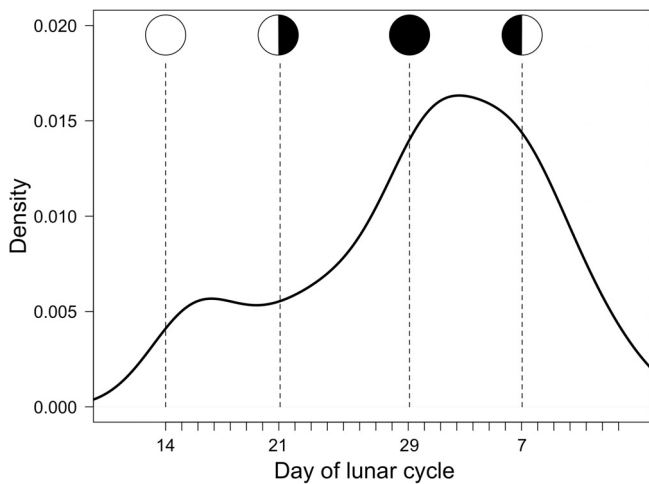


Fig. 11. The probability density function of intense *D. acuta* blooms (>3000 cells L⁻¹) through the lunar cycle at station P2 in the Ría de Pontevedra based on 30-year time series (n = 65). Lunar phases are shown above.

phase. The probability distribution showed a main mode (bloom maxima), on day 3 of the lunar cycle, corresponding to the transition period between new moon and first quarter and characterized by moderate tidal range (~2.5 m).

3.6. Seasonal patterns of *Dinophysis* (*D. acuminata* + *D. acuta*) bloom development

Based on the 30-year time series (1985–2014) of *Dinophysis acuta* and *Dinophysis acuminata* occurrence in Ría de Pontevedra, three seasonal patterns were identified which take place under different climatic scenarios (Fig. 12). The first seasonal pattern is characterized by the occurrence of only *D. acuminata*, with a clear bimodal distribution, with two maxima, in late spring and in late summer-early autumn. This pattern is observed during years with summers cooler than the historic mean (e.g. 1994, 1998, 2002, 2007) (Fig. 12A). In the second seasonal pattern, short-lived blooms of *D. acuta*, associated with longshore transport (e.g. 1987, 2005, 2013), follow *D. acuminata* during the autumn transition (October–November) (Fig. 12B). This second pattern is observed during years with moderate temperatures (above or below the mean) where the balance between heating (warm summer) and upwelling intensity (strong, breaking stratification) did not lead to the appropriate vertical structure. Finally, in the third seasonal pattern, *D. acuta* replaces *D. acuminata* in late summer (August–September) (Fig. 12C). In these cases (e.g. 1989, 1990, 2006) *D. acuta* shows a bimodal distribution, with a first maximum in late summer due to *in situ* growth and another maximum in the autumn transition linked to physical transport. This pattern occurs in years with very hot summers combined with moderate upwelling conditions which lead to increased stratification and deepening of the thermocline.

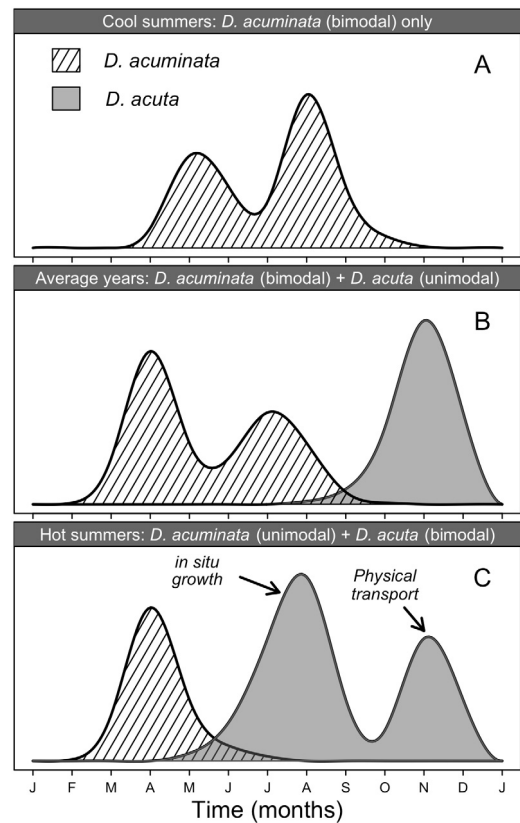


Fig. 12. Seasonal conceptual model representing the evolution of *D. acuminata* and *D. acuta* in the Galician Rías Baixas under three different climatic scenarios: (A) cool summers; (B) average years and (C) hot summers.

Table 1
Akaike's information criterion (AIC) value, generalized cross validation (GCV), R^2 -squared for the fitted model (R^2) and deviance explained (%) for 14 final generalized additive models (GAMs). Low AIC and GCV values indicate best model fit (bold). (CUI_{JJA} = Cumulative Upwelling Index from June to August; SST_{JJA} = monthly average of SST from June to August; Tide = tidal range; Inoculum = *D. acuta* cell densities in July).

Candidate models	AIC	GCV	R^2	Deviance explained (%)
~s(CUI _{JJA})	107.62	2.12	0.03	13.0
~s(SST _{JJA})	103.67	1.83	0.11	14.2
~s(Tide)	85.81	0.99	0.54	57.4
~s(Inoculum)	89.08	1.11	0.46	48.1
~s(CUI _{JJA}) + ~s(SST _{JJA})	102.55	1.81	0.22	32.9
~s(CUI _{JJA}) + ~s(Tide)	86.78	1.04	0.54	59.0
~s(CUI _{JJA}) + ~s(Inoculum)	88.42	1.12	0.52	59.4
~s(SST _{JJA}) + ~s(Tide)	81.44	0.86	0.61	65.6
~s(SST _{JJA}) + ~s(Inoculum)	90.05	1.15	0.46	50.0
~s(Tide) + ~s(Inoculum)	79.20	0.80	0.64	67.9
~s(CUI _{JJA}) + ~s(SST _{JJA}) + ~s(Inoculum)	87.86	1.12	0.55	63.4
~s(CUI_{JJA}) + ~s(SST_{JJA}) + ~s(Tide)	76.03	0.76	0.71	77.3
~s(CUI _{JJA}) + ~s(Tide) + ~s(Inoculum)	80.91	0.86	0.63	68.2
~s(SST _{JJA}) + ~s(Tide) + ~s(Inoculum)	77.35	0.76	0.67	71.7

3.7. Statistical model and predictors for *D. acuta* summer blooms

GAM models based on individual explanatory variables (predictors) showed that four predictors—CUI_{JJA}, SST_{JJA}, tidal range and inoculum—chosen from the descriptive analysis, explained 13%, 14.2%, 48.1% and 57.4% respectively of the deviance in *Dinophysis acuta* summer bloom intensity (Table 1). Using as predictors CUI_{JJA}, SST_{JJA} and tidal range, the model explained 77.3% of the deviance ($R^2 = 0.71$), with tidal range being the most important of them ($p < 0.01$). Likewise, using as predictors SST_{JJA}, tidal range and inoculum, the model explained 71.7% of the deviance ($R^2 = 0.67$). Response plots indicated that the occurrence of moderate to high (10^3 – 10^4 cells L^{-1}) densities of *D. acuta* in summer (“response”) was associated with average (35,000–50,000 $m^3 s^{-1} km^{-1}$) values of CUI_{JJA} (Fig. 13A) and dome-shaped relationship, SST_{JJA} > 17 °C (Fig. 13B), moderate values (~2.5 m) of the tidal range (Fig. 13C) and presence of *D. acuta* cells (inoculum) since early July (Fig. 13D).

4. Discussion

Several studies have suggested a significant global increase of HABs in recent decades (Smayda, 2002a; Hallegraeff, 2010). An increase in HAB impacts has been reported in the Galician Rías associated with a weakening of the Iberian coastal upwelling and increase of water renewal times (Álvarez-Salgado et al., 2008), but there is controversy concerning the weakening trend of the Iberian upwelling (Barton et al., 2013), and interpretations are affected by the geographic location of the observations and the precise interval of time considered (González-Nuevo et al., 2011). Further, HAB reports (all kinds) and days of Galician mussel harvesting closures are very biased due to intensification of monitoring since the early 1990s, and the implementation of new regulations, i.e. control of domoic acid in shellfish since the mid 1990s. Other points to consider are that Álvarez-Salgado et al. (2008) related renewal times with days of harvesting closure during a short period (1998–2006), irrespective of the kind of syndrome (paralytic, diarrhetic or

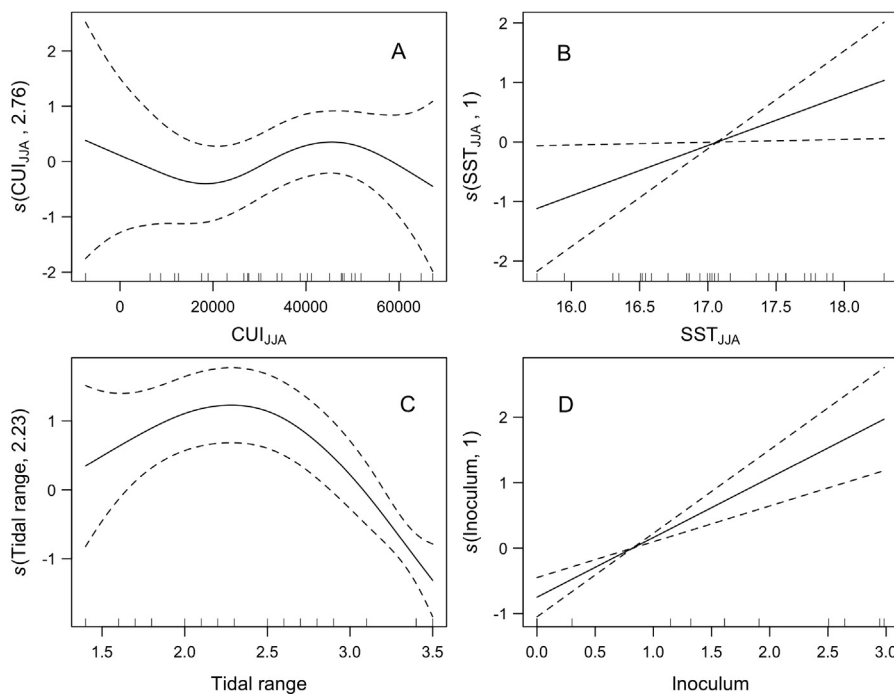


Fig. 13. Final generalized additive models (GAMs) based on single predictors to explain summer blooms of *D. acuta* in the Galician Rías Baixas (A) CUI_{JJA}; (B) SST_{JJA}; (C) Tidal range and (D) Inoculum. Solid lines denote smoothed values and dashed lines on each plot represent 95% confidence intervals. Short vertical lines along the X–X' axes indicate the values at which observations were made. Note that x-scale in D (Inoculum) is a logarithmic scale.

amnesic toxins), and that toxin accumulation by mussels is a complex process affected not only by the cell density and toxin content of the causative agent, but also by the ratio between toxic cells and the total phytoplankton available for filter feeders (Reguera et al., 2011). Hence, decreased primary production and biomass associated with reduced upwelling may indirectly affect toxin accumulation during the upwelling season, when diatoms are dominant, by increasing the toxic algae:total phytoplankton ratio. Nevertheless, the same effect is unlikely during the most intense autumn outbreaks, at the end of the upwelling season, when downwelling circulation brings large swimming dinoflagellates into the Rías and diatoms are displaced to the bottom.

The development of predictive capabilities for HABs requires species-specific predictions of toxic or harmful blooms and knowledge of the species properties which provide competitive advantage under different scenarios (Pitcher, 2012). In the present study we describe the seasonal and interannual variability of *Dinophysis acuta* blooms in relation to climate and test a statistical model using climate indicators as predictors of these blooms.

4.1. Local conditions preceding *D. acuta* bloom development

Descriptive analysis of the 30-year time series of *Dinophysis acuta* in the Galician Rías Baixas, sampled in the same area with the same sampling (tube) method, showed significant interannual variability characterized by some years with only autumn blooms (transport), years with summer (stratified conditions) and autumn blooms, and a predominance of years (20 out of 30) where *D. acuta* cells were hardly detected ($<1 \times 10^2$ cells L⁻¹) or even absent. The most outstanding feature was the exceptional summer–autumn blooms, in terms of early initiation and intensity, recorded in the late 1980s.

Dinophysis acuta blooms in the Galician Rías Baixas and in particular the *in situ* development of summer (August) blooms during the upwelling season, have previously been associated with hotter than average summers and persistent thermal stratification (Reguera et al., 1993; Reguera et al., 1995). These conditions prevailed in July–August during the years (1989, 1990) of exceptional summer blooms. Nevertheless, even more extreme air temperature and SST anomalies were observed in 2003 and 2004 but *D. acuta*, although present in the area, showed negligible summer growth. The main difference between 1989 and 1990 versus 2003 and 2004 was the strong negative anomaly in summer upwelling during the latter. Thus persistent, thermally driven stability on its own is not enough to guarantee summer blooms of this highly seasonal species if it is not accompanied by moderate (close to the mean) summer upwelling. This can be explained by the nutritional behaviour of *Dinophysis* species, obligate mixotrophs that require live ciliate prey and light for sustainable growth (Park et al., 2006), and which can often be prey-limited in the field (Harred and Campbell, 2014; Velo-Suárez et al., 2014). In years of weak summer upwelling, lack of nutrients might limit production of cryptophytes and ciliates, essential to trigger *Dinophysis* growth, and *D. acuta* populations present would only reach low densities, as was the case in summers 2003 and 2004.

The exceptional blooms observed in the summers of 1989/90 exhibited common oceanographic conditions in the Rías during the preceding ~6 weeks: (i) high SST reaching values >21 °C; (ii) moderate (average or slightly above average) summer upwelling pulses; (iii) strong thermal stratification and deepened thermoclines resulting from the previous two and (iv) occurrence of *inoculum* populations detected in the local monitoring samples in early summer. The combination of these environmental conditions seems to have created an optimal scenario that can be exploited by *Dinophysis acuta*. Concerning autumn blooms of *D. acuta*, associated with longshore transport at the end of the upwelling

season (Escalera et al., 2010), these were preceded by the build up of populations off northern Portugal, with its epicentre between Aveiro and Figueira da Foz (Fig. 1B). Conditions in that region, with a wider continental shelf and more stability, are optimal for summer growth of *D. acuta* populations later transported to the Galician region (Moita et al., 2006, 2016).

In addition, we found that *Dinophysis acuta* blooms may be amplified by other factors, such as tidal phase. Exceptional summer blooms took place during the transition from new moon to first quarter, characterized by moderate tidal ranges close to 2.5 m. Several previous studies have identified a relationship between phytoplankton blooms and lunar cycles (Cloern, 1991; Blauw et al., 2012). In a 10-year time series from San Francisco Bay, Cloern (1991) observed an increment in phytoplankton biomass during neap tides and a decline coinciding with spring tides. In contrast in the southern North Sea, Blauw et al. (2012) found that phytoplankton fluctuated in phase with multiple-scales of variability (diurnal, semidiurnal and fortnightly) of the tidal cycle. In the Gulf of Maine, Balch (1981) observed that, in general, diatom blooms coincided with and dinoflagellate blooms followed spring tides. Using historical records of different dinoflagellate species and comparing them with lunar phases and tidal range, Balch identified important geographic differences and ruled out the existence of global patterns (Balch, 1986). More specifically, Cusack et al. (2014) found tides to be the main factor controlling the initiation of *Dinophysis* blooms in Killary Harbour, western Ireland, where the onset of *Dinophysis* events is linked to the spring-neap tidal cycle and the modulation of entrainment. In the Ría de Pontevedra, Díaz et al. (2014) found that short-term variability of *Pseudo-nitzschia* populations and stratification was modulated by semidiurnal and spring–neap tidal signals. Our data support the view that specific lunar phases modulate *D. acuta* bloom intensity in north-western Iberia. Geographic differences are to be expected because maximum tidal range is not always synchronous with the new or full moon, with lags (called “age of the tide”) from hours to days (Souza and Pineda, 2001). These lags exist because tides are determined by the moon phase, but their mode is site specific and related to bottom topography, basin resonance and geographic location (Pond and Pickard, 1978).

4.2. Interannual climate variability and trends in *Dinophysis* populations

Interannual fluctuations related to long-term climate cycles, such as the NAO, affect coastal upwelling systems through modification of seasonal upwelling–downwelling strength (GEO-HAB, 2011).

Results here show that the intense summer blooms of *Dinophysis acuta* observed in the late 1980s coincided with the highest solar activity and positive phase of the NAO in the last three decades. Subsequent solar cycles have been weaker (Fig. 2A), and there have been no corresponding summer blooms of *D. acuta*. Belgrano et al. (1999) linked abundance of *D. acuta* in the Skagerrak, western Sweden, to periods of positive values of the NAO, and suggested that large-scale climatic processes govern the interannual variability of *D. acuta*, ruling out the hypothesis of an increasing trend in recent decades. Naustvoll et al. (2012) observed a decrease of *D. acuta* numbers on the southern Norwegian coast on the basis of a 25-year time series (1985–2010). Concerning *Dinophysis* spp. blooms in the North Sea, a spatial shift of their epicentre from the east to the west, rather than increased frequency or abundance, was reported by (Edwards et al., 2006).

There is evidence that variations in solar activity affect different biological processes including pelagic fisheries yields (Guisande et al., 2004), recruitment of fish populations (Santos et al., 2012) and phytoplankton cycles (Bondarenko and Evstafeyev, 2006).

Despite the fact that variation in total solar irradiance through the 11-year solar cycle (sunspot cycle) is only ~0.1%, its effects on climate may be important (Lean, 2010), and include changes in sea surface temperature (White et al., 1997) and zonal wind shifts affecting upwelling patterns (Rind et al., 2008). Information on HABs and solar activity is limited and their relationship with solar cycles is unknown. No clear relationships between *Dinophysis acuta* bloom frequency or intensity and solar activity (sunspot cycles) or NAO indices were found in the time series studied here.

The exceptional summer blooms of *Dinophysis acuta* observed in the late-1980s, in terms of early initiation and intensity, seem to be coupled to a short-term weather anomaly driven by large-scale atmospheric and oceanographic processes. Exceptional hydroclimatic conditions linked to exceptional dinoflagellate blooms were recorded, also in the late 1980s, in other Atlantic European regions (Edwards et al., 2006), which suggests that these events were modulated by mesoscale atmospheric processes (Kerr, 1997). This is supported by further studies documenting hydroclimatic anomalies (positive NAO index and warm SST) in the 1989/91 period, affecting a large portion of the European Atlantic coast, and which take place episodically over a time scale of decades (Becker and Dooley, 1995; Edwards et al., 2002). In addition, Becker and Dooley (1995) described strong positive SST and salinity anomalies along the Atlantic coasts during December 1988.

It is known that density stratification suppresses turbulence and creates stable vertical gradients optimal for development of *Dinophysis* populations (Maestrini, 1998; Reguera et al., 2012). Results here show that strong thermal stratification and deepened thermoclines, combined with average upwelling conditions observed during July–August 1989/90 promoted *Dinophysis acuta* growth on the adjacent shelf, the region where this neritic species reaches maximal densities (Palma et al., 1998; Moita et al., 2006). The “pelagic seed banks” (sensu Smayda, 2002b) of *D. acuta* then inoculated near shore habitats, leading to formation of intense summer blooms detected in all the Galician Rías Baixas (Reguera et al., 1995). These anomalous conditions, which were most intense during summer 1989, also triggered exceptionally high density green tides of a naked green dinoflagellate—misidentified as *Gyrodinium* cf. *aureolum* (Jiménez et al., 1992)—later identified as *Lepidodinium viride* (S. Fraga pers. comun.) and other dense blooms of an unidentified *Gymnodinium* species. The green dinoflagellate bloom, which later co-occurred with patches of *Heterosigma akashiwo*, formed conspicuous olive-green patches within a microphytoplankton community dominated by diatoms (*Leptocylindrus* spp.) (Pazos et al., 1995; Reguera et al., 1995). These anomalies were observed in Iberian coastal waters from June to August 1989, coinciding with the summer development of the *D. acuta* bloom. Cloern et al. (2005) described a similar mechanism to explain an exceptional summer bloom of *Akashiwo sanguinea* in San Francisco Bay associated with an upper-level high-pressure anomaly off the US west coast resulting in weak coastal upwelling. These authors observed that positive anomalies in thermal stratification coincided with four consecutive days of high air temperature and weak winds coupled with a low-energy neap tide.

In coastal upwelling systems, large-scale climatic anomalies may produce changes in the timing of upwelling (Pierce et al., 2006; Schwing et al., 2006; Bograd et al., 2009), triggering eventual ecosystem responses (Barth et al., 2007), the intensity of which may vary across functional groups and multiple trophic levels (Edwards and Richardson, 2004). Wyatt and Zingone (2014) reviewed how dynamical behaviour of biological populations is the sum of effects due to events with different frequencies in combination with endogenous regulation. Thus, the impact of environmental forcing will depend on the relative magnitude of intrinsic population growth versus environmental forcing.

In Galician coastal waters, changes in upwelling rates and their effects on different trophic levels are well documented (Guisande et al., 2001; Álvarez-Salgado et al., 2008; Pérez et al., 2010). Díaz et al. (2013) found that exceptional early spring blooms of *Dinophysis acuminata* were associated with anomalous winter wind patterns (dominance of northerlies) promoting an early onset of the upwelling season. The exceptional summer blooms of *Dinophysis acuta* described here did not appear as a simple linear response to specific upwelling patterns, but promoted by a combination of favourable physical drivers, such as a moderate upwelling index and strong thermal stratification, creating “windows of opportunity” sensu Lasker (1978) for this species. Thus, the two species of *Dinophysis* may show phenological changes and develop exceptional blooms under different kinds of anomalies: unusual (out of season) predominance of upwelling in winter in the case of *Dinophysis acuminata* and a combination of average (close to the historic mean) upwelling intensity, positive SST anomalies and stable thermal stratification in summer in the case of *D. acuta*. In fact, phenological changes (early initiation) and an increasing trend in *D. acuminata* bloom intensity have been observed in the last years in the Galician Rías Baixas (Fig. S2) along with a reversal of the “weakening trend” in upwelling strength (data not shown) reported by Álvarez-Salgado et al. (2008).

4.3. Statistical models and implications for predictive capabilities

There is a need to apply models to determine the influence of long-term changes on the presence of HABs and assess the possible use of climate indicators as predictors of HABs in different hydrodynamic systems (GEOHAB, 2011). A main gap in our knowledge of the population dynamics of *Dinophysis acuta* in the Galician Rías is to identify climate factors, operating over multiple time scales, which affect its interannual variability, in particular the development of exceptional summer blooms.

Raine et al. (2010) proposed a conceptual model for prediction of *Dinophysis* blooms in south-western Ireland, based on the sequence of winds that result in water exchanges advecting populations into the bays. Vale (2012) proposed two simple models to explain accumulation of diarrhetic shellfish poisoning toxins (DSTs) using a 10-years time series based on control by rainfall and wind forcing in Aveiro lagoon, Portugal. Recently, Velo-Suárez et al. (2014) presented a conceptual model that combined physical (upwelling) and biological (predator–prey interactions) drivers to explain initiation and maintenance of *Dinophysis acuminata* blooms in the Galician Rías during the whole upwelling season. Here we propose a statistical model (GAM) to help explain exceptional summer blooms of *D. acuta* in the Galician Rías Baixas on the basis of three-predictors—SST_{JJA}, CU_{JJA} and tidal range (proxy for the lunar cycle)—provided the inoculum (*D. acuta* cells in early July) is present. This information can be very useful for prediction purposes and management decisions.

The presence of inoculum cells is an obvious requirement, but is perhaps the most difficult factor to predict; *Dinophysis acuta* cells seem to disappear from the whole northwestern Iberia region in some years. Moita et al. (2016) suggest that a strong positive upwelling anomaly in 2008 probably caused an equatorward displacement of the core population, which may explain a four-years gap (2009–2012) of *D. acuta* blooms in the following years in northern Portugal. This putative displacement of the core population coincided with the absence of *D. acuta* from Galician waters from 2007 to 2012. The presence/absence of the species during summer in the epicentre region (Aveiro-Figueira da Foz), reported from the Portuguese monitoring programme, may therefore be used as a valuable tool for early warning of *D. acuta* blooms in Galician waters.

Finally, we should note that circulation models are able to describe the response of shelf stratification and along- and across-shore transport to variations in atmospheric and tidal forcing (Ruiz-Villarreal et al., 2016), factors that we have identified in this work as drivers of interannual variability in *Dinophysis acuta* populations. Therefore, circulation model outputs combined with *D. acuta* reports from its epicentre area in Portugal, would make it possible (a) to use hindcast simulations of interannual variability of oceanographic conditions to study *D. acuta* ecology and (b) develop predictive simulations on the variability of oceanographic conditions that might serve as early warning of *D. acuta* events.

5. Conclusions

Stable thermal stratification during July–August is necessary for the build up of summer (August) populations of *Dinophysis acuta* in the northwest Iberian coastal upwelling region. The development of these populations to form exceptional summer blooms in the Galician Rías appears related to an optimal combination of SST ($>17^{\circ}\text{C}$), deepened thermoclines (>6 weeks) and values of upwelling close to or slightly higher than the historical average. The first two conditions accompanied by weak upwelling lead to bloom failure presumably due to prey limitation. A dome-shaped relationship was found between summer upwelling intensity and *D. acuta* blooms. A clear signal appears in the local response associated with lunar phase (bloom maxima 3 days after neap tides). The application of a generalized additive model based on biological (*D. acuta* inoculum) and environmental predictors (Cumulative June–August upwelling CUI_{JJA} , average June–August SST_{JJA} , and tidal range) explained more than 70% of deviance for these exceptional summer blooms, through a combination of moderate ($35,000\text{--}50,000\text{ m}^3\text{ s}^{-1}\text{ km}^{-1}$) summer upwelling (CUI_{JJA}), $\text{SST}_{\text{JJA}} > 17^{\circ}\text{C}$, moderate tidal range ($\sim 2.5\text{ m}$) and July occurrence of *D. acuta* cells on the Galician shelf.

There was no evidence of an increasing trend in *Dinophysis acuta* bloom frequency or intensity but of intensity of *Dinophysis acuminata* blooms; this supports the need of a species-specific approach to the study of HABs and climate.

The exceptional summer blooms of 1989–1990 were linked to extreme hydroclimatic anomalies affecting most of the European Atlantic coast and which take place episodically on decadal time scales.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.hal.2015.11.007](https://doi.org/10.1016/j.hal.2015.11.007).

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