Environmental drivers of mussels flesh yield in a coastal upwelling system

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ABSTRACT

Eastern boundary coastal upwelling ecosystems (EBUEs) are highly sensitive to climate variability, particularly to coastal wind change. Here, we test the response of the flesh yield of blue mussels cultured in the northern boundary of the Iberian–Canary current EBUE to climate-related variables. Significant relationships were found between the annual mean, seasonal build-up and phenology of the mussel flesh yield with meteorological variables such as continental runoff, intensity and direction of coastal winds, and solar radiation. Our analysis shows that better flesh yields occur during years characterised by dry winters, accompanied by early springs and followed by summers dominated by strong northerly winds that produce intense upwelling. Compared with other EBUEs, upwelling has weakened in the study area over the last fifty years, implying an overall decrease in mussel

flesh yield. However, future climate scenarios suggest that coastal upwelling will intensify over the 21th century, particularly during the summer months, which would lead to a recovery of mussel flesh yield.

1. Introduction

The flesh yield, i.e. the portion of the total weight that is soft-tissue, is a routinely used condition index of commercial bivalves feeding in dynamic coastal environments (Orban et al., 2002; 2007; Knights, 2012; Filgueira et al., 2013). The flesh yield provides a cost-effective indicator of bivalve culture performance (Sasikumar and Krishnakumar 2011) and is commonly used as a benchmark for management strategies (Halpern et al., 2008; Polasky et al., 2011) and to assess their monetary value (Pérez-Camacho et al., 2013; 2014). The bivalve flesh yield has been also applied in environmental monitoring programs (Smaal and Widdows, 1994) as it integrates physiological responses to food availability and quality with changes in somatic growth associated to the reproductive cycle of bivalves (e.g. Mathieu and Lubet 1993; Fernández-Reiriz et al., 1996; Orban et al., 2002; 2007; Baek et al., 2014; Irisarri et al., 2015). Lucas and Beninger (1985) recommended that the flesh yield of adult bivalves would be adopted for most routine aquaculture work.

The Galician rías, a group of coastal embayments in the NW coast of Spain (**Fig. 1**), are a World-leading producer of blue mussels, with an annual yield of about 220,000 tons, which represents 40% of the European and 15% of the World production (Labarta et al., 2004). The intricate orography of the region, its oceanographic regimen dominated by coastal upwelling–downwelling episodes, and the particular cultivation method on hanging ropes is behind the success of these ecosystems as one of the major producers of marine

proteins per square meter in the World (Tenore and González 1975; Álvarez-Salgado et al., 2011). The high productivity of the region attracted ambitious ecosystem approach studies since the 1970's in the rías of Arousa and Muros (Tenore and González, 1975; Tenore et al., 1982) (**Fig. 1**). In this context, Blanton et al. (1987) reported for the first time a positive linear relationship between coastal upwelling intensity and mussel flesh yield, i.e. between the regional scale weather pattern and the commercial value of mussels harvested in the Galician rías. Given this dependence, knowledge of regional changes in weather conditions under present (Álvarez-Salgado et al., 2008; Pérez et al., 2010) and future (Álvarez et al., 2016) climate scenarios would be helpful for the management of the local mussel farm industry.

Despite the importance of the Galician rías for the world production of blue mussels, studies relating the mussel flesh yield with the regional weather conditions are scarce (Blanton et al., 1987). In this work, we have used an extensive dataset of flesh yield values from mussels cultured in different areas of the Ría de Ares-Betanzos (**Fig. 1**) collected between the years 2001 and 2012. With this dataset, we have modelled the seasonal variability of the flesh yield and examine its inter-annual variability in the light of the weather conditions in the study area, using solar radiation, coastal winds and river discharge as explanatory variables. These meteorological variables are proposed as proxies of sea surface temperature and food availability, the latter being the environmental variables that control bivalve growth according to previous studies in the area (Aguiar et al., 2015). Our results demonstrate the usefulness of linking mussels flesh yield with the climate conditions of the area to use them as an indicator of the seasonal and interannual variability of mussel meat content.

2. Materials and Methods

2.1. Mussels flesh yield

Flesh yield values used in this work were the condition index (*CI*) values provided by the mussel farmer PROINSA, who owns 95 of the 147 mussel rafts / long-lines anchored in the two cultivation areas, Arnela and Lorbé, of the Ría de Ares-Betanzos (**Fig. 1**). PROINSA has been monitoring the size and flesh yield of the cultured mussels that have achieved the commercial size (> 50 mm), as well as, the mussels already extracted for commercialization from their mussel rafts since 2001. The flesh yield is calculated as the percentage of the total weight of 1 kg of live mussels collected in a mussel raft that is meat weight after opening the valves with water vapour. It should be noted that this monitoring programme has been based on the strategic management of the farmer rather than a preconceived scientific design. This resulted in an uneven temporal and spatial coverage of the flesh yield data because the mussel rafts monitored and the times that they were visited depended on the presence of commercial size mussels (> 50 mm) in the trays and the occurrence of red tide events that produced a closure of the mussel cultivation areas. **Table A1** and **Figure A1** in the Appendix summarises the temporal and spatial coverage of the data used in this work. The crude database, consisting of 2749 flesh yield values obtained from samples of 1 kg of live mussels, was organised in two groups, coinciding with the cultivation areas of Arnela (964 values) and Lorbé (1785 values), located in the innermost and central segments of the embayment (**Fig. 1**). Individual values were aggregated to obtain monthly time series over the period 2001–2012 for the two areas. This data-gathering approach allowed us to partly overcome the irregular temporal and spatial distribution of the data.

2.2. Continental runoff

Rivers Eume and Mandeo (**Fig. 1**) are the main tributaries of the Ría de Ares-Betanzos. The flow at the mouth of River Mandeo was estimated from gauge station nº 464 at Irixoa, hold by Augas de Galicia (Galician Government). The total drainage basin of this river is 456.97 Km² and the gauge station intercepts only 249.21 Km². Therefore, the ratio of total to gauged areas was used to estimate the flow at the mouth following the Horton's Law (Strahler, 1963). Concerning River Eume, its flow 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 just 94.04 Km². Daily values of continental runoff over the period 2001–2012 were averaged to obtain monthly river flows (Q_r) to allow direct comparison with the time series of flesh yield.

2.3. Offshore Ekman transport

The West-East (Q_x , in m² s⁻¹) and South-North (Q_y , in m² 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 ($1.4 \cdot 10^{-3}$); 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 $-Q_L$ indicates an offshore Ekman transport and a negative value of Q_L and onshore Ekman transport in this coastal inlet. As for the case of Q_r , daily values were averaged to obtain monthly mean $-Q_L$ over the period 2001–2012.

2.4. Global radiation

Global radiation (G) data was taken from the meteorological station of CIS Ferrol (**Fig. 1**), run by the Galician Meteo Agency Meteogalicia (<http://www.meteogalicia.com>), where a pyranometer Schenk 8101 is installed. Again, measurements recorded every 10 minutes were averaged to obtain monthly mean values of G .

2.5. Statistical analyses

The seasonal cycles of the mussel flesh yield or condition index (CI), continental runoff (Qr), offshore Ekman transport parallel to the main axis of the Ría de Ares-Betanzos ($-Q_L$) and global radiation (G) were modelled with a simple harmonic function to obtain the corresponding fitting coefficients for the whole study period (2001–2012) and for each individual year by minimising the residuals in the least squared sense. For the particular case of the CI , the equation to be fitted is:

$$CI = b_1 + b_2 \cdot \sin\left(\frac{2 \cdot \pi}{12} \cdot t + b_3\right) \quad (3)$$

Where b_1 is the mean value of the condition index (Avg , in %); b_2 is the amplitude of the harmonic; and b_3 is the diphas (month when the seasonal minimum is achieved). The average increase rate of CI (Rat , in % month⁻¹) was calculated as $Rat = (2 \cdot b_2)/6$. The denominator of Rat , 6 months, is the time interval between the seasonal maximum and minimum of CI as fitted with Eq. 3. Finally, the month when CI was halfway between the seasonal minimum and the seasonal maximum (φ , in month) was calculated as $\varphi = b_3 + 3$. For some particular years, mean CI values are not available for certain months (see **Table A1** in the Appendix) because mussels were not of commercial size or the farms were closed to exploitation due to a red tide event. In any case, there were enough monthly mean CI values data each year to produce seasonal cycles with statistically significant values of Avg , Rat and φ . Note that the same harmonic function has been also used to model the seasonal cycles of Qr , $-Q_L$ and G .

Furthermore, linear models, with location as a factor, were tested to model the inter-annual variability of the fitting parameters Avg , Rat and φ of the mussel CI in the

cultivation sites of Arnela and Lorbé with the environmental variables Q_r , $-Q_L$ and G . The effect of location was tested by means of F-tests for nested linear models. The goodness of fit of the different models was tested with the determination coefficient (R^2), the standard error of the fitting coefficients, and the standard deviation of the residuals. Data analysis was performed using the statistical software R 2.15.2 (R Development Core Team 2011).

3. Results and Discussion

3.1. Seasonal and interannual variability of mussels flesh yield

Monthly mean flesh yield values for both cultivation areas describe a well-defined seasonal cycle (**Fig. A2a & b** in Appendix) that can be modelled with a simple harmonic equation (see Eq. 3) characterised by three parameters: the annual mean CI (Avg , in %), the average increase rate of CI (Rat , in % month⁻¹) and the month when the CI was halfway between the seasonal minimum and the seasonal maximum (φ , in month). The values of Avg , Rat and φ that best fit the field data to Eq. 3 were obtained for the whole period 2001–2012 and also for each individual year.

Harmonic Eq. 3 explained 54% and 42% of the variability of the monthly-mean CI values over the whole study period in the cultivation areas of Arnela and Lorbé, respectively (**Table 1**). The 2001–2012 mean CI (Avg) in Arnela, $23.4 \pm 0.4\%$, was significantly higher ($p < 0.01$) than in Lorbé, $21.9 \pm 0.3\%$. The 2001–2012 seasonal increase rate (Rat) was also significantly higher ($p < 0.05$) in Arnela, 2.0 ± 0.2 % month⁻¹, than in Lorbé, 1.4 ± 0.2 % month⁻¹. Therefore, mussels cultured in Arnela grew faster and of better commercial quality than in Lorbé. When considering the whole study period, both sites followed the same timing in the increase rate of CI , with the seasonal minimum being

in mid-March (month 3.3–3.6), the seasonal maximum in mid-September (month 9.3–9.6) and φ in month 6.3–6.6 (**Table 1**).

This seasonal cycle is primarily dictated by the reproductive biology of mussels. In this regard, the reproductive cycle of mussels in the Galician rías starts with the development and ripening of the gonads during autumn-winter. A major spawning event takes place during the spring and, subsequently, gonad restoration leads to a secondary spawning event during late summer or early autumn (Villalba, 1995; Peteiro et al., 2011; Suarez et al., 2013; Irisarri et al. 2015). Therefore, to reflect the biology of the species, harmonic Eq. 3 for the individual years was fitted considering 12 month periods starting on October and ending on the next September instead of a Gregorian calendar (January–December) (see **Fig. A3** in the Appendix). Eq. (3) for each individual year explained from 62% to 95% of the variability of the monthly-mean *CI* values. Significant inter-annual differences were observed in the values of *Avg*, *Rat* and φ in both cultivation sites (**Fig. 2**). Seasonal mean *CI* values ranged from 20.8 ± 0.6 % (2007) to 25.8 ± 0.7 % (2011) in Arnela and from 19.5 ± 0.9 % (2007) to 23.8 ± 1.0 % (2011) in Lorbé (**Fig. 2a**). Both sites evolved in parallel, *Avg* values being generally higher in Arnela than in Lorbé, and no significant inter-annual trend over the period 2001–2012 was observed. The increase rate (*Rat*) varied from 0.7 ± 0.2 (2012) to 3.3 ± 0.3 % month⁻¹ (2011) in Arnela and from 0.8 ± 0.4 (2012) to 2.8 ± 0.4 % month⁻¹ (2011) in Lorbé (**Fig. 2b**). Again, Arnela and Lorbé evolved in parallel, *Rat* was usually higher in Arnela than in Lorbé, and there was no significant inter-annual trend over the period 2001–2012. φ varied over a wide range of about four months: between months 4.7 ± 0.4 (2004) and 8.9 ± 0.7 (2002) in Arnela and between months 5.7 ± 0.8 (2004) and 9.6 ± 0.4 (2002) in Lorbé (**Fig. 2c**). Once more, both sites showed similar

patterns throughout the year and there was no significant inter-annual trend over the period 2001–2012. The marked interannual differences observed in the three parameters of the harmonic equation, (*Avg*, *Rat* and φ) is the reason behind the relatively low percentage of the total variability (44–54%; **Table 1**) explained by the harmonic equation when the entire study period is fitted to Eq. 3.

3.2. Environmental drivers of the interannual variability of mussel flesh yield

In order to model the three parameters that define the seasonal cycle of mussel *CI*, we have analysed the correlation of *Avg*, *Rat* and φ with selected indices that define the seasonal cycles of the primary meteorological variables that define the climate of the study area: continental runoff (*Qr*), offshore Ekman transport parallel to the main axis of the Ría de Ares-Betanzos ($-Q_L$) and global radiation (*G*).

It has been broadly reported in the literature the seasonality of continental runoff and coastal winds in the NW Iberian upwelling system (Nogueira et al., 1997; Álvarez-Salgado et al., 2008). For the particular period studied in our work, the harmonic equation (Eq. 3) but applied to *Qr* explained 41% of the variability of continental runoff (**Fig. A2c** in the Appendix), resulting in a 2001-2012 mean flow of $29 \pm 2 \text{ m}^3 \text{ s}^{-1}$, a seasonal amplitude of $24 \pm 2 \text{ m}^3 \text{ s}^{-1}$ and a seasonal minimum occurring at month 7.2 ± 0.2 , which means that the transit from the humid to the dry season occurred in early April (**Table 1**). **Figure 3a** shows the time course of the annual mean of *Qr* for each individual year over the study period, with values ranging from $17 \pm 3 \text{ m}^3 \text{ s}^{-1}$ (2012) to $51 \pm 5 \text{ m}^3 \text{ s}^{-1}$ (2007) and no significant inter-annual trend. For the case of the coastal winds (**Fig A2d** in the appendix), the harmonic equation explained only 23% of the total variability of $-Q_L$ over the study

period. The 2001-2012 mean was not significantly different from zero ($-46 \pm 48 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$), the seasonal amplitude was $433 \pm 68 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ and the seasonal minimum occurred at month 0.3 ± 0.6 (**Table 1**). This means that, on average over the period 2001–2012, the time of the year when $-Q_L$ was positive —i.e. the upwelling-favourable season— extended from month 3.8 (late march) to month 9.4 (early September). Therefore, the average value of $-Q_L$ from April to August is a suitable index of the intensity of the upwelling season on each particular year (**Fig. 3b**), which ranged from a downwelling-favourable value of $-269 \pm 116 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ (2012) to an upwelling-favourable value of $582 \pm 116 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ (2011). Again, there was not a significant inter-annual trend of this index over the study period. Concerning the global radiation (G), the harmonic equation explained 94% of the variability of the monthly time series over the period 2001 to 2012. The 2001-2012 annual mean was $12.7 \pm 0.1 \text{ MJ m}^{-2} \text{ d}^{-1}$, the seasonal amplitude was $8.4 \pm 0.2 \text{ MJ m}^{-2} \text{ d}^{-1}$ and the seasonal minimum was at month 0.28 ± 0.04 , i.e. in early January (**Table 1**). February revealed as the winter month that exhibited the largest inter-annual differences in G (**Fig. 3c**), with values ranging from $6 \text{ MJ m}^{-2} \text{ d}^{-1}$ (2000) to $10 \text{ MJ m}^{-2} \text{ d}^{-1}$ (2004) and a increasing inter-annual trend over the study period, although not statistically significant.

Our analyses of the correlation of the fitting parameters of mussel CI (Avg , Rat and φ) with the explanatory meteorological variables (Qr , $-Q_L$ and G) yielded that the annual mean value of CI (Avg) depended inversely on the annual mean value of the continental runoff (**Fig. 2d**; $R^2 = 0.57$, $n = 22$, $p < 0.001$), the amplitude of CI (Rat) depended directly on the mean offshore Ekman transport from April to August (**Fig. 2e**; $R^2 = 0.44$, $n = 22$, $p < 0.05$) and the dipphase of CI (φ) depended directly on the average global radiation in February (**Fig. 2f**; $R^2 = 0.42$, $n = 22$, $p < 0.001$). Linear models with mussel farm location

as a factor were used to run these analyses (see materials and methods). It resulted that the effect of location was significant for the models of *Avg* and *Rat*, but not for the case of the model of φ .

Although the correlation between the annual average mussel flesh yield and continental runoff is not exceptionally high ($R^2 = 0.57$), it is remarkable that such a significant ($p < 0.001$) correlation has been obtained between an intricate physiological variable and a simple meteorological variable. The negative dependence of the annual average of *CI* on continental runoff is probably related to the transport of mineral particles of terrestrial origin by rivers, which leads to an increase in the total concentration of particles available for filter feeders but dilutes the amount of organic particles suspended in the water column (Aguilar et al., 2015). Therefore, although the relatively low coefficient of determination (R^2) of the linear relationship between flesh yield and continental runoff prevent us to make quantitative predictions, it is expected that in those years when continental runoff is higher during the wet season (November to March) the flesh yield of the mussels before the upwelling season is lower, leading to a lower annual mean flesh yield.

The connection between upwelling intensity and mussel quality (**Fig. 2e**) was first established by Blanton et al (1987) in the Ría de Arousa. According to their conceptual model, the higher the intensity of upwelling, the higher the nutrient fertilisation, which leads to enhanced primary production, greater food availability and, consequently, improved flesh yield of the cultured mussels. The first three steps of this conceptual model (from wind to primary production) was tested and demonstrated in the field, specifically in the Ría de Arousa, a decade latter (Álvarez-Salgado et al. 1996). And the close relationship

between coastal upwelling, food availability and mussel growth was also verified empirically (Pérez-Camacho et al. 1995, 2014). In the case of the Ría de Ares-Betanzos, the annual mean flesh yield seems to be not dictated by the upwelling intensity but by the average continental runoff (**Fig. 2d**). What the intensity of upwelling seems to affect is the net increase of the *CI* of the mussels cultured in the Ria de Ares-Betanzos throughout the year (**Fig. 2e**). Orographic, hydrological and hydrographic differences are behind the contrasting oceanographic behaviour of the rías of Arousa and Ares-Betanzos (Alvarez-Salgado et al., 2011). Our work suggests that the difference in the oceanography of both embayments translates to the quality of cultured mussels too. Again, the low coefficient of determination of the seasonal increase of the flesh yield with the average upwelling index over the upwelling season ($R^2 = 0.44$), prevent us to forecast, but supports the premise of the influence of upwelling on mussel commercial quality posed by Blanton et al. (1987).

The timing of the seasonal minimum of mussels *CI* is associated with the timing of the early spring spawning event (Villalba et al., 1995; Peteiro et al., 2011; Fuentes- Santos et al., 2016) that, in turns, appears to be conditioned by the average total radiation received by the Ría de Ares-Betanzos during February (**Fig. 2f**). Global radiation is used here as a foretaste of seawater temperature, which is the variable that dictates the timing of the reproductive cycle of bivalves (Phillipart et al., 2003). Therefore, higher radiation in late winter (February) produces an earlier warming of the surface waters that results in an earlier spring spawning event and a timelier value of ϕ , the month when the flesh yield was halfway between the seasonal minimum and the seasonal maximum.

3.3. Spatial differences in mussel flesh yield

Numerous studies have reported that the mussel flesh yield can vary substantially among bivalves cultured in nearby sites within the same embayment (Fernández-Reiriz et al., 1996; Marin et al., 2003; Norkko et al., 2006; Baek et al., 2014), or in proximate locations in a given coastal ecosystem (Okumus and Stirling 1998; Kang et al., 2000; Pérez-Camacho et al., 2013; Irisarri et al., 2015). In this case, our results indicate that the annual mean and seasonal amplitude of the flesh yield is significantly higher in Arnela than in Lorbé. This seems counterintuitive if one considers that Arnela is located in the inner part of the embayment, i.e. closer to the river mouth, and continental runoff has a negative impact on the inter-annual variability of the annual mean *CI*. However, it has been recently suggested that the variability of seston food quality in the Ría de Ares-Betanzos can be explained by an appropriate combination of nutrient loads, pycnocline development and flushing time that is met in the cultivation area of Arnela (Aguilar et al., 2015), where the flushing time is twice than in Lorbe (Duarte et al., 2014). Furthermore, it has been also suggested that the better flesh yield of the mussels from Arnela is related to the lower mussel biomass in that area, with only 40 of the 147 mussel rafts (Alvarez-Salgado et al., 2011), which exerts lower pressure in the standing stock of food available (Fernandez-Reiriz et al. 1996).

3.4. Mussels flesh yield under climate change

The empirical relationships obtained in this work between the annual average, seasonal built-up and phenology of the mussel flesh yield with river discharge, coastal

winds and solar radiation provided us with a tool to argue about the quality of harvested mussels in response to future climate scenarios in the study area.

The NW coast of the Iberian Peninsula is located in a transitional zone between the subtropical and temperate regimes of the Eastern North Atlantic. Therefore, this area is particularly sensitive to climate change. In fact, a challenged decrease of the intensity and persistence of upwelling favourable winds over the last 50 years has been reported (Barton et al., 2013). Such a decrease seems to be the reason behind the increase in the number of days that the mussel cultivation areas are closed to exploitation because of the occurrence of diarrheic (DSP) and paralytic shellfish poisoning (PSP) toxicity in mussel flesh in the wind-governed southern rías of Vigo, Pontevedra, Arousa and Muros (Alvarez-Salgado et al., 2008) (**Fig. 1**). In the case of the northern Ría de Ares-Betanzos, which is both river and wind-governed, it has been found that the number of days that Arnela and Lorbé are closed to exploitation during the summer depends on spring continental runoff and the number of days closed during the autumn depends on NE winds intensity during the summer (Alvarez-Salgado et al., 2011). Concurrently, whereas according to Blanton et al. (1987) mussel flesh yield is related to coastal wind patterns in the southern Ría de Arousa, it is affected not only by coastal winds but also by continental runoff in the Ría de Ares-Betanzos. Our results suggest that an overall decrease of the flesh yield of mussels cultured in the Ría de Ares-Betanzos should have to occur in parallel to the decrease in upwelling intensity observed from the middle 1960's (Alvarez-Salgado et al., 2008; Pérez et al., 2010). Conversely, future climate scenarios predict a significant intensification of coastal upwelling in the study area during the summer months through the 21st century (Alvarez et al., 2016), which would lead to a recovery of mussel flesh yield.

4. Conclusions

The interannual variability observed in the seasonal cycle of the flesh yield of mussels cultured in the Ría de Ares Betanzos, NW Iberian upwelling system, was linked to the primary variables that define the climate of the area: continental runoff, offshore Ekman transport and solar radiation. We observed that (1) continental runoff affected inversely the annual mean flesh yield; (2) offshore Ekman transport affected positively the seasonal increase of the flesh yield through the spring and summer; and (3) solar radiation affected positively the timing of the spring spawning and, therefore, the timing of the seasonal increase of the flesh yield. The linear correlations obtained between the response and explanatory variables do not present high determination coefficients, which prevent us to make quantitative predictions. However, they can be helpful indicators of the seasonal and interannual variability of mussels flesh yield or being used to argue about the impact of future climate scenarios on mussel flesh yield in our area.

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Figure legends

Fig. 1. The mussel cultivation areas of Arnela and Lorbé (Ría de Ares-Betanzos, NW Iberian Peninsula) are shown. Rivers Eume and Mandeo, the $2^{\circ} \times 2^{\circ}$ cell centred at 43°N 11°W where geostrophic winds were calculated and the meteorological station of CIS Ferrol are also positioned.

Fig. 2. Time course of the (A) annual mean, (B) seasonal amplitude and (C) diphas of the mussel flesh yield or condition index (*CI*) in the cultivations areas of Arnela and Lorbé; and relationship of (D) the annual mean *CI* with the annual mean continental runoff (Q_r), (E) the seasonal amplitude of *CI* with average offshore Ekman transport from April to August ($-Q_L$), and (F) the diphas of *CI* with the average global radiation during February (G). White dots and continuous lines correspond to Arnela and blank dots and dashed lines correspond to Lorbé.

Fig. 3. Time-course of the (A) annual mean of the continental runoff, (B) average April–September offshore Ekman transport and (C) average February global radiation.

488 **Table 1.** Fitting parameters of the average seasonal cycles of mussel flesh yield or
 489 condition index (CI), freshwater discharge (Qr), offshore Ekman transport ($-Q_L$) and global
 490 radiation (G) over the period 2001–2012. Annual mean, seasonal amplitude and diphase
 491 are the parameters b_1 , b_2 and b_3 in Eq. 1. The parameter b_3 indicates the month when the
 492 seasonal minimum of each variable is achieved.

	Annual mean	Seasonal amplitude	Diphase	R^2	p
CI (Arnela)	23.4 ± 0.4	6.0 ± 0.6	3.3 ± 0.2	0.54	<0.001
CI (Lorbé)	21.9 ± 0.3	4.3 ± 0.5	3.6 ± 0.2	0.42	<0.001
Qr	29 ± 2	24 ± 2	7.2 ± 0.2	0.41	<0.001
$-Q_L$	-46 ± 48 (n.s.)	433 ± 68	0.6 ± 0.3	0.23	<0.001
G	1267 ± 12	841 ± 17	0.28 ± 0.04	0.94	<0.001

493

Appendix

Table A1. Monthly average mussel flesh yields (in %) for the cultivation areas of Arnela and Lorbé in the Ría de Ares-Betanzos (NW Spain) between 2001 and 2012. Each flesh yield data was calculated as the percentage of the total weight of 1 kg of mussels that is meat weight.

Numbers in brackets indicate the number of flesh yield data used to obtain the monthly average values.

Arnela

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2001									36.6 (11)	25.3 (1)		31.5 (3)
2002	28.4 (21)					22.9 (6)	19.2 (1)	24.5 (13)	25.8 (19)		29.0 (2)	
2003			20.9 (3)	17.6 (3)	14.9 (15)		23.9 (6)	27.7 (1)	30.1 (12)			
2004		17.5 (3)		24.8 (6)	24.6 (5)	27.2 (13)	29.6 (9)		29.6 (6)		25.9 (19)	
2005		16.5 (2)	19.5 (3)		17.7 (11)	21.3 (18)	26.3 (4)	30.9 (4)	28.0 (4)		27.6 (29)	
2006			17.5 (8)		17.6 (7)	20.6 (40)	20.5 (7)			26.9 (15)	25.1 (5)	
2007	22.0 (7)			16.6 (4)	18.0 (9)	17.7 (7)	17.5 (10)	17.9 (3)	24.9 (9)	25.3 (17)	24.7 (5)	22.8 (3)
2008	21.1 (17)	18.3 (6)	15.2 (9)	17.2 (18)	14.6 (9)	23.0 (27)	28.1 (14)	28.7 (5)	34.6 (4)	29.5 (18)	24.1 (22)	
2009	18.7 (8)		21.9 (3)	12.4 (2)	24.6 (8)	28.3 (30)	31.6 (3)	29.2 (5)	27.9 (6)	28.0 (11)	26.1 (30)	27.1 (1)
2010			12.9 (9)	15.7 (6)	13.9 (14)	16.1 (34)	22.4 (19)		34.1 (4)			24.6 (14)
2011	21.2 (12)	17.6 (7)	15.0 (1)	15.6 (4)	21.4 (33)	30.4 (5)	35.0 (15)	37.0 (1)	32.9 (19)	30.4 (14)	26.9 (13)	23.9 (16)
2012	24.1 (4)	22.0 (1)			24.6 (3)	24.1 (9)	25.1 (14)		26.7 (7)		25.5 (21)	

Lorbé

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2001							23.7 (3)	27.1 (5)	32.0 (24)	27.6 (60)	22.1 (19)	26.8 (7)
2002	26.6 (3)	25.4 (5)				18.0 (1)	13.8 (4)	17.5 (4)	21.0 (20)	24.2 (13)	21.6 (71)	20.8 (32)
2003				23.9 (2)	19.4 (8)	17.1 (12)	19.0 (2)		27.6 (10)	29.1 (86)		
2004		18.3 (1)		22.5 (30)	22.5 (11)	19.8 (22)	24.4 (15)	26.2 (21)	27.1 (2)	24.4 (63)	24.7 (34)	
2005		18.5 (3)	20.4 (7)		14.0 (14)	21.8 (37)	25.0 (6)	23.6 (7)	27.9 (4)	25.1 (10)	23.3 (30)	22.2 (16)
2006	22.5 (2)		18.6 (6)	18.5 (10)	13.1 (10)	15.9 (13)					22.8 (69)	20.1 (57)
2007	19.4 (21)			15.1 (5)	21.0 (22)		17.0 (25)	17.7 (18)	22.1 (6)	24.5 (1)	20.8 (37)	19.4 (20)
2008	20.2 (19)	17.7 (17)	19.9 (3)	13.9 (13)	14.3 (5)	21.1 (16)	28.0 (20)		31.4 (28)	28.5 (22)	25.4 (10)	23.3 (24)
2009	21.6 (12)		18.3 (3)	13.0 (3)		25.5 (20)	28.8 (6)	25.5 (25)	26.4 (42)	25.0 (26)	21.3 (8)	23.2 (3)
2010	22.2 (6)	18.8 (14)	17.2 (4)	18.4 (11)	15.2 (8)	15.7 (5)	24.4 (7)	22.9 (18)		27.2 (19)	24.0 (50)	22.5 (11)
2011		19.1 (6)	16.6 (14)	16.3 (29)	20.0 (32)	19.8 (30)	29.7 (3)	37.0 (3)	32.0 (1)	29.9 (39)	27.4 (38)	26.2 (14)
2012	22.9 (14)	20.5 (10)			19.3 (2)	20.6 (5)	26.0 (1)		21.5 (8)	22.5 (4)		25.9 (8)

Figure A1. Spatial distribution of the mussel flesh yields data for the cultivation areas of Arnela and Lorbé in the Ría de Ares-Betanzos (NW Spain). Each mark corresponds to an individual mussel raft /long-line where the mussel flesh yield was obtained. The symbols (see legend) indicate the number of times that each raft/long-line was visited to obtain the flesh yield over the study period 2001–2012. This chart illustrates that the data were not obtained on a regular temporal and spatial basis but according to the management strategy of the farmer.

Figure A2. Time series of the monthly box plots of the (a) mussel flesh yield of Arnela; (b) mussel flesh yield of Lorbé; (c) volume discharged by the rivers Eume and Mandeo; and (d) offshore Ekman transport.

Figure A3. Individual year seasonal cycles of the mussel flesh yield for the cultivation areas of Arnela and Lorbé. Note that the years are defined from November to October. Solid and dotted lines represent the fitting of monthly average data to the harmonic Eq. 3 for Arnela and Lorbe, respectively.