Control of lipophilic shellfish poisoning outbreaks by seasonal upwelling and continental runoff

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Abstract

Closures of mussel rafts in the Ría de Ares–Betanzos (NW Spain) because of the occurrence of lipophilic shellfish poisoning outbreaks over the period 1999–2007 have been studied in relation to the coastal wind and precipitation regimes of the area. More than 85% of the episodes concentrate on the summer and autumn that coincide with the upwelling–favourable/dry season and the transition to the downwelling–favourable/wet season, respectively. We obtain that the percentage of days closed in summer can be predicted by the average continental runoff (Q_r) during the preceding spring (86% of the variance explained by the average Q_r of May) and the percentage of days closed in autumn by the average offshore Ekman transport (Ek_L) during the preceding summer (91% of the variance explained by the average Ek_L of August). A rainy spring will produce extensive closures in summer and a windy summer extensive closures in autumn. We speculate that this seasonal lag between atmospheric forcing and lipophilic shellfish poisoning outbreaks, which provides a chance to forecast mussel toxicity, is compatible with the obligate mixotrophic nutritional mode of the *Dynophysis acuminata* complex, the dominant lipophilic shellfish poisoning species in the Ría de Ares–Betanzos.

Keywords: HABs, lipophilic shellfish poisoning, upwelling, continental runoff, NW Spain

1. Introduction

The eastern boundary coastal upwelling systems of W Iberia–NW Africa, Namibia–Benguela, Peru–Chile and California–Oregon are among the most productive marine ecosystems: they represent <1% of the ocean surface area but support >10% of the ocean new production (Chavez and Togweiler, 1995) and >20% of the global fish catches (Rykaczewski and Checkley, 2008). However, harmful algal blooms (HABs) frequently occur in these areas under suitable hydrographic and dynamic conditions (Pitcher et al., 2010) causing major economic losses in fisheries and aquaculture (GEOHAB, 2005), a circumstance that strongly motivates research directed to improve our capability to forecast HAB incidence in upwelling systems (e.g. Lane et al., 2009).

The Galician coast (NW Iberia) is at the northern limit of the eastern boundary upwelling system of the NE Atlantic. At these latitudes, 42°–44°N, coastal winds describe a seasonal cycle characterised by upwelling favourable north–easterly winds from March–April to September–October and downwelling favourable south–westerly winds the rest of the year (Wooster et al., 1976; Torres et al., 2003). The topography of the Galician coast is particularly intricate, with a total of 18 coastal inlets, named rías, of varied topography and hydrographic regime (Fig. 1). The rías are extraordinary sites for the culture of the blue mussel *Mytilus galloprovincialis* on hanging ropes: on the one side, high quality plankton biomass is produced into the rías due to fertilisation by coastal upwelling; and, on the other side, the topography of the rías provides protection to the mussel rafts against intense northerly winds during the upwelling season and storms during the downwelling season (Figueiras et al., 2002; Álvarez-Salgado et al., 2008). In fact, about 250,000 tons of blue mussels are extracted from the rías of Vigo, Pontevedra, Arousa, Muros–Noia and Ares–Betanzos every year (Labarta et al., 2004). The main threat for the mussel raft culture is the recurrent appearance of HAB species that produce lipophilic toxins that are transferred through the food web,

and even at low densities ($<10^3$ cell l^{-1}) can be accumulated by shellfish above regulatory levels, causing the closure of the cultivation areas to mussel extraction. Okadaic acid and pectenotoxins mainly produced by *Dinophysis acuminata* + *Dinophysis sacculus*, i.e. the *D. acuminata* complex, and *Dinophysis acuta*, are the main responsible of those closures (Reguera et al., 2003; 2007). Both species are present, though habitually in low numbers, in the Galician rías over the upwelling season, and *D. acuta* also appears during the short downwelling episodes that occur at the end of the upwelling season in September and October (Reguera et al., 1995). Dense blooms of the yessotoxins producer *Lingulodinium polyedrum* are also common in the northern rías in summer (Arévalo et al., 2006).

The Ría de Ares–Betanzos is one of the V-shaped inlets located in the Galician coast (Fig. 1). The topography of this embayment is complex, with a shallow (<10 m) inner part divided in two branches, Ares and Betanzos, and a deeper outer part, where both branches converge that is freely connected to the adjacent shelf. The total volume of the ría is 0.65 km^3 , the surface area 52 Km^2 , and the maximum depth of 43 m is reached at the open end. From the hydrographic point of view, the two inner branches can be considered as estuaries: Ares being the estuary of River Eume, with a long-term average flow of $16.5\text{ m}^3\text{ s}^{-1}$, and Betanzos being the estuary of River Mandeo, with a long-term average flow of $14.1\text{ m}^3\text{ s}^{-1}$ (Prego et al., 1999; Sánchez-Mata et al., 1999; Gómez-Gesteira and Dauvin, 2005). On the contrary, the outer ría behaves like an extension of the adjacent shelf and responds to the intensity, persistence and direction of coastal winds (Bode and Varela, 1998). Mussel cultivation areas are located in the southern side of this ría, specifically in Arnela and Lorbé (Fig. 1), with a total of 40 and 107 rafts respectively, which produce about 10,000 metric tons of mussels per year (Labarta et al., 2004). The recurrence of lipophilic shellfish poisoning episodes over the

summer and autumn dramatically affects the commercial exploitation of this culture (Mariño et al., 1985; Reguera et al., 2007).

Recently, Álvarez-Salgado et al. (2008) have shown that the closures of mussel cultivation areas in the rías of Vigo, Pontevedra, Arousa and Muros-Noia, collectively known as Rías Baixas, are linked to the wind pattern of the adjacent shelf, which controls the flushing times of these large coastal inlets. The present work will show a somewhat different picture for the relationship between the meteorological conditions and the incidence of harmful phytoplankton species on the mussel culture in the comparatively smaller Ría de Ares-Betanzos. Coastal wind and continental runoff regimes will be raised as descriptor variables to forecast the closure of mussel raft polygons to extraction because of lipophilic shellfish poisoning toxicity.

2. Materials and Methods

2.1. Ekman transport off NW Spain

The West-East (Q_X , in $\text{m}^2 \text{s}^{-1}$) and South-North (Q_Y , in $\text{m}^2 \text{s}^{-1}$) components of the Ekman transport off NW Spain have been calculated following Bakun's (1973) method:

$$-Q_X = -\frac{\rho_A \cdot C_D}{\rho_W \cdot f} \cdot \sqrt{V_X^2 + V_Y^2} \cdot V_Y \quad (1)$$

$$Q_Y = -\frac{\rho_A \cdot C_D}{\rho_W \cdot f} \cdot \sqrt{V_X^2 + V_Y^2} \cdot V_X \quad (2)$$

where ρ_A is the density of air (1.22 kg m^{-3} at 15°C); C_D is an empirical dimensionless drag coefficient ($1.4 \cdot 10^{-3}$ according to Hidy, 1972); f is the Coriolis parameter ($9.946 \cdot 10^{-5} \text{ s}^{-1}$ at 43° latitude); ρ_W is the density of seawater ($\sim 1025 \text{ kg m}^{-3}$); and V_X and V_Y are the average daily westerly and southerly components of the geostrophic wind in a $2^\circ \times 2^\circ$ cell centred at $43^\circ\text{N } 11^\circ\text{W}$, representative for the study area (Fig. 1). Average daily geostrophic winds were estimated from atmospheric surface pressure charts,

provided at 6-hour intervals by the Spanish Institute of Meteorology. Upwelling-favourable offshore Ekman transport matches up positive values of $-Q_x$ and Q_y in the western and northern coasts, respectively. Conversely, negative values of $-Q_x$ and Q_y indicate downwelling-favourable onshore Ekman transport in the western and northern coasts, respectively.

$-Q_x$ and Q_y were rotated 30° clockwise to produce a longitudinal ($-Q_L$) and a transversal (Q_T) component of the Ekman transport to the main axis of the Ría de Ares-Betanzos (Fig. 1). Therefore, a positive value of Ek_L ($= -Q_L$) indicates an offshore Ekman transport and a negative value of Ek_L and onshore Ekman transport in this coastal inlet.

2.2. Continental runoff to the Ría de Ares-Betanzos

Continental runoff to the Ría de Ares-Betanzos is mostly a combination of the discharges of rivers Eume and Mandeo (Fig. 1). The flow at the mouth of River Mandeo was estimated from gauge station n° 464 at Irixoa, hold by Augas de Galicia (Galician Government). The Horton's Law (Strahler, 1963) was applied by considering the proportion between the corresponding drainage basin areas: 248.21 Km² at the gauge station and 456.97 Km² at the river mouth. The volume of River Eume is a combination of regulated and natural flows. Daily volumes of the Eume reservoir, which controls 80% of the drainage basin, were provided by ENDESA S.A., the company in charge of the management of the reservoir. The natural component of River Eume flow was estimated from the River Mandeo flow by applying again the Horton's Law, considering that the drainage basin of River Eume not controlled by the reservoir is 94.04 Km².

2.3. Safety of the cultivation of blue mussels in Ría de Ares–Betanzos

In compliance with European Directives, and using the standard mouse bioassay method of Yasumoto 1978 entrusted to the “Instituto Tecnolóxico para o Control do Medio Mariño” (INTECMAR), mussel extraction is forbidden by the Galician Government when toxin levels exceed the regulatory level. Mussel rafts in the Ría de Ares–Betanzos are grouped in two areas: Lorbé and Arnela (Fig. 1). Over the period 1999–2007, mouse bioassays were performed by INTECMAR in 1 sampling point in Arnela and 2 sampling points in Lorbé. The toxins causing the closures, Amnesic Shellfish Poisoning (ASP), Lipophilic Shellfish Poisoning or Paralytic Shellfish Poisoning (PSP) were also reported.

3. Results

3.1. Seasonal and interannual variability of the duration of shellfish harvesting closures in mussel cultivation areas

Over the period 1999–2007, the cultivation area of Lorbé was closed to mussel extraction a total of 1143 days (34.8% of the time) because of the occurrence of HAB episodes, with lipophilic shellfish poisoning toxicity causing 85.7% of the closures (Fig. 2a). In contrast, the area of Arnela was closed 846 days (25.7% of the time), 80.5% of them due to lipophilic shellfish poisoning toxicity (Fig. 2b).

A consistent seasonal cycle was observed in the number of days per month that the mussel cultivation areas were closed to extraction because of lipophilic shellfish poisoning outbreaks: more than 85% of the days concentrate in the summer and autumn (Fig. 3a). Marked interannual differences occurred in the closures, ranging from 13.9 to 57.8% of the year in Lorbé and from 3.0% to 40.5% of the year in Arnela over the study period (Fig. 3b).

Significant positive correlations were observed between the two sites at both the seasonal (Fig. 3c; $r^2 = 0.92$, $p < 0.001$, $n = 12$) and interannual (Fig. 3d; $r^2 = 0.94$, $p < 0.001$, $n = 9$) time scales.

3.2. Seasonal and interannual variability of offshore Ekman transport and continental runoff

Monthly average values of Ek_L (Fig. 2c) over the study period describe a seasonal cycle characterised by negative figures over the autumn, winter and spring, which are minimum in December and January (below $-0.60 \text{ m}^2 \text{ s}^{-1}$; Fig. 4a), and positive figures over the summer, which are maximum in August (above $0.25 \text{ m}^2 \text{ s}^{-1}$; Fig. 4a). This seasonal cycle explains 28% of the total variability of the monthly time series ($r^2 = 0.28$, $p < 0.001$, $n = 108$). At the annual time scale, downwelling-favourable onshore Ekman transport dominate over upwelling-favourable offshore Ekman transport periods, resulting in negative annual average values of Ek_L ranging from -0.46 in 2002 to 0.00 in 2005 (Fig. 4b). A significant increase of the annual average Ek_L is observed from 1999 to 2007 ($r^2 = 0.45$, $p < 0.05$, $n = 9$). Therefore, strictly speaking, the Ría de Ares-Betanzos should be classified as a coastal downwelling rather than a coastal upwelling system.

For the case of the monthly average values of continental runoff, calculated as the sum of the flows of the rivers Eume and Mandeo (Fig. 2d), wet and dry seasons can be defined encompassing the downwelling- and upwelling-favourable seasons observed in Ek_L (Fig. 2c). A significant negative correlation was observed between Q_r and Ek_L at the monthly time scale ($r^2 = 0.42$, $p < 0.001$, $n = 108$). The seasonal cycle of Q_r (Fig. 4c) explains 34% of the total variability of the monthly time series ($r^2 = 0.34$, $p < 0.001$, $n = 108$). Annual average Q_r ranges from $54 \text{ m}^3 \text{ s}^{-1}$ in 2001 to $23 \text{ m}^3 \text{ s}^{-1}$ in 2005 (Fig. 4d).

3.3. Linking the occurrence of lipophilic shellfish poisoning outbreaks to meteorological conditions

More than 80% of the closures of the mussel raft cultivation areas of the Ría de Ares-Betanzos over the period 1999–2007 were due to lipophilic shellfish poisoning episodes and more than 85% of those closures concentrate on the summer and autumn months (Fig. 3a). As a result, we will focus this section on lipophilic shellfish poisoning toxicity in Lorbé, where 73% of the mussels rafts are located, from June to November.

Since Ek_L and Q_r describe well-defined coupled seasonal cycles, with June–August being the upwelling-favourable/dry season (Fig. 4a, c), closure days have been grouped using this criterion. Therefore, we have considered, on one side the percentage of the time that the mussel raft cultivation areas were closed during the summer (June–July–August, JJA) and, on the other side, the percentage of the time that they were close during the autumn (September–October– November, SON), which is part of the downwelling favourable/wet season. To asses the dependence of the percentage of the summer and autumn that mussel raft cultivation areas were close to extraction on the meteorological conditions, a correlation analysis with Ek_L and Q_R was preformed.

For the case of the summer, the best descriptor of the percentage of days closed to extraction in Lorbé was the continental runoff during the previous spring, specifically the average Q_r for May. This simple positive relationship (Fig. 5a), was able to explain 86% of the interannual variability from 1999 to 2007 ($r^2 = 0.86$, $p < 0.0003$, $n = 9$). Therefore, the higher Q_r , the higher the number of days that the rafts were closed to mussel extraction over the next summer. In the particular case of the year 2006, the average Q_r of April and May was used as a predictor variable. Note that the ratio of the continental runoff in May versus April was >0.50 , except for 2006 when an anomalously low value of 0.25 was obtained (Fig. 2 c). If the continental runoff of May

is used for 2006, the relationship between Q_r and the percentage of days closed to extraction in Lorbé would be still highly significant ($p < 0.005$) but it would explain only 70% of the interannual variability.

For the case of the autumn, the best descriptor was the offshore Ekman transport over the preceding summer, specifically the average Ek_L for August (Fig. 5b), that explains 91% of the observed interannual variability ($r^2 = 0.91$, $p < 0.0002$, $n = 8$) for $Ek_L > 0$, i.e. for those years when coastal upwelling prevails in August. Again, the higher Ek_L , the higher the number of days that the rafts were closed to mussel extraction over the next autumn. In 2004, when the average Ek_L was $-0.4 \text{ m}^2 \text{ s}^{-1}$ (black dot in Fig. 5a), the percentage of days closed was 30%. This percentage is about the same than when Ek_L is nil, suggesting that it would be considered as a threshold for the Ría de Ares–Betanzos independently of the wind regime.

4. Discussion

4.1. Ecological basis for the meteorological control of lipophilic shellfish poisoning toxicity in the Ría de Ares–Betanzos

The observed seasonal lag between spring continental runoff, summer upwelling and the closure of mussel rafts in the Ría de Ares–Betanzos can hardly be explained on basis of the traditional arguments of in situ growth in a stratified water column or accumulation by advection processes (Reguera et al., 1995; Pitcher et al., 2010). Given that the flushing time of water in the Ría de Ares–Betanzos is about 1 week (Villegas-Rios et al., accepted), haline stratification in the summer as a consequence of spring continental runoff or thermal stratification in the autumn as a consequence of moderate summer upwelling are not valid arguments. We hypothesize the explanation for the seasonal lag requires appealing to microplankton species able to produce lipophilic shellfish poisoning that display a mixotrophic nutrition mode. In

this sense, the *D. acuminata* complex is the lipophilic shellfish poisoning species repeatedly recorded in the Ría de Ares–Betanzos (Mariño et al., 1985; Reguera et al., 1993). *D. acuta* is usually limited to the south of Cape Fisterra, showing higher abundances in the Rias Baixas at the time of the seasonal upwelling–downwelling transition (Reguera et al., 1993; 1995) and peaking in its main growing area off Aveiro (Portugal) in late summer during the upwelling season (Moita et al., 2006). Although isolated cells of the *D. acuminata* complex can be found in the water column during the whole year, higher abundances in the Ría de Ares–Betanzos roughly coincide with the growing season of phytoplankton (Mariño et al., 1985; Reguera et al., 1993). Specifically, the *D. acuminata* complex begins to be important after the diatom spring bloom and remains as a significant component of the microplankton community until October–November. It often shows a second maximum in abundance at the end of the summer, coinciding with a second diatom maximum. Thus, the *D. acuminata* complex is a regular member of the microplankton community of the rías that flourishes following the spring bloom and in which dinoflagellates and ciliates, including *Myrionecta rubra* (*Mesodinium rubrum*), progressively acquire importance (Figueiras and Pazos, 1991; Figueiras and Ríos, 1993; Figueiras et al., 2002).

D. acuminata, as well as other species of the genus *Dinophysis* containing chloroplasts (Hallegraeff and Lucas, 1998; Nagai et al., 2008; Nishitani et al., 2008a; 2008b), is an obligate mixotroph that grows well in the presence of its prey (*Myrionecta rubra*) and light (e.g. Park et al., 2006; Kim et al., 2008). However, it shows lower growth rates at high light without prey and fails to grow in darkness. As observed with other species of *Dinophysis* (Nishitani et al., 2008a; 2008b), enhanced growth of *D. acuminata* without prey could also occur during a few days following heavy feeding, to then decline progressively. Therefore, *D. acuminata* in natural environments could grow actively when food is enough and would use photosynthesis for maintenance at

lower growth rates in the absence of food (Gisselson et al., 2002; Carvalho et al., 2002; Riisgaard and Hansen, 2009). Mixotrophy has been also reported for the yessotoxins producer *Lingulodinium polyedrum* (Burkholder et al., 2008), which from occasionally forms dense blooms in the Ría de Ares-Betanzos in summer (Arévalo et al., 2006).

This interpretation is, at present, highly speculative because it mainly comes from culture observations in the laboratory and no other potential preys have been identified yet. However, it could be useful to understand the relationships reported here between continental runoff, upwelling and lipophilic shellfish poisoning toxicity in mussel rafts in the Ría de Ares-Betanzos. Both spring continental runoff and summer coastal upwelling would fertilize the ría with the inorganic nutrients needed to support phytoplankton blooms (Prego et al., 1999), which could supply the food required by the *D. acuminata* complex to grow actively and, therefore, cause mussel toxicity. Note that the offshore Ekman transport is negative, i.e. unfavourable for the development of the diatom spring bloom, until May (Fig. 4a). By contrast, continental runoff in May is still high enough, average ± 1 std of $28 \pm 19 \text{ m}^3 \text{ s}^{-1}$ (Fig. 4c), to provide the nutrients required for phytoplankton growth. Considering that the inorganic nitrogen concentration in the rivers draining into the Ría de Ares-Betanzos is about 65 mmol m^{-3} (Prego et al., 1999), the average nitrogen supply to the ría during May would be about 1.8 mol s^{-1} . Distributing this flux over the 42.4 Km^2 of free surface area from the inner reaches of the ría to Lorbé, the resulting concentration would be $3.7 \text{ mmol m}^{-2} \text{ d}^{-1}$ of N. Assuming that the phytoplankton of the Ría de Ares-Betanzos follows the Redfield composition $\text{C}_{106}\text{H}_{274}\text{O}_{46}\text{N}_{16}\text{P}$ (Fraga et al., 1998), complete consumption of the inorganic nitrogen supplied by continental runoff would lead to a new production of about $300 \text{ mg C m}^{-2} \text{ d}^{-1}$ or $9.1 \text{ g C m}^{-2} \text{ month}^{-1}$. The influence of other factors than inorganic nutrients supplied by runoff can not be disregarded (e.g. organic nutrients; Carlsson et al., 1999). In the summer, the offshore Ekman transport is relatively intense

only in August, average ± 1 std of $0.25 \pm 0.43 \text{ m}^2 \text{ s}^{-1}$ (Fig. 4a). Again, considering that the inorganic nitrogen concentration in the Eastern North Atlantic Central Water (ENACW) that upwells in the Ría de Ares-Betanzos is 5 mmol m^{-3} (Prego et al., 1999) and that the wideness of the ría at Lorbe is 5 Km, the average nitrogen supply during August would be about 6 mol s^{-1} or $12.7 \text{ mmol m}^{-2} \text{ d}^{-1}$ of N. Since only 50% of the inorganic nitrogen supplied to the Ría de Ares-Betanzos under upwelling conditions is consumed there (Villegas-Rios et al., accepted), a new production of about $500 \text{ mg C m}^{-2} \text{ d}^{-1}$ or $15 \text{ g C m}^{-2} \text{ month}^{-1}$ is obtained.

The prevalence of toxicity in the mussel rafts during the 3 months following the nutrient supplied by the continental runoff of May and the coastal upwelling of August, when presumably the abundance of the *D. acuminata* complex is low, could be related to the high cell toxicity that is commonly observed at low cell abundance (Lindahl et al., 2007; Pizarro et al., 2008).

4.2. Oceanographic basis for the contrasting patterns of lipophilic shellfish poisoning toxicity between the Ría de Ares– Betanzos and the Rías Baixas

Whereas in the Ría de Ares-Betanzos both continental runoff and offshore Ekman transport reveal as predictor variables for the occurrence of lipophilic shellfish poisoning episodes, in the Rías Baixas only the second is significant (Álvarez-Salgado et al., 2008). The Ría de Ares-Betanzos, located in the Artabro Gulf, exhibits marked geomorphologic, hydrographic, and dynamic differences with the Rías Baixas, located between the River Miño and Cape Fisterra (Fig. 1). According to Torre-Enciso (1958), whereas the Ría de Ares-Betanzos was formed mainly by the erosive action of the rivers Eume and Mandeo, the origin of the Rías Baixas is essentially tectonic. Consistently, the relevance of continental runoff for the hydrography and dynamics of the Ría de Ares-Betanzos is larger than for the Rías Baixas: the relationship between

the annual average river discharge (Q_r , in m^3) and the volume (V , in m^3) of the Ría de Ares-Betanzos is $Q_r/V = 1.5$ and for the Rías Baixas the ratio is <0.7 (Table 1). It is also noticeable the gradient observed in the Rías Baixas: the ratio is about 0.7 for Muros-Noia and Arousa, the northernmost rías, and about 0.2 for Vigo and Pontevedra, the southernmost rías (Fig. 1). Therefore, considering these Q_r/V values and the role of rivers supplying nutrients, it seems reasonable that continental runoff arises as a predictor variable of DSP episodes only in the Ría de Ares-Betanzos.

Another relevant geomorphologic difference between the Ría de Ares-Betanzos and the Rías Baixas is the orientation of the coast: the main axis of the former is oriented in the NW-SE direction and the mouth of its open end is perpendicular to the main axis, whereas the latter are oriented in the SW-NE direction and their open ends are oriented in the N-S direction (Fig. 1). As a consequence, while north-easterly winds are the most favourable for coastal upwelling in the Ría de Ares-Betanzos, northerly winds dictate upwelling in the Rías Baixas. In this sense, the 1999-2007 average upwelling season was 50% shorter (3 versus 6 months) and about 40% weaker (0.10 versus $0.16 \text{ m}^2 \text{ s}^{-1}$) in the Ría de Ares-Betanzos (as calculated from $-Q_L$) than in the Rías Baixas (as calculated from $-Q_X$) (Table 1). However, as for the case of continental runoff, to properly compare the impact of wind-driven upwelling on the rías, the ratio $D \cdot E_k/V$ has been used. D is the wideness of the open end of the ría under consideration and E_k is the average volume of water upwelled in the ría during the upwelling season, i.e. $-Q_X$ for the case of the Rías Baixas and $-Q_L$ for Ares-Betanzos (Table 1). Following Álvarez-Salgado et al. (2008), D has been corrected for the effect of the islands on the free exchange of water with the shelf in Vigo, Pontevedra and Arousa (Fig. 1). The ratio $D \cdot E_k/V$ for the Ría de Ares-Betanzos, 8.5, is from 50% to 225% larger than for the Rías Baixas, despite the reduced extension and intensity of the upwelling season there. This means that the upwelled waters renews the Ría de Ares-

Betanzos much faster than the Rías Baixas, in such a way that upwelled nutrients are cycled more efficiently in the latter. A more efficient cycling is synonymous with an enhanced regeneration within the embayment (Álvarez-Salgado et al., 2010) that, in turns, should favour the development of harmful dinoflagellate species with high affinity for regenerated nutrients (Le Corre et al., 1993; Ríos et al., 1995; Kudela and Cochlan, 2000; Seeyave et al., 2009). This could explain the contrasting response of lipophilic shellfish poisoning toxicity to coastal upwelling in the different rías. For the case of the Rías Baixas, lipophilic shellfish poisoning closures can be predicted from the inverse of the offshore Ekman transport, $-1/Q_x$, a proxy to the average renewal time of the rías, which is long enough to allow phytoplankton populations succeed until dinoflagellates (Álvarez-Salgado et al., 2008). By contrast, such a relationship seems to be lost in the Ría de Ares–Betanzos because the average renewal time is under the threshold that permits a complete phytoplankton succession.

Apart from the renewal times, the different quality of the Eastern North Atlantic Central Water (ENACW) that upwells along the Galician coast also conditions the contrasting nutrient regimes experienced by the rías. Two ENACW branches are observed: (1) subtropical ENACW, formed to the south of 40°N in winter mixed layers of <150 m and transported northwards by the Iberian Poleward Current; and (2) subpolar ENACW, formed to the north of 45°N in winter mixed layers of >400 m and transported southwards by the Iberian Current (Alvarez-Salgado et al., 2009). The isotherm of 13°C separates the warmer subtropical from the colder subpolar ENACW. They present contrasting nutrient levels: preformed nutrients are higher in the subpolar than in the subtropical waters (Pérez et al., 1993) but a more intense organic matter mineralization occurs in the subtropical branch (Castro et al., 2006). Subpolar ENACW upwells preferentially to the North of Cape Fisterra and subtropical ENACW to the south. Therefore, the new nutrient-rich subpolar ENACW is the dominant water

mass in the Ría de Ares–Betanzos, whereas the regenerated nutrient-rich subtropical ENACW prevails in the Rías Baixas. In this sense, diatom blooms use to be associated to fertilisation with new nitrate-rich waters and dinoflagellate blooms with regenerated ammonium-rich waters (Nogueira et al., 1997).

Finally, a fourth factor to take into consideration in any study of the ecology of harmful microalgae is the relative importance of tidal and residual (subtidal) currents. The dimensionless ratio between the volume of water flowing up any embayment through a given section during the flood tide, i.e the tidal prism (P), and the volume of freshwater flowing into that embayment above the section during a complete tidal cycle (Q_r) has been suggested as a rough index of the dominant estuarine circulation pattern (Morris 1985). The average tidal range for the Galician rías (2.40 m, ranging from 1.05 to 3.75 m), the average river discharges, and a tidal cycle of 12 hours 25 minutes has been used to produce the P/Q_r values in Table 1. The P/Q_r ratio of Ares–Betanzos (91) is about 70% the value obtained in Muros–Noia and Arousa and about 25% the value obtained in Vigo and Pontevedra (Table 1). Note that a P/Q_r ratio between 10 and 100 (the case of the Ría de Ares–Betanzos) would be characteristic of a partially stratified estuary, with strong vertical mixing and a 2-layered residual horizontal circulation, and a ratio between 100 and 1000 (the case of the Rías Baixas) would be characteristic of a vertically homogeneous estuary where the circulation is mainly dominated by the tide (Pritchard, 1955; Boden, 1980; Beer, 1983; Morris, 1985). However, the ratio P/Q_r implies that the river flow is the main forcing agent of the 2-layered estuarine circulation when it is well-known that wind-induced coastal upwelling should also be considered in the particular case of the Galician rías (Rosón et al., 1997; Álvarez-Salgado et al., 2000; Pardo et al., 2001). In this sense, Rosón et al. (1997) suggested the corrected index $P/(Q_r + D \cdot E_k)$ shown in Table 1. The resulting values of the ratio $P/(Q_r + D \cdot E_k)$, ranged from 7 to 17 (Table 1), which suggests that

the influence of the tide on turbulent mixing in all the rías is of minor importance (Morris, 1985).

5. Conclusions

The occurrence of harmful microalgae in the Ría de Ares-Betanzos strongly depends on the meteorological conditions, being different for the summer than for the autumn. Since there is a seasonal lag time between atmospheric forcing and toxicity of the plankton community, this gives a change for forecasting, helping the mussel farmers to manage their exploitation: a rainy spring will produce extensive closures in summer and a summer with intense north-easterly winds will produce extensive closures in the autumn. The observed relationships between meteorological conditions and mussel rafts closures allow inferring long term trends on basis of climate predictions of the evolution of precipitation and intensity of coastal winds off NW Spain.

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Table 1. Surface area (A), volume (V), wideness of the open end (D), annual average river discharge (Qr), upwelling season average offshore Ekman transport (Ek), Qr/V ratio, D · Ek/V, P/Qr and P/(Qr+D · Ek) ratios, where P is the tidal prism, for the rías of Ares–Betanzos, Muros–Noia, Arousa, Pontevedra and Vigo.

	Ares–Betanzos	Muros–Noia	Arousa	Pontevedra	Vigo
A (Km ²)	52	125	230	147	176
V (Km ³)	0.65	2.47	4.34	3.45	3.12
D (m)	3450	5690	8620	4480	3320
Qr (m ³ s ⁻¹)	30.6	54.1	95.6	21.2	20.4
Ek (m ² s ⁻¹)	0.10	0.16	0.16	0.16	0.16
$\frac{Qr}{V}$ (dimensionless)	1.5	0.7	0.7	0.2	0.2
$\frac{D \cdot Ek}{V}$ (dimensionless)	8.5	5.6	4.8	3.2	2.6
$\frac{P}{Qr}$ (dimensionless)	91	124	129	372	463
$\frac{P}{Qr + D \cdot Ek}$ (dimensionless)	7.2	7.1	8.5	10.9	17.4

Figure captions

Figure 1. Map of the Ría de Ares Betanzos showing to topography of this coastal inlet and the main geographic features of the area. The shaded area in the inset is the $2^{\circ} \times 2^{\circ}$ cell where the geostrophic winds were calculated.

Figure 2. Time series of monthly average number of days that the mussel raft cultivation areas of Lorbe (a) and Arnela (b) are closed to extraction because of the occurrence of toxic phytoplankton; monthly average total continental runoff to the ría, Q_r (c); and offshore Ekman transport, Ek_L (d).

Figure 3. Incidence of DSP toxicity on the extraction of mussels in the raft cultivation areas of Arnela and Lorbe over the period 1999–2007. Average percentage of days per month of closure (a); interannual variability of the number of day per year closed to extraction (b); relationship between the percentage of days per month that Lorbe and Arnela have been closed (c); and relationship between the number of days per year that Lorbe and Arnela have been closed (d).

Figure 4. Average seasonal evolution of the offshore Ekman transport Ek_L (a); and continental runoff, Q_r , over the period 1999–2007 (c); and interannual variability of the offshore Ekman transport, Ek_L (b); and continental runoff, Q_r , over the period 1999–2007 (d).

Figure 5. Linear relationship between the percentage of days that the mussel raft cultivation of area of Lorbe was closed to extraction because of DSP toxicity during the summer (June, July and August) with the average continental runoff of the preceding May (a); and during the autumn (September, October and November) with the offshore Ekman transport of the preceding August. The average Q_r of April and May was used in 2006 (black dot in panel a) and the negative Ek_L of 2004 was not used in the regression (black dot in panel b). See section 3.3 for more details.

Álvarez-Salgado et al., Figure 1

Álvarez-Salgado et al., Figure 2

Álvarez-Salgado et al., Figure 3

Álvarez-Salgado et al., Figure 4

Álvarez-Salgado et al., Figure 5