

Nutrient limitation can explain a rapid transition to synchrony in an upwelling-driven diatom community

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Abstract

Identifying the mechanisms controlling the temporal dynamics of ecological communities is key to understand their vulnerability to natural and anthropogenic impacts and to identify early warnings of critical transitions. At community level, inter-specific synchrony is an important indicator of ecosystem stability and variation in function. Using wavelet analysis on time-series of abundance of 12 dominant diatom species, sampled monthly (1994–2009) in a coastal upwelling embayment at the northern limit of the Canary Current Upwelling System, we find a sudden onset of synchrony between 1998 and 2002, concomitant with an increase in the amplitude of the upwelling index at different temporal scales. To better understand the underlying mechanism that could generate this sudden onset of synchrony among competitors, we analyzed a general model of competition between two species for two essential nutrients (e.g., nitrogen and silicate). We incorporate environmental variation by varying the concentration of one of the essential nutrients entering the system. Increase in the amplitude of environmental variation always leads to greater synchrony among competitors. This occurs because the system shifts from a state in which species are limited by different nutrients to one where species are often limited by the same nutrient. We show that the transition from asynchronous to synchronous dynamics can occur suddenly as the amplitude of environmental variation increases. While it is not possible to rule out alternative mechanisms, our model demonstrates that sudden changes in the extent of synchronization should be a common feature when species compete for essential nutrients in variable environments.

Understanding the processes that drive population fluctuations and bring sudden abrupt changes within communities is a key topic in ecology. This is especially required to sharpen predictions under global change, including climate warming, overexploitation of resources, and pollution (Clements and Ozgul 2018). Most studies of abrupt transitions focus on

changes in population abundance in response to abiotic factors, but such transitions have also been observed at meta-population and community levels, concerning emergent properties related to ecosystem dynamics (e.g., stability, resilience), or function (food-web complexity, connectivity), which are often difficult to detect (e.g., Kuiper et al. 2015). In addition, the effect of abiotic factors in population dynamics does not depend on mean conditions only (Parmesan et al. 2003); changes in the variance or amplitude of environmental oscillations may have stronger impacts on ecological process (Stenseth 2012) and may be particularly important for inducing transitions in biological systems (Scheffer et al. 2009). In Eastern Boundary Upwelling Ecosystems (EBUEs), changes in the frequency and strength of upwelling events are expected due to climate change (Bakun 1990; Sydeman et al. 2014; Wang et al. 2015). This has important implications since EBUEs, usually dominated by diatoms (Smayda and Trainer 2010) adapted to profit environmental windows of high turbulence and high nutrient concentrations (Margalef 1978), exhibit some of the highest rates of primary production in the ocean (Ryther 1969), and sustain between 20% and 25% of world fish catches while

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Additional Supporting Information may be found in the online version of this article.

Author Contribution Statement: Conceived and wrote: L.B. and D.A.V.; editorial comments: all.

In Memoriam: This work is dedicated to the memory of our colleague Dr. Manuel Varela, a renowned phytoplankton ecologist and taxonomist who conducted research at the Centro Oceanográfico de A Coruña and passed away recently (23 October 2019).

Special Issue: Nonlinear dynamics, resilience, and regime shifts in aquatic communities and ecosystems

occupying less than 1% of the ocean surface. Furthermore, theoretical frameworks (Legendre and Rassoulzadegan 1996) and empirical studies (Chavez and Messié 2009) suggest that the frequency of upwelling events (nutrient inputs) and its consequences in the temporal dynamics of primary production are key factors on the efficiency toward high trophic levels (e.g., fisheries). Understanding how the variability of amplitude and frequency of upwelling events impact phytoplankton community assembly and primary production become therefore crucial.

One feature that has strong consequences for community stability is the association among the dynamics of their constituent populations (i.e., inter-specific synchrony; e.g., Pimm et al. 1988; Tilman et al. 1998; Inchausti and Halley 2003; Vasseur and Gaedre 2007; Gonzalez and Loreau 2009; Gouhier et al. 2010). Here, synchrony typically refers to positive correlations among species temporal dynamics whereas negative correlations lead to anti-synchrony or “compensatory” dynamics. Compensatory dynamics can occur if species exhibit temporal niche differentiation, which is required for certain mechanisms of coexistence (Hubbell 2001; Lande et al. 2003; Loreau and de Mazancourt 2008; Kalyuzhny et al. 2014). Compensatory dynamics buffer the effects of abiotic disturbances and therefore maintain ecological properties and stabilize functions at the community level (Gonzalez and Loreau 2009). However, compensatory dynamics appear to be rare in natural populations and recent meta-analyses of temporal dynamics suggest that synchronous fluctuations among populations are relatively more common (Houlahan et al. 2007; Vasseur et al. 2014) suggesting that environmental forcing may be a particularly important driver of dynamics. Overall, there is still controversy about the relative strength of abiotic and biotic forces needed to shift a community from compensatory to synchronous dynamics. It is especially difficult to assess those questions in natural systems as it requires an understanding of their functioning as well as statistical tools able to cope with the non-stationary nature of ecological systems (Cazelles et al. 2008).

In systems that are dominated by cycles, the shift to synchronization (via phase-locking of the different oscillations) has been proposed to be an early warning of critical transition (Scheffer et al. 2009). Indeed, recent empirical work has shown that an increase in synchrony among plankton populations facilitated a regime shift by disrupting community structure (Jochimsen et al. 2013). Synchronization has been shown to occur in a zooplankton community over many years following experimental acidification in Little Rock Lake, USA (Keitt 2008), and a recent analysis of plankton dynamics in the North Sea demonstrated clear changes in synchrony concurrent to climate induced regime shift in the 1980s (Defriez et al. 2016). In addition, the vast majority of models that have been used to examine the synchrony of competitors in the presence of environmental noise have demonstrated that synchrony tends to change smoothly in response to the parameters representing environmental or competitive attributes (Kendall et al. 2000;

Loreau and de Mazancourt 2008) but this can differ in models where dynamics are cyclic or chaotic (Greenman and Benton 2001; Vasseur 2007). Experiments aimed at assessing the synchrony of populations across space or among different species typically do not incorporate the regression design necessary to observe non-linearity transitions in synchrony. To date, little work has examined the variation in synchrony that is exhibited by communities or sought to explain its origins. Yet, it is crucial to understand the mechanisms that cause populations to transition into and out of synchrony as these transitions may provide early warning of approaching destabilization and regime shifts.

In the present study, we examine the temporal synchrony of the most abundant diatom species in “Ría de A Coruña,” one of the coastal embayments or rías (flooded tectonic valleys) distributed along the Galician coast (Northwest Iberian Peninsula) (Fig. 1). The region is located at the northern limit of the Canary Current Upwelling System (Aristegui et al. 2009), and thus, is subject to the seasonal occurrence of upwelling events, from ca. March to September, of varying duration (between ca. 3 and 14 d) (Gilcoto et al. 2017; Buttay et al. 2017). In mid-latitude shelf-coastal ecosystems, phytoplankton usually exhibit a bi-modal seasonal pattern, with two main annual peaks of population growth in spring and autumn, during the period of transient thermoclines when water column mixing allows nutrients to be available in the surface layer. In summer, stratification limits the input of nutrients to the surface and consequently their depletion leads to a strong decrease of the phytoplankton population. In the Galician shelf and rías, the occurrence of upwelling events during the stratified period promotes event-scale physical intrusions of cold, nutrient-rich sub-surface Eastern North-Atlantic Central Water (ENACW) to the surface. The enrichment of the surface layer during the spin-up phase of upwelling events stimulates phytoplankton growth and primary production (Bode et al. 2019). Diatoms are particularly well adapted to upwelling systems as they are able to respond quickly to the sudden availability of inorganic nutrients (Nogueira et al. 2000). The dynamics of phytoplankton species during upwelling cycles are then modulated by their stoichiometric requirements for nutrients, especially nitrate and silicate for diatoms (Nogueira et al. 1997), and variation in nutrient availability can lead to discrete shifts in the factor limiting growth (e.g., Liebig’s law) (Kaiser et al. 1994).

To better understand the mechanistic basis of the transition between asynchronous and synchronous periods, we analyze a model of competition among two species for two essential resources, which availabilities fluctuate regularly. In contrast to other two species models, such as Lotka-Volterra, consumer-resource models do not assume linear interaction coefficients and as such perform better to scale up to multispecies communities (Letten and Stouffer 2019). We find that a likely explanation for the transition to and from periods of phytoplankton population synchrony in the Galicia system stems from a shift in the identity of limiting resources for some populations, leading to a reduction

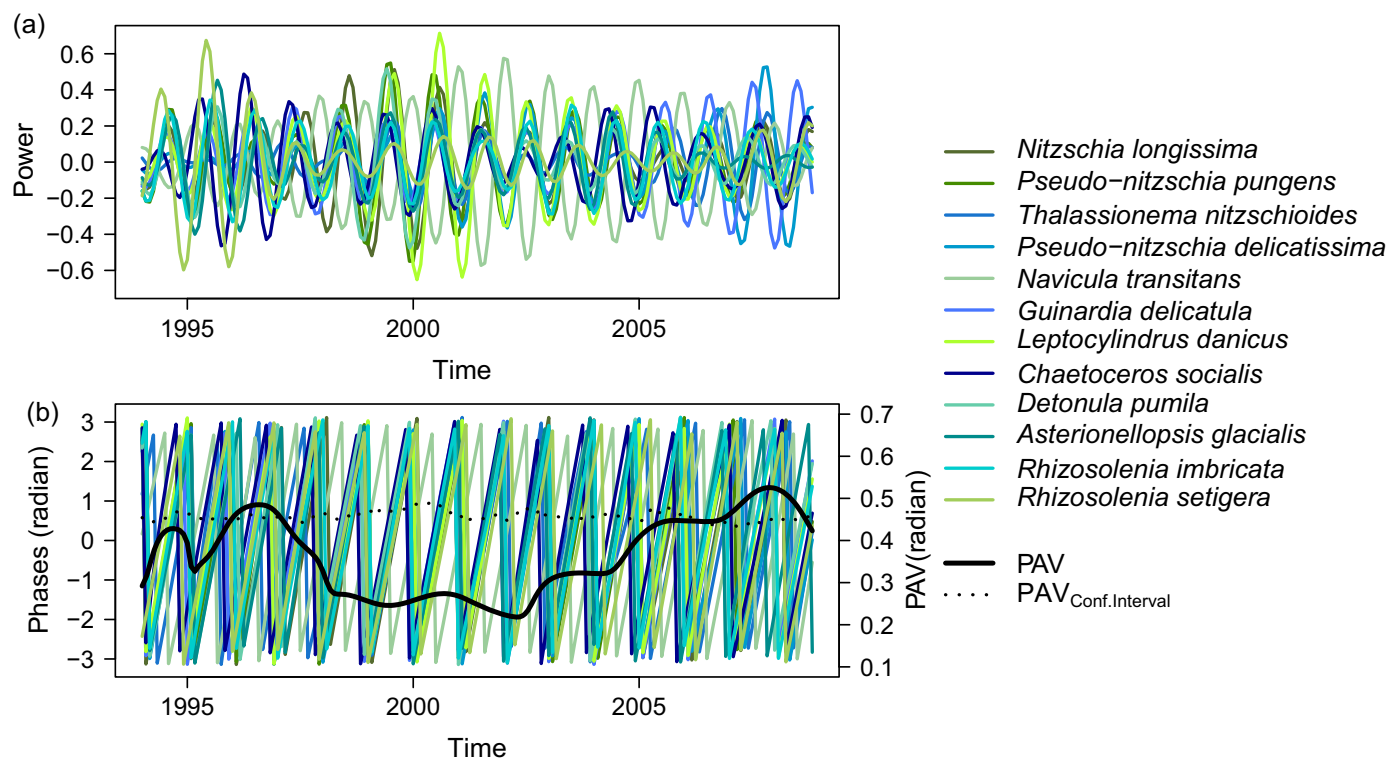


Fig. 1. Time series of the seasonal mode of diatom abundance. **(a)** Normalized seasonal mode and **(b)** seasonal phase (in radians) extracted from the series of each of the selected diatom species. Each color line represents a species. The black line represents the phase angle variance (PAV) of the seasonal component, and the black dotted line represents the 95% confidence interval of the PAV (computed with a bootstrapping scheme based on hidden Markov chains, HMM) to show its statistical significance.

in niche differentiation when amplitude of the upwelling fluctuations are high. Given the expectation for increasing environmental variation and more frequent and lasting extreme events, such transitions to and from a synchronized state may become a more prevalent feature in upwelling communities.

Material and methods

Study site and data

The Galician coast is located at the northern limit of the Canary Current upwelling system (Aristegui et al. 2009), one of the four major Eastern Boundary Upwelling Ecosystems (EBUEs) in the world's oceans. From mid-spring to early-autumn, driven by the predominance of along-shore equatorward winds, coastal upwelling injects inorganic nutrients to the euphotic zone, fueling phytoplankton growth and enhancing primary production. During the rest of the year, south and westerly winds predominate, inducing coastal downwelling over the shelf and rainfall (and associated continental runoff) over the western Iberian Peninsula. The relevance of upwelling dynamics in the structure of the plankton community, acting at multiple time scales from short-term events and seasonal cycles to long-term variability, has been extensively studied in the area (Nogueira et al. 2000; Alvarez et al. 2009; Ospina-Alvarez et al. 2010; Buttay et al. 2017).

Time series of daily upwelling index (UI, $\text{m}^3 \cdot \text{s}^{-1} \cdot \text{km}^{-1}$) were provided by the Instituto Español de Oceanografía (<http://www.indicedeafloramiento.ieo.es/>). The UI was calculated by the Ekman transport equation (Bakun 1973) from geostrophic winds estimated at 43°N , 11°W , which is considered a representative location for the characterization of wind driven coastal upwelling/downwelling dynamics for the northern Galician shelf (Lavín et al. 1991). The UI time-series is represented in Supplementary Fig. S1. Upwelling events have a strong influence on nutrient availability, being responsible for > 70% of total dissolved inorganic nitrogen inputs in the Galician rías (Villegas-Ríos et al. 2011), the seasonal dynamics is presented in Supplementary Fig. S2.

Phytoplankton have been sampled on a monthly basis off A Coruña (Northwest Iberian shelf) (E2CO Station: 43.422°N – 8.437°W) since 1994 as part of the hydrographic, biogeochemical, and plankton observing program “RADIALES,” a time-series monitoring project run by the Instituto Español de Oceanografía (IEO) in the Northwest and North Iberian coastal-shelf (www.seriestemporales-ieo.net) (Nogueira et al. 2004; Bode et al. 2012; Valdés et al. 2021). Phytoplankton samples were taken by means of Niskin bottles and preserved in Lugol's solution (ca. 0.5% final concentration) for their subsequent identification in the laboratory using the Utermöhl method (Casas et al. 1997). Diatoms play a recognized prominent role in EBUEs and are responsible

for the bulk of primary production and other functions such as silicate and carbon cycling (Benoiston et al. 2017). In this study, we focus on diatom species that were present in more than 40% of the samples in the surface layer (averaged abundance from samples acquired at ca. 2, 5, and 10 m depth). This cutoff allows us to obtain consistent estimates of the wavelet spectrum (see below). The resultant 12 species that met this criterion are distributed in 8 diatoms families (Table 1) and make up on average 73% of the diatom abundance. The local wavelet power spectrum (WPS) of each diatom time series (Supplementary Fig. S3) revealed that seasonality accounted for an important part of the total variability, ranging from 31% (*Thalassionema nitzschioides*) to 68% (*Leptocylindrus danicus*).

Wavelet extraction of annual amplitudes and phases

The wavelet transform provides a time and scale specific measure of the ability of a chosen wavelet to describe fluctuations in a dataset. It has been successfully used to identify synchrony among species at particular scales and times that are otherwise obscured by patterns at other scales or by temporal averaging (e.g., Cazelles et al. 2008; Rouyer et al. 2008; Sheppard et al. 2016; Buttay et al. 2017). Wavelet analysis overcomes the problem of non-stationarity, found in this and many other ecological time-series, by performing a local time-scale decomposition of the signal (Daubechies 1992; Torrence and Compo 1998; Cazelles et al. 2008). Prior to the application of wavelet analysis, the time series of abundance of diatoms species were regularized using the “regul” function from the Pastecs R package (Ibanez and Grosjean 2013) based on the area method (Fox and Brown 1965). This method provides a linear interpolation considering all observations located at the vicinity (i.e., within 2 time-steps) of the missing observation. Low-frequency components having periods greater than one-third of the time-series length (i.e., 5 years for the diatom

abundance time-series and 18 years for the upwelling index time-series) that could not be well resolved were removed using low-pass filter (Shumway and Stoffer 2006). Finally, the regularized monthly time series of phytoplankton abundance were normalized by square root transformation and subsequently all series were standardized to zero mean and unit variance.

We employed the Morlet wavelet, a continuous and complex function that enables the extraction of the amplitudes and phases of sinusoidal components at each time and frequency combination (Cazelles et al. 2008). The relative importance of these components is resolved in the time–frequency plane to form the local WPS. The local WPS of each of the 12 diatom species is presented in Supplementary Fig. S3. Classical methods to estimate synchrony are based on the covariance between species time series. Those methods, however, fail to distinguish between scales, and as synchrony and compensatory dynamics can occur simultaneously at different scale (Vasseur et al. 2005; Keitt et al. ; Vasseur and Gaedke), we used the scale-specific wavelet quantities to estimate diatom synchrony. As such, oscillations at the annual scale were extracted to compare their amplitude and phase throughout the time series in order to characterize the temporal synchrony between the annual signals. We extracted, for each of the 12 species time series, the phases of the annual oscillation (in radian, from $-\pi$ to π) for each time-step and computed the Phase Angle Variance (PAV) among the phases of the 12 species time series using the MATLAB Circular Statistics toolbox (Berens 2009). The PAV summarizes the dispersion of the phase angle among diatom species and is thus a measure of the synchronicity (Keitt 2008): the lower the PAV, the higher is the synchronicity (i.e., Lower dispersion of phases).

To assess whether the wavelet-based quantities (either for WPS or PAV) were not only due to random processes, we determined the 5% significance level through a bootstrapping

Table 1. List of the dominant diatom species in the surface layer, showing their median abundance (cell·mL⁻¹), percentage of occurrence along the monthly time series for the period 1994–2008 and contribution of the annual variance to total variance extracted from the local wavelet power spectrum of the specie time series.

Species	Family	Median abundance (cell·L ⁻¹)	Occurrence (%)	Annual variance contribution (%)
<i>Nitzschia longissima</i>	Bacillariaceae	2.4×10^4	93	40
<i>Pseudo-nitzschia pungens</i>	Bacillariaceae	3.0×10^4	81	46
<i>Thalassionema nitzschioides</i>	Thalassionemataceae	2.1×10^3	71	31
<i>Pseudo-nitzschia delicatissima</i>	Bacillariaceae	1.3×10^4	63	41
<i>Navicula transitans</i>	Naviculaceae	6.1×10^2	60	49
<i>Guinardia delicatula</i>	Rhizosoleniaceae	9.2×10^3	58	52
<i>Leptocylindrus danicus</i>	Leptocylindraceae	1.0×10^5	56	68
<i>Chaetoceros socialis</i>	Chaetocerotaceae	1.9×10^5	51	61
<i>Detonula pumila</i>	Skeletonemaceae	7.9×10^3	43	45
<i>Asterionellopsis glacialis</i>	Fragilariaceae	1.1×10^4	41	39
<i>Rhizosolenia imbricata</i>	Rhizosoleniaceae	3.5×10^2	41	34
<i>Rhizosolenia setigera</i>	Rhizosoleniaceae	2.2×10^3	40	52

scheme that used a hidden Markov model (HMM) (Cazelles and Stone 2003). For this purpose, we tested the null hypothesis that the observed time-series patterns were different from those expected by chance alone, by generating a surrogate time-series that mimicked the original time-series, thus presenting the same distribution of values and identical short-term autocorrelation structure (Cazelles et al. 2014).

Model of competition for essential (non-substitutable) resources

Competition for essential resources is common among phytoplankton (e.g., Tilman 1980) and thus a major driver of community structure in planktonic systems. To assess the relationship between the amplitude of fluctuation of resources and the degree of synchrony between competing populations, we simulated the dynamics of two consumers that compete for two essential resources that fluctuate due to exogenous forcing. The model follows that of Leon and Tumpson (1975), describing competition among two consumers that have fixed stoichiometric demand for two essential resources (e.g., silicate and nitrogen for diatoms) and further developed in Fox and Vasseur (2008) and Vasseur and Messinger (2015).

The model is given by a system of ordinary differential Eq. (1) in which the concentration of essential resources R_i ($i = 1, 2$) is renewed according to a chemostat-dynamic with flow rate D , and supply concentration (S_i). Consumers (C_j) take-up resources according to a Droop function (g), where y_{ij} is the yield coefficient that gives the units of consumer j produced from a unit of resource i , and u_j defines the uptake rate of consumer j for resource 1. We assume a strict tradeoff between uptake rates of resources 1 and 2 for both consumers. Finally, consumers experience constant per-capita loss m_j either through wash-out or death.

$$\begin{aligned} \frac{dR_i}{dt} &= D(S_i - R_i) - R_i \sum_j C_j \frac{g_j}{y_{ij} \times R_i} \\ \frac{dC_j}{dt} &= C_j (g_j - m_j) \\ g_j &= \min(y_{1j} u_j R_1, y_{2j} \times (1 - u_j) R_2) \end{aligned} \quad (1)$$

Much is known about the conditions favoring equilibrium coexistence of competing consumers under this framework (León and Tumpson 1975; Abrams 1987; Fox and Vasseur 2008; Vasseur and Messinger 2015). The key consideration for coexistence is that consumers must be limited by different resources and must ingest a greater fraction of the resource that is most limiting to their growth. The region of equilibrium coexistence, when defined in the two-dimensional space of uptake rates u_i and u_j , is bounded by a set of 4 inequalities that determine the feasibility and stability of the community equilibrium (see Fox and Vasseur 2008).

To simulate the seasonal pattern of upwelling in the Galician system, we incorporate sinusoidal variation in the

inflow supply concentration of R_1 with an amplitude a_1 (where $0 \leq a_1 < 1$) and period τ :

$$S_1(t) = a_1 \cos(2\pi t/\tau) + 1 \quad (2)$$

Importantly, this introduces fluctuations into the densities of both competing consumers and can generate qualitative changes in the factors limiting the growth of each competitor. We analyze the change in dynamics and synchrony that occur as the amplitude of supply concentration is varied to assess how the strength of external forcing (e.g., upwelling) can alter the synchronization of competitors (e.g., diatoms). Notably, our choice of parameters describing the underlying dynamics of the system will have no qualitative impact on our results provided that stable coexistence is possible in the absence of external fluctuations.

Simulations were conducted using the “NDSolve” package in *Mathematica v11* (Wolfram Research) over the region of u_1, u_2 parameter space, which supports coexistence in the absence of external fluctuations. Simulations were run for 2500 time-steps beginning from the initial point $R_1 = R_2 = C_1 = C_2 = 0.1$. To quantify the synchrony of consumers, we calculated the Pearson correlation of the dynamics using the final 250 time-steps, which ensured that transient dynamics were no longer apparent. If the abundance of either consumer did not surpass 10^{-4} during the final 250 time-steps, we assumed that coexistence was not supported and did not calculate the correlation. The range of parameters employed is specified in the Supplementary Table S1.

Results

Natural system observations

The annual oscillations of each diatom species varied in amplitude through time (Fig. 1a). In general terms, the higher amplitudes were found from 1998 to 2005, even though some species differed from this general pattern. This was the case, for instance of *Rhizosolenia setigera* and *Chaetoceros socialis* that showed their higher amplitudes at the beginning of the series (1995 and 1996), or *Guinardia delicatula* toward the end (2006–2009). Some differences in the temporal association among those 12 species were also noticeable.

To better highlight differences in their patterns of variation, we extracted the phases of the annual oscillation from the wavelet transformation of each species' time-series and we plotted those in Fig. 1b. Angular phases locate the observed oscillation, for each time-step, on the trigonometric circle, fluctuating therefore between $-\pi$ and π radian. From 1998 to 2002, the angular phases get closer than during the rest of the time series, indicating higher synchrony during this period at the annual scale. Only one species (*Navicula transitrans*) does not follow the same pattern, maintaining temporal distance with the other species. It corresponds to a benthic, epiphytic species, which presents different life history traits (Round et al. 1990) and exhibits higher abundances during winter in the studied area (Ospina-Alvarez et al. 2014) and thus it is not likely to compete with the other

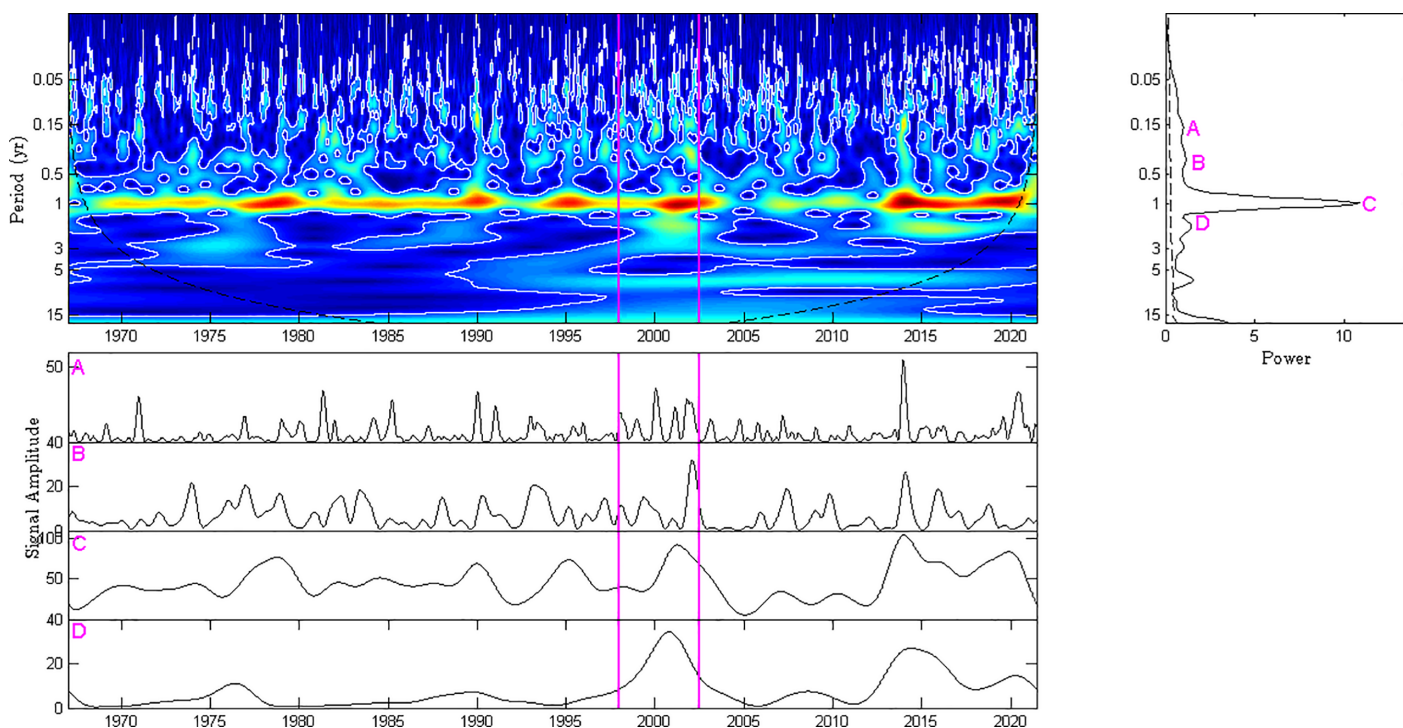


Fig. 2. Wavelet decomposition of daily upwelling index time series. **(a)** Local wavelet power spectrum (WPS); color code for power values is graded from blue (low values) to dark red (high values), and the black dashed line defines the cone of influence below which the information is affected by the edge effect, the white lines surround the 5% significance areas determined with a bootstrapping scheme based on hidden Markov chains (HMM) (Cazelles et al. 2014); **(b)** global WPS. The black line corresponds to the global power, the black dotted lines denote the 5% significance limit, the magenta letters represent the periodicities extracted and plotted in panel c; **(c)** amplitude of the extracted periodicities A: 0.14–0.15, B: 0.32–0.37, C: 0.9–1.1, D: 1.4–1.6. The magenta vertical lines on panels a and c depict the start of 1998 and the middle of year 2002, where higher diatom synchrony was found (lower PAV in Fig. 1b).

pelagic diatom species. In order to quantify the degree of synchrony, we have calculated the Phase Angle Variance (PAV) and computed, through a bootstrap approach, the 5% confidence interval below which the synchrony is higher than expected by chance alone. The PAV is almost always below the confidence interval unless in 1994 and between 2005 and 2007 because the diatom species fluctuations are mainly synchronized. Yet, the lowest values of PAV (i.e., higher synchrony) were found from 1998 to 2002, when an abrupt decrease in the PAV was observed. Another representation of the changes in all diatom species phases is shown in Supplementary Fig. S4.

Nutrient inputs in the study area are mainly driven by the dynamics of coastal upwelling, whose intensity may be estimated by means of the Ekman transport equation from the velocity of the components of geostrophic winds. We performed a wavelet transformation on the daily time series of upwelling intensity (Fig. 2). The main mode of variability was the annual (Fig. 2a), noticeable by a band of high power (predominantly red and orange colors) for a period of 1 yr in the local WPS. While its amplitude varied through time, it was significant throughout the whole series. Indeed, the annual component is also the highest peak in the global WPS (Fig. 2b) as it retained most of the variability. An important part of the variability is retained in components whose period is lower than 0.5 (i.e., 6 months) and

was present sporadically. Among those components of short periodicities, most of the power is encountered for period between 0.14–0.15 and 0.32–0.37 (approximately 1.5 months and 4 months, respectively, “A” and “B” peaks on the global WPS). Another part of the variability retained in components whose period is above the year and in particular the 1.5-year component (peak “C” in the global WPS), which was intermittently significant through the time-series. Thus, in Fig. 2c we highlighted the variability for four band-periods. The band-period “A” (1.5 month) presents high variability, with the highest amplitudes observed in 1981, 2000, and 2014. The highest amplitude for the band-period “B” (4 months) was observed in 2002 and 2014. The band-period “C” (annual component) presented high amplitude in 1979, 2001, and 2014 while the period band “D” presents its maximum amplitude around 2001. Overall between 1998 and 2002, the power was high in all the main periodic components, presenting the highest values for the period of time covered by plankton data (1994–2009) and in the case of A, C, and D among the highest for the whole 54-year upwelling index time series.

Model of competition for essential resources

Given that synchronous dynamics among diatom species (Fig. 1) arise concomitantly to changes in upwelling amplitude

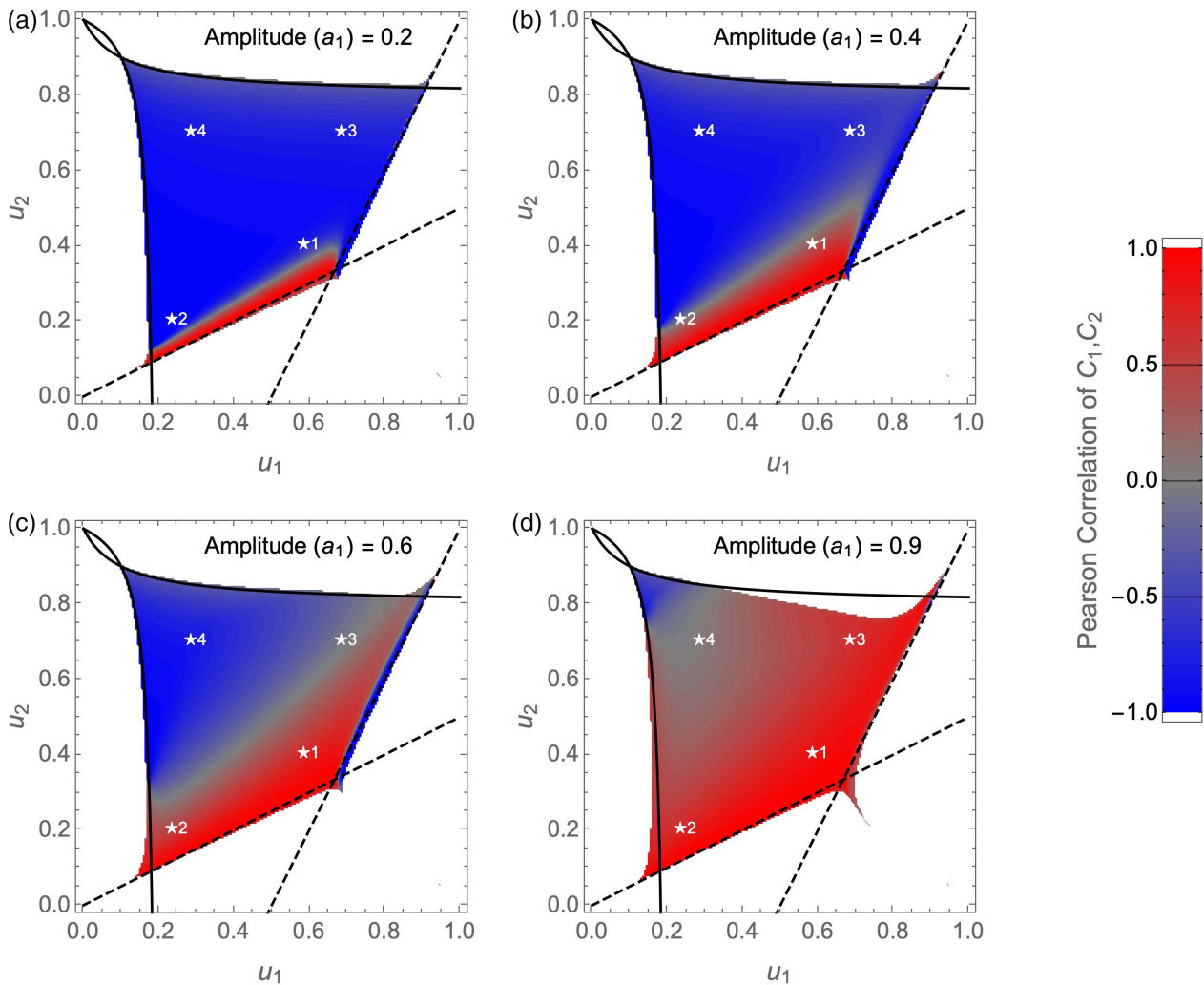


Fig. 3. Correlation between consumer populations (C_1 and C_2) within the space of equilibrium coexistence that is framed by the persistence boundaries (solid lines) and the feasibility boundaries (dashed lines). Along the persistence boundaries, consumers do not attain enough resources to achieve growth due to a mismatch between uptake and demand. Along the feasibility boundaries, consumers are not differentially limited and therefore cannot coexist at equilibrium. With the addition of sinusoidal perturbations in R_1 , synchrony first emerges along the lower feasibility boundary as this is where the smallest changes in R_1 can yield changes in resource limitation. Panels show amplitude values (a_1) of resource 1 (R_1): (a) 0.2, (b) 0.4, (c) 0.6, and (d) 0.9. The four labeled points in each scenario correspond to the parameter values used in subsequent figures; respectively these are $(u_1, u_2) = (0.6, 0.4)$, $(0.25, 0.2)$, $(0.7, 0.7)$, $(0.3, 0.7)$.

at several scales (Fig. 2), we explored the potential for transitions to synchrony to emerge in our model of competition for essential resources. Figure 3 shows the correlation between the dynamics of consumers within the parameter space, where long-term coexistence occurred for four different amplitudes of resources supply fluctuations. With small amplitude fluctuations in the supply of R_1 (Fig. 3a, $a_1 < 0.2$), the coexistence space is dominated by asynchronous oscillations of competitors with a correlation close to -1 .

Increasing the amplitude of supply of resource R_1 results in a transition to synchrony (positive correlations), which appears first near the “feasibility boundary” that denotes a transition from differential resource limitation to synonymous limitation of both competitors (at equilibrium). As the

amplitude of fluctuations is further increased, the transition to synchrony sweeps across parameter space (Fig. 3b–d). Notably, the transition from strongly asynchronous (correlation near -1) to strongly synchronous (correlation near 1) can be very sharp, suggesting that when external fluctuations are sufficiently strong, the transition to synchrony can be non-linear and rapid.

To better assess how rapid the transition to synchrony is across the space of co-existence, we selected four pairs of values of the resources uptake rates (u_1, u_2) in the coexistence region (see Fig. 3) and varied the amplitude of variation in S_1 across the full gradient values (Fig. 4). In all four cases, the correlation increases with the resource supply amplitude in a non-linear fashion (Fig. 4a). In particular, the two cases near

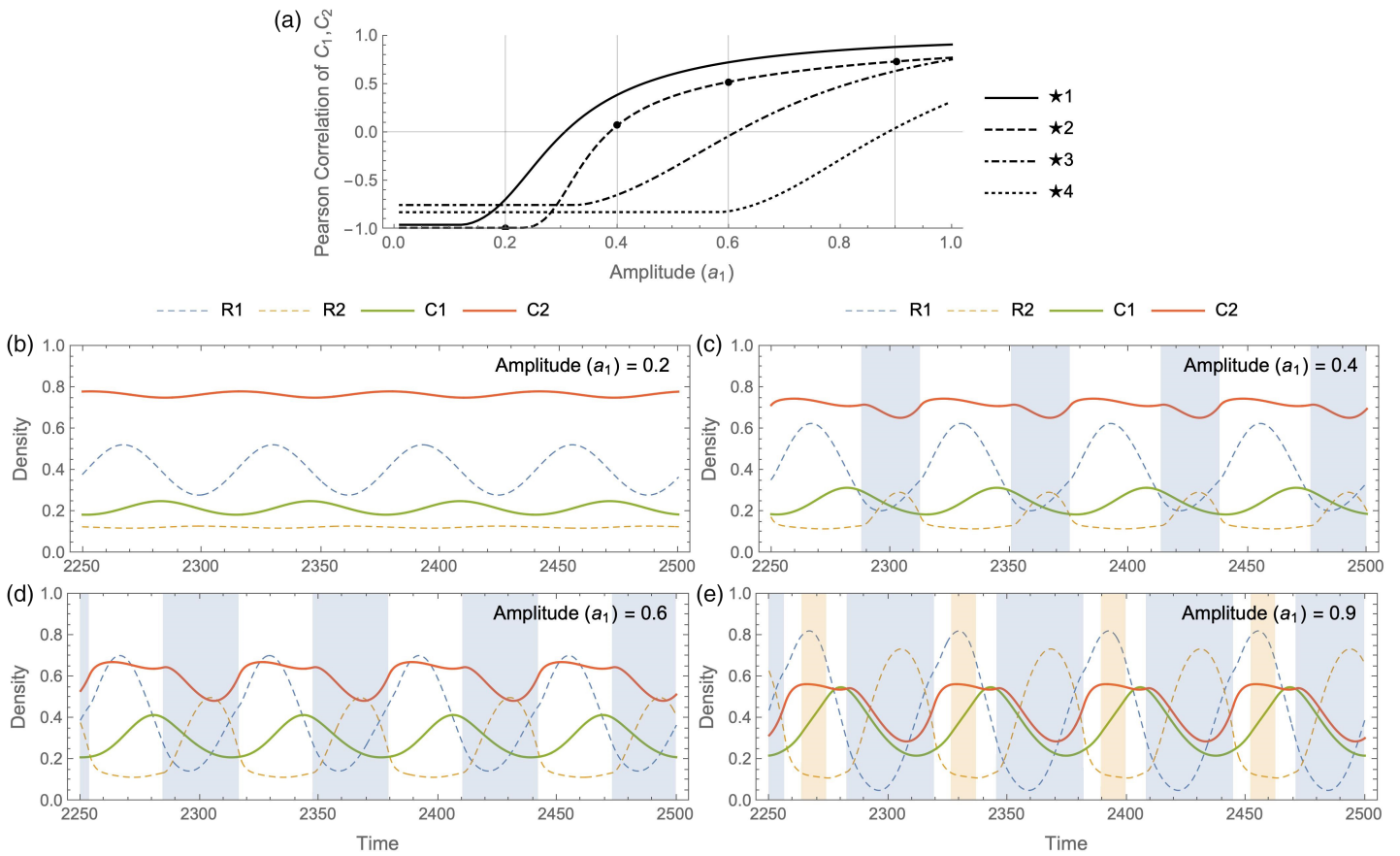


Fig. 4. Correlation between competitors and examples of resource and competitor dynamics. **(a)** Correlation between competitors C_1 and C_2 as a function of the amplitude of external fluctuations in R_1 with each line corresponding to one of the points in Fig. 3, **(b–e)** for the second parameter combination ($\star 2$) we plot the dynamics of the model at each of the four amplitudes shown by the dots in the upper panel and corresponding to the plots in Fig. 2. Here the transition to synchrony is clearly visible and coupled to an increase in the duration of periods of synonymous limitation by R_1 (blue-shaded regions) and by R_2 (tan-shaded regions). The unshaded regions of these panels correspond to periods where consumers are limited by different resources.

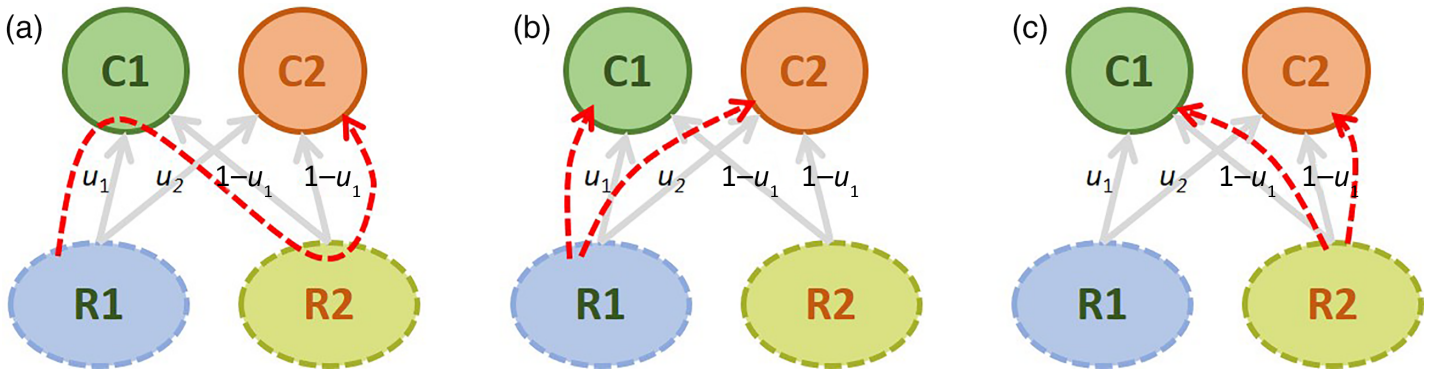


Fig. 5. The three pathways by which the limitation in R_1 impacts the consumers in our model. **(a)** Asynchronous pathway: When C_2 is limited by R_2 , R_2 is supplied in excess and therefore small fluctuations in R_1 do not directly impact the growth of C_2 . Rather, these fluctuations are transmitted by the red arrows and introduce a temporal lag that inhibits synchronization. **(b)** Synchronous pathway: When fluctuations in R_1 are large enough, R_1 can be limiting for both consumers near the lower part of the cycle. **(c)** Synchronous pathway: When R_1 is very abundant near the upper part of the cycle and both consumers are limited by R_2 .

to the lower feasibility boundary (cases 1 and 2) demonstrate an earlier and relatively sharper transition to synchrony. The mechanism driving this transition is clearly visible when looking at the temporal dynamics of the system (Fig. 4b–e). At small amplitudes of fluctuations in S_1 , the consumers maintain their equilibrium pattern of differential limitation; however, as fluctuation amplitudes increase, temporal periods of low R_1 availability generate synonymous limitation by R_1 and temporal periods of high R_1 availability generate synonymous limitation by R_2 (Fig. 4). During these periods of co-limitation, both C_1 and C_2 exhibit largely coherent dynamics, declining in response to declines in R_1 , and increasing in response to increases in R_1 .

The abrupt change of state described in the Galician ecosystem and in our model relies on the tendency for anti-synchronous dynamics to emerge when external perturbations are small. In our model, coexistence relies on niche differentiation and requires that each competitor consumes more of the resource that limits its growth (León and Tumpson 1975). At equilibrium, it is impossible to measure correlation due to the absence of fluctuations in density. However, the equilibrium behavior can easily explain the patterns observed for small amplitude fluctuations in S_1 . Fluctuations in S_1 directly generate fluctuations in R_1 albeit with a small time-lag (our model could impose fluctuations in R_1 and yield the same result). Because the growth of C_1 is limited by R_1 , these fluctuations impact C_1 directly causing it to fluctuate. In contrast, the growth of C_2 is limited by R_2 and R_1 is available in excess, thus it does not respond to the fluctuations in R_1 . It does, however, experience some of the fluctuations in its competitors' density because C_1 uses a varying amount of resource R_2 to balance its stoichiometric requirements for growth. This generates a relatively longer pathway for C_2 to experience the external fluctuations relative to C_1 (Fig. 5) and as a consequence a temporal lag is introduced in the dynamics of C_1 and C_2 resulting in an anti-synchronous (negative correlation) dynamic. The two path diagrams shown in Fig. 5 represent two dominant modes that the system can alternate between as S_1 fluctuates. A third mode can also emerge to reinforce synchrony when R_1 is very abundant and both consumers are limited by R_2 (see Fig. 4e).

Discussion

The rapid transition to and from synchrony that we describe for the diatom community in the shelf waters of Galicia (sta. E2 off A Coruña) could arise through a multitude of mechanisms that combine both the impact of biotic and abiotic controls on population dynamics. While the model that we present above is not intended to accurately depict the precise nature of abiotic and biotic interactions among competitors in this system, it does provide a parsimonious explanation for the sudden onset of synchrony that arises when upwelling (or another input mechanism) increases the periodic availability of nutrients.

The key mechanism we describe is Liebig's law of the minimum, which ensures that phytoplankton growth occurs at a rate governed by the resource that is most limiting (Kaiser et al. 1994) and generates a discontinuous change in population dynamics when limitation shifts from one resource to another. Given that there is documented variation in stoichiometric requirements among diatom species (Lomas et al. 2019), identifying the transition values for dominant species may be particularly important for both validating our hypotheses and predicting critical transition to synchrony in phytoplankton communities. Theory and empirical work both predict that there are a variety of different factors influencing the temporal structure and dynamics of plankton communities. On one hand, abiotic forcing is expected to promote synchrony among species that have similar functional traits (Rocha et al. 2011); however, density-dependent processes, such as competition or predation, have an antagonistic effect that can force populations to separate in time in order to coexist (i.e., temporal niche differentiation) (e.g., Vallina et al. 2017). Phytoplankton populations' growth depends on several factors such as light, temperature, and nutrient availability. In the Galician coast, the availability of nutrients, such as nitrate and silicate, is highly controlled by wind-driven upwelling cycles of nutrient-rich waters (Nogueira et al. 1997; Doval et al. 2016). Inter-specific competition for nutrients operates when they are depleted in the euphotic layer, giving rise to succession between species with different stoichiometric requirements. Therefore, it is expected that when nutrients are not limited, the strength of competition relaxes, allowing different species of the community to grow simultaneously. Previous work in temperate lakes has shown a seasonal transition from synchrony during winter and spring, when nutrients are non-limiting, to compensatory dynamics (asynchrony) during summer and fall, when phosphorus is in short supply (Vasseur et al. 2005). From our observations, the period of high synchrony occurring from 1998 to 2002 among diatom species corresponds to a period in which upwelling amplitudes increased at several of the dominant temporal scales. It is likely that the higher input of nutrients between 1998 and 2002, such as nitrate and silicate, relaxes the intensity of competition for these essential nutrients for the growth of diatom species, thereby allowing a previously obscured factor to influence their dynamics in a fashion that favors synchrony.

Although, our model includes only two species of competitors and two resource types, the transition to synchrony that we observe under resource fluctuations generalizes well to more species-rich communities. We have demonstrated that the transition to synchrony begins when resources fluctuations are large enough that they generate periods of synonymous limitation, where both competitors are limited by the same resource (Fig. 4). This result extends to more species-rich communities; provided that all competitors have an essential requirement for the fluctuating resource, there is a threshold at which all competitors will be limited by the same resource and will therefore synchronously track fluctuations in that resource. We employ an explicit model of competition in

order to capture the importance of resource limitation. The more widely used Lotka-Volterra framework, which assumes that competition scales linearly with the density of heterospecifics, cannot adequately capture the effect of essential resources; however, a recent study demonstrated that the inclusion of higher-order terms in Lotka-Volterra models can allow them to more accurately depict the dynamics of explicit resource competition Letten and Stouffer (2019). Further research into the impact of resource fluctuations on synchrony will undoubtedly offer greater insight into how the assumptions governing resource uptake and competition are reflected in community-level patterns.

Numerous works have proposed to classify communities on whether they fluctuate in synchrony or in compensatory dynamics (e.g., Keitt and Fischer 2006; Houlahan et al. 2007; Vasseur and Gaedre 2007; Downing et al. 2008; Keitt 2008; Gonzalez and Loreau 2009; Jochimsen et al. 2013; Vasseur et al. 2014) and only some of them have discriminated different scales of variability (Vasseur and Gaedke 2007; Vasseur et al. 2014). It is not surprising that synchronous dynamics is the main mode of variation observed at the annual scale in latitudes where seasonal variations of abiotic and biotic factors control, to a large extent, the abundance of organisms. In our study system, located at intermediate latitude and strongly influenced by coastal upwelling processes, we have shown that diatom species tend to fluctuate in synchrony, presenting high abundances from April to September (i.e., during the upwelling favorable season). Indeed, the phase angle variance (PAV; metric of temporal association, inverse of synchrony) is only sporadically above the confidence interval, even though the temporal association among diatoms varied over time. A previous study on zooplankton dynamics in a southernmost location of the Galician coast (Ría de Vigo) also revealed that the synchrony was the main mode of variation at the annual scale (Buttay et al. 2017). Other studies that have been carried out on plankton communities have also revealed that the temporal structure of the community can change through time and, in particular, they have shown that such changes can occur suddenly (Keitt 2008; Jochimsen et al. 2013; Buttay et al. 2017).

It is worth noting that synchronous and compensatory dynamics can occur simultaneously but at different timescales (Vasseur and Gaedke 2007; Downing et al. 2008) or at different periods (Vasseur and Gaedke 2007; Jochimsen et al. 2013; Jochimsen 2013; Vasseur et al. 2014; Buttay et al. 2017). The sampling frequency of phytoplankton in our study does not allow us to study periodicities below 3 months (such as the 2–3 weeks or 6 weeks periodicities depicted in the upwelling index series). Even though other scales have been explored, synchrony among diatom species has been detected only at the annual scale, while the changes in upwelling were noticeable at several scales. In a previous work carried out in the southern part of the Galician coast on zooplankton communities, the upwelling high-frequency mode was also indicated to

have favored synchrony among zooplankton species at the annual scale (Buttay et al. 2017). Indeed, it has been shown that the effects of a perturbation occurring at a specific scale can be redistributed to other frequencies (Greenman and Benton 2005) although there is no clear evidence of the underlying mechanisms.

Synchrony has been proposed to alter the stability of the community and although Scheffer et al. (2009) state that there is little empirical evidence, they proposed that in cyclic systems the phase locking of different oscillators may provide an Early Warning Signal (EWS) of critical transition. Since then, some examples have arisen. Jochimsen et al. (2013) showed that the plankton community of the Constance lake (Switzerland), affected by a long-term decrease in phosphate, started fluctuating in synchrony. They hypothesized that the subsequent regime shift they observed was favored by the loss in compensatory dynamics. In the southern Galician coast, zooplankton community presented a shift in abundances between two stable states, which started with all the components of the community fluctuating in synchrony (Buttay et al. 2016, 2017). More recently, the results of a long-term experiment on nutrient enrichment in alpine grassland revealed that nutrient enhancement induced an increase of the synchrony between the dominant plant species, which in turn contributed to a decline of the ecosystem stability (Song et al. 2019). In a recent study base on the same study area, Bode et al. (2020) showed that the plankton community off A Coruña experienced two important changes described as regime shift, one between 1997 and 1998 affecting zooplankton taxonomic groups and phytoplankton species abundances and one between 2001 and 2002 affecting the abundance of micro-zooplankton groups and zooplankton community assemblages. Interestingly those changes occurring in 1997–1998 and 2001–2002 delimited the period of high synchrony observed in the diatom community. Diatom community does not show evidence of sustained change; the abundances varied during the synchrony period, but get back to average values soon afterwards. This may potentially indicate a higher resilience of the diatom community.

Regime shifts can happen due to alternative stable states. One classical example comes from the dynamics of shallow lakes moving back and forth from a clear state dominated by aquatic vegetation to a turbid state dominated by algae (Scheffer et al. 1993). Strong non-linearity could arise in response to a change in some parameters, as we observed here with the sudden enhancement of synchrony associated to small variations in the amplitude of nutrient input. Since synchrony has been suggested to impact communities' stability, abrupt increase of synchrony could potentially also trigger a regime shift. Early warning signals of regime shifts are notoriously hard to detect (Clements and Ozgul 2018). Classical methods to identify EWSs of regime shifts consist in searching for a critical slowing down (CSD) that occurs when the system is close to a tipping point. As the system takes more time to

bounce back for small perturbations close to a tipping point, variance and autocorrelation are expected to increase (Scheffer et al. 2009). It is often difficult to distinguish trends in summary statistics, such as variance and autocorrelation, from noise because they are highly dependent on the sampling frequency and the method employed to aggregate data (Clements and Ozgul 2018). Synchrony, which can be computed by different methods, might therefore provide an additional suitable EWS.

Acknowledgments

This study was conducted within the framework of the LOTOPEL project (CTM2013-16053. Ministerio de Ciencia e Innovación, Spain). L.B. was supported by an FPI Ph.D. grant from the Instituto Español de Oceanografía. The authors acknowledge the phytoplankton taxonomic identification carried out by Manuel Varela and the nutrients analysis carried by both Nicolás González and Rosario Carballo. The authors also thank the crew of RV Lura and their colleagues from the Centro Oceanográfico de A Coruña that carry out the monthly monitoring of the hydrography, biogeochemistry, and plankton in the Ría de A Coruña within the framework of the time series monitoring program RADIALES (www.seriestemporales-ieo.net).

Data availability statement

All the data used within this study are available in PANGAEA (<http://doi.pangaea.de/10.1594/PANGAEA.855901>).

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Conflict of interest

None declared.

Submitted 14 February 2021

Revised 17 November 2021

Accepted 17 January 2022

Guest editor: James B. Heffernan