Environmental multi-scale effects on zooplankton inter-specific synchrony

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Abstract

Knowledge on the mechanisms that drive population dynamics and shape community structure is a key issue in ecology. Using wavelet methods, we analyzed 17-yr of monthly time-series of marine zooplankton (taxonomic composition, total abundance, and biomass) and their relationship with environmental factors (upwelling index and river outflow). The main mode of variation in all series was annual, and exhibited year-to-year variability. The dynamics of zooplankton aggregated properties showed a strong association with upwelling index and river outflow. The annual oscillation of biomass and abundance increased in 2000 corresponding to the highest amplitudes of environmental forcing. Concomitantly, enhanced synchrony was observed among the main taxonomic groups of zooplankton and among copepod species, the most relevant group in terms of occurrence and abundance. The degree of synchrony appeared to be correlated with the upwelling index and, more closely, with the duration of the upwelling events. The amplified seasonality of the environmental variables from 2000 to 2004, combined with a reduction of off-shore exportation by shortening of upwelling events, favored retention in winter, and primary production in summer. These changes modulated community aggregated properties and affected the stability of the zooplankton community through an increase in inter-specific synchrony allowing the community to shift to another state and likely a reorganization of the community size structure.

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fluctuations can strongly modify system dynamics instead of just increasing system variance (Chesson 2003). Those findings suggest that community composition data is needed in order to assess the biological effects of environmental disturbances.

Determining the relative strength of biotic and abiotic forces needed to shift between compensatory and synchrony dynamics remains controversial. One of the reasons is the difficulty to identify and model the effect of key environmental drivers (Mutshinda et al. 2009) and the need to use quantitative methods able to cope with the nonstationary nature of the data, given that community properties and environmental forcing response are susceptible to fluctuate in time. Wavelet analysis is a suitable numerical tool for nonstationary time-series that performs a local time-scale decomposition of the signal (Lau and Weng 1995; Torrence and Compo 1998; Cazelles et al. 2008) and allows to determine the dominant modes of variability and track their change through time (Kláva et al. 2004). It also permits a scale-dependent analysis of the coupling between drivers and response variables (Ménard et al. 2007) and the inspection of the level of synchrony among signals (Keitt et al. 2006; Vasseur et al. 2014).

The functioning of the Galician ecosystem has been intensely studied (e.g., Bode et al. 1998; Nogueira et al. 2000; Cabal et al. 2008; Ospina-Alvarez et al. 2010; Roura et al. 2013). The region, influenced by contrasted seasonal fluctuations in upwelling and precipitation, offers a good case study to infer the relationship between environmental forcing and community dynamics. Additionally, zooplankton has been proposed to be a good sentinel of environmental changes (Taylor et al. 2002; Hays et al. 2005) being therefore an appropriate biological model to study the effects of abiotic factors on population dynamics. For instance, competitive interactions between two marine zooplankton species, giving rise to compensatory dynamics at decadal scale, have been identified in the North Atlantic (Fromentin and Planque 1996). However, investigations focusing on the dynamics of whole zooplankton communities have been based mainly on freshwater ecosystems (Keitt et al. 2006; Keitt 2008; Vasseur et al. 2014), so there is a scarcity of studies dealing with zooplankton dynamics of natural marine populations. A previous analysis of the dataset used in the present work described significant changes on the zooplankton community (Buttay et al. 2016). More precisely, an important increase of the abundance of the whole zooplankton community as well as all the main taxa studied was observed from 2001 onwards. Some meteo-climatic variables were highlighted as possible drivers for such long-term increment, but the methods employed did not allow us to explore in depth neither the coupling between zooplankton abundances and environmental drivers nor the temporal scales involved in such coupling.

In the present study, we pursue three main objectives: (1) to analyze the main components of temporal variability in zooplankton aggregated properties and meteo-hydrographic variables, how their periodic components fluctuate in time and their possible association; (2) to quantify the synchrony at the annual scale and its changes through time at two community levels: among major taxonomic groups and among copepod species; and (3) to explore the relationship between synchrony and the multi-scale variability of the environmental drivers in order to infer the processes that shape the structure of the zooplankton community.

**Material and methods**

**Study area**

The northwest Iberian shelf is located in a temperate latitude, at the northern limit of the Canary current upwelling system (Aristegui et al. 2009). As such, the region is characterized by a strong seasonality mainly driven by the alternation, at the annual scale, of wind regimes. From mid-spring to early-autumn, the predominance of northerly winds promotes the upwelling of sub-surface waters, injecting inorganic nutrients to the surface layers that fuel primary production. Upwelling dynamics interact with the circulation within the rías, reinforcing across-shelf export. The rest of the year, southerly and westerly winds predominate, inducing downwelling over the shelf and rainfall over the western Iberian Peninsula. The combination of river runoff and downwelling favor the establishment of the western Iberian buoyant plume (WIBP) (Peliz et al. 2002), which further contributes to shelf retention processes. Nevertheless, a large fraction of upwelling–downwelling and river outflow variability occurs at short-term scales (from days to weeks), also affecting plankton dynamics (Nogueira et al. 2000).

**Zooplankton community and environmental variables**

Zooplankton was sampled monthly from 1994 to 2011 within the framework of the ongoing RADIALES monitoring program (http://www.seriestemporales-ideo.com/), at two stations on the southern part of the Galician sub-region: in the central part of the Ría de Vigo (Sta. 1; 42.213°N, 8.850°W; ca. 40 m isobath), and in the adjacent mid-shelf, off the ría’s mouth (Sta. 3; 42.142°N, 8.958°W; ca. 100 m isobath). Samples were taken by means of oblique hauls with a double 40 cm diameter Bongo net of 200 μm mesh size from the surface down to 5 m above the sea floor. Methods for sampling and sample processing were consistent throughout the time series. The sample from one cod-end of the net was preserved in 4% tetraborate-buffered formaldehyde. Subsequently, zooplankton organisms from a subsample (at least 1000 individuals) were identified under a stereoscopic microscope at the lowest possible taxonomic level and counts were converted to full-sample number of individuals per m$^{-3}$. The sample from the second cod-end of the net was filtered and
subsequently dried during 24 h at 60°C in order to estimate the sample biomass as mg dry weight m⁻³.

Different levels of zooplankton community assembly were considered: aggregated properties (total zooplankton biomass and total abundance) and abundance of the zooplankton taxonomic groups and of the species of copepods, which is the most relevant taxa in terms of occurrence and contribution to total zooplankton abundance (Supporting Information Tables S1, S2).

Meteo-hydrographic variables, which are known to play a significant role on ecosystem dynamics in the studied area, were also analyzed (Buttay et al. 2016). Time series of daily upwelling index (m³ s⁻¹ km⁻¹) were provided by the Instituto Español de Oceanografía (http://www.indicedealforamiento.ieo.es/). The index was calculated by the Ekman transport equation (Bakun 1973) from geostrophic winds estimated at 43.8°N, 11.8°W, which is considered a representative location for the characterization of wind driven coastal upwelling/downwelling (forced by northerly/southerly winds) along the Galician coast (Lavin et al. 1991). Also, the short-term variability of upwelling was estimated by calculating the duration of upwelling events, defined as the number of consecutive days with positive upwelling index. Daily outflow (m³ s⁻¹) from river Miño at the gauge station of Frieira, which covers 86% of the total drainage basin of the river system (17,570 km²) that outflows in the study area, were provided by the Confederación Hidrográfica del Miño-Sil (http://www.chminosil.es/es/).

Data preparation
Upwelling and river outflow data had daily resolution whereas zooplankton sampling was carried out on an approximately monthly basis (32 ± 7 d). Prior to the application of wavelet analysis, the time series of environmental variables were monthly averaged and those of zooplankton abundance were regularized using the “regul” function from the Pastecs R package (Ibanez and Grosjean 2013) based on the area method (Fox and Brown 1965). Low-frequency components having periods greater than 6 yr (corresponding to one-third of the total length of the time-series) could not be well resolved, and so they were removed using a 6-yr low-pass filter (Shumway and Stoffer 2006). Finally, the monthly time series of zooplankton abundance and Miño outflow were normalized by square root transformation and subsequently all series were standardized to mean zero and unit variance due to their different units and scales of measurement.

Wavelet analysis
For all time-series, we used the Morlet wavelet, a continuous and complex wavelet that enables the extraction of time-dependent amplitude cycles and whose scales are related to frequencies (Ménard et al. 2007; Cazelles et al. 2008). The relative importance of frequencies for each time step may be represented in the time–frequency plane to form the local wavelet power spectrum (WPS) on a 2D plot. Discontinuities, however, exist at the border of the data, and the corresponding affected region growing in extent as the scale increases, is delimited by the cone of influence (Tessereau and Compo 1998). Therefore, the information below the cone lacks accuracy and should be interpreted with caution. We also computed the global WPS as the time-average of the local WPS for each frequency component, which provides an unbiased, consistent alternative to the Fourier spectrum in order to summarize the dominant periodicities of the series (Percival 1995) and to calculate the relative contribution of the annual component through the time-series.

The wavelet coherence (WCo) is suited to analyze the transient patterns of co-variation between pairs of signals (Grinsted et al. 2004; Cazelles et al. 2008) by representing, in a time–frequency plane, information on where two non-stationary time series are locally linearly correlated. In the present work, it was applied to compare meteo-hydrographic variables (i.e., upwelling index and river outflow) with total zooplankton biomass and, additionally, their phases for the seasonal mode were extracted and compared (Cazelles et al. 2008). To assess whether the wavelet-based quantities (either for WPS or WCo) were not only due to random processes, we determined the 5% significance level through a bootstrapping 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).

The metrics classically employed to quantify the temporal associations between species are based on covariance quantities (e.g., Loreau and de Mazancourt 2008; Gouhier and Guichard 2014) and did not allow to distinguish between the different scales of variation (Vasseur et al. 2014). In the present work, wavelet decomposition has been applied to the abundance time series of taxonomic groups and copepod species which occurred in more than 30% of the samples: 15 taxonomic groups and 12 copepod species in Sta. 1 (15 taxonomic groups and 15 copepod species in Sta. 3). A description of the selected taxonomic groups and copepod species cycles is provided in the Supporting Information Table S1. The oscillations that corresponded to the annual scale were then extracted from all series to compare their characteristics (i.e., amplitude and phase) throughout time.

We quantified the dispersion of the phases in order to characterize the temporal synchrony between the annual signals (Cazelles and Stone 2003; Keitt 2008). To this aim, we computed the angular variance from the extracted phase angles of the annual modes at each time step using the MATLAB Circular Statistics toolbox (Berens 2009): the lower the phase angle variance, the higher is the synchrony among series. The HMM bootstrap method was also used to determine whether the variances of the phase angle values...
observed (i.e., degrees of synchrony) were lower from those expected by chance alone, simply by putting the one-sided 95% confidence interval. Additionally, we explored the relationship between environmental variability and the degree of synchrony by comparing the phase angle variance from a precise date each year (1st July) with the annual averaged environmental variables.

The results presented here correspond to the sampling location within the ría (Sta. 1). Results for Sta. 3 (mid-shelf, off the ría’s mouth) are shown in the Supporting Information. In general terms, similar zooplankton dynamics were observed in both spatial domains, but between-site differences worth to mention are discussed. The numerical analyses were mainly performed using a MATLAB wavelet package (www.biologie.ens.fr/~cazelles/bernard/Research.html).

**Results**

**Dynamics of zooplankton aggregated properties and environmental variables**

The time series of zooplankton aggregated variables (total biomass and abundance) and environmental drivers (upwelling index and Miño outflow) are presented in Fig. 1. The local WPS of total zooplankton biomass (Fig. 1a) and abundance (Fig. 1b) revealed the presence of a 1-yr periodic component which, despite its presence throughout the entire 17-yr time series, varied in power from year-to-year and was statistically significant from 2000 onwards. The highest power at the annual scale was recorded between 2002 and 2006 for abundance and between 2005 and 2010 for biomass. Similar patterns were observed in the mid-shelf site (Sta. 3), with the exception of the year 2005 during which the 1-yr periodic component was absent in biomass and a 2-yr periodic component that was present in the abundance series (Supporting Information Fig. S1). The annual component represented on average 61% of the variance of total zooplankton biomass and 67% of the variance of total zooplankton abundance at Sta. 1 (at Sta. 3, it represented 63% and 61% of total zooplankton biomass and abundance, respectively).

River Miño outflow showed one main periodic component (Fig. 1c), which was annual and intermittent, being disrupted from 1998 to 2000 and between 2005 and 2009. This component represented on average 61% of the variance of total zooplankton biomass and 67% of the variance of total zooplankton abundance at Sta. 1 (at Sta. 3, it represented 63% and 61% of total zooplankton biomass and abundance, respectively).
to important river discharges during that period, especially in 2001. The local WPS of the monthly time series of upwelling index (Fig. 1d) presented a unique significant 1-yr periodic component that was more marked from 2000 to 2004 and interrupted between 2004 and 2006. This annual component represented on average 53% of the total variance of the monthly time series. Thus, the highest annual amplitudes in the time series of upwelling index and outflow from river Miño occurred between 2000 and early 2004, and were concurrent with the beginning of the period (from 2000 onwards) characterized by enhanced annual cycles of zooplankton aggregated variables.

The WCo corroborated the strong association between meteo-hydrographic variability and zooplankton total biomass and abundance. The coherence is particularly consistent at the annual scale (Fig. 2a,b). The comparison of phases for the annual component revealed that total zooplankton biomass (and abundance, not shown) fluctuated in synchrony with upwelling. In contrast, a phase difference of $\pi$ radians (i.e., 6 months) was observed between the annual phases of total zooplankton biomass and outflow from river Miño series (Fig. 2c,d).

**Dynamics of zooplankton taxa and copepod species**

A description of the significant periodic components present in the time series of zooplankton taxa and copepod species, derived from the inspection of the respective global and local WPS, is given in Supporting Information Table S1. All taxa used in this study presented an annual cycle, consistent in both the local and global WPS. In addition, Cirripedia larvae and Polychaeta (only in Sta. 3) presented shorter periodic components of the order of 6 months. They also presented, as was the case for most of the major taxonomic groups of meroplankton (larvae of Bivalvia, Gasteropoda, and Decapoda), significant periods of 2 yr. The time series of copepod species were also dominated by the annual oscillation; oscillations at shorter scales were observed sporadically in *Pseudocalanus elongatus* and *Oithona similis*. Multi-annual periodicities were more frequent; cycles of 1.5 yr to 3 yr were observed for the time series of *Calanus helgolandicus*,
P. elongatus, Euterpeina acutifrons, Oncaea media, Oithona nana and O. similis.

The annual component extracted from each zooplankton taxa and copepod species are shown in Fig. 3a,b, respectively. The amplitude of the seasonal mode of all taxonomic groups series increased from 2000 to 2003, and decreased afterwards showing, in 2011, amplitude values that were similar to those found at the beginning of the series (Fig. 3a). The amplitude of the seasonal mode of copepod species showed a similar pattern (Fig. 3b).

The time series of the angular variance among zooplankton taxa and among copepod species (red line on Fig. 3a,b, respectively) showed a common general pattern. Both series presented an abrupt decrease after 1999, followed by a period of significantly low angle variance values between 2000 and 2004. During this period, the annual phases were closer, which is indicative of a higher degree of synchrony among zooplankton taxa and copepod species. While the phase angle variance among taxonomic groups was significant through the whole series, for the copepod assembly significance was lost from January 1999 to June 2000 and from February 2005 to June 2006. We further explored the relationship between environmental variability and the degree of synchrony (i.e., annual phase angle variance) among zooplankton community components. All environmental variables tested are described in the Supporting Information Fig. S4. We found no significant relationship between the annual average of upwelling intensity and the phase angle variance among copepod species ($r = 0.44$; $p$-value $= 0.09$) or among taxonomic groups ($r = 0.36$; $p$-value $= 0.18$). A significant relationship was found, however, between the phase angle variance and the annual average duration of upwelling events, defined as the consecutive number of days of upwelling occurrence between downwelling episodes). The annual mean duration of upwelling events (Fig. 4) ranged between 7 d (in 2003) to 13 d (in 1995 and 2005), and the shorter the duration of events, the lower the angle variance (i.e., the stronger the synchrony) among population abundances. This relationship was statistically significant at both community assembly levels, but higher for copepod species ($r = 0.60$, $p$-value $= 0.02$) than for main taxonomic groups ($r = 0.51$, $p$-value $= 0.05$). The period between 2000 and 2004 corresponded to the highest degree of synchrony and shorter duration of upwelling events. In Sta. 3 (mid-shelf), despite a concurrent period of low phase angle variance between 2000 and 2004, no significant relationships with upwelling index or with the duration of upwelling events were found.
In the present work, we have studied the dynamics of a natural marine zooplankton community at different levels of organization and their relationship with fluctuating abiotic factors. To this aim, we applied wavelet methods to 17-yr (1995–2012) monthly time series of community aggregated properties (biomass and abundance), species composition and meteo-hydrographic factors (coastal upwelling and river runoff). Long-term data of zooplankton represent a considerable effort in taxonomic identification, and to our knowledge no previous studies have focused on the scale-dependent fluctuations of aggregated properties or interspecific synchrony within a natural, non-manipulated marine zooplankton community.

**Temporal patterns and coupling between aggregated zooplankton properties and environmental variables**

The principal mode of temporal variation observed in all zooplankton and environmental time series was annual. It represented between 53% and 67% of the total variance of the monthly time series and exhibited in all cases a significant year-to-year variability in amplitude. In both time-series of aggregated zooplankton properties (biomass and abundance), the statistical significance of the annual component started in 2000, pointing to an increase in amplitude at the annual scale. A previous study on the same data set that used classical methods unable to distinguish between scales (Cumulative sums to identify long-term trends in the series combined with Generalized linear model to model the main temporal patterns—long-term, seasonal, and autocorrelation structure), described a stepped increase in the abundance series occurring in 2001, followed by a light decrease in 2006 (Buttay et al. 2016). Similarly, the wavelet transform depicted a decrease in the annual component for the abundance series after 2006. In contrast, the total biomass series continued increasing, suggesting a possible structural change within the community towards larger sized organisms. This pattern was observed in both costal and mid-shelf stations but additional data of organisms’ size would, however, be necessary to corroborate those changes.

The relationship between the annual cycles of total biomass (and abundance) of zooplankton and upwelling/downwelling index and river outflow revealed by the WCo confirmed the major importance of these weather-induced factors on the seasonal dynamics of zooplankton in the studied area. It is worth noting that the seasonality of zooplankton aggregated properties arose when the annual amplitude of upwelling and river outflow were maximal. The higher amplitudes of the annual signals of these abiotic factors observed between 2000 and 2004 are indicative of enhanced contrast between the winter and summer seasons, due to changes in wind patterns at regional scales and related to sustained trends of large-scale climatic patterns in the North Atlantic during that period (Buttay et al. 2016). Within this configuration, strong upwelling and dry/sunny weather in summer cause higher primary production, while strong downwelling and precipitation in winter promote the reinforcement of the WIBP that, by influencing shelf circulation and across-shelf transport processes, favors the retention of planktonic organisms at the coast (Peliz et al. 2002; Otero et al. 2008). Those changes in the winter conditions may have important ramifications for the plankton community because small variations in the overwintering stock of organisms are magnified by exponential growth and can cause major changes in the summer populations (Colebrook 1979). The shortening of upwelling events, also observed during the same 2000–2004 period, could have favored the retention of organisms at the coast by diminishing the strength of the across-shelf exchanges processes as well (Iles et al. 2012). Indeed, a previous study conducted in the Galician region described a decrease in zooplankton abundances within the oceanic domain and pointed out to the reduction of the offshore exportation of organisms as a possible mechanism (Bode et al. 2009).

![Fig. 4. Annual phase angle variance computed on the seasonal mode of copepod species abundances (red), taxonomic groups (red dotted line) and annual average duration of upwelling events (black) at Sta. 1. (r = 0.60, p-value = 0.02 and r = 0.51, p-value = 0.05 for copepod and taxonomic groups, respectively).](image-url)
Inter-specific synchrony: variability and possible drivers

In a changing environment, coexisting species should tolerate similarly environmental variability and consequently, natural selection exerted by environmental drivers on functionally similar species can lead to synchronous dynamics, where all species rise and fall together (Rocha et al. 2011). In the Galician coast, which is considered a highly variable environment, it is not surprising that zooplankton populations fluctuate in a relative level of synchrony, presenting high abundances from late spring to early autumn during the upwelling favorable period of the year (Valdés et al. 1990; Buttay et al. 2016). The use of wavelet methods in this study allowed us to detect temporal changes in the degree of synchrony by computing the time evolution of the angular variance among the species annual phases. It is worth noting that concomitantly with the enhanced seasonality in upwelling and river outflow observed from 2000 to 2004 and the substantial increase in zooplankton aggregated properties, higher synchrony was observed among copepod species and taxonomic groups at the annual scale in both sampling stations. It is also notable that the selected taxonomic groups are functionally diverse. Indeed, different feeding habits (predators, filter-feeders...) are represented and while most of the groups are part of the holoplankton, some pertain to the meroplankton (those that are planktonic only for a part of their life cycle: e.g., Cirripedia larvae, Echinodermata larvae). Despite the fact that some different dynamics may occur within the taxonomic groups and blur synchrony detection, similar patterns in synchrony were observed among copepod species and taxonomic groups. The degree of synchrony and the duration of upwelling events appeared to be significantly correlated and higher synchrony was indeed associated with an increase of upwelling frequency. Even though high synchrony was encountered in both stations during the period of shorter upwelling events (2000–2004), the relationship was not statistically significant at the mid-shelf station. We hypothesize that this station, being located at the interface between coastal and oceanic domains (Roura et al. 2013), receives occasionally oceanic influences that may blur the effect of coastal upwelling.

It has been shown that the effects of an environmental driver 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: Did shorter upwelling events prevent compensatory dynamics from occurring by increasing the frequency of disturbances? Or did shorter upwelling events support higher primary production leading to a reduction of interspecific competition and thus the need of temporal differentiation among populations? Additional data on phytoplankton production would have been necessary to answer those questions however.

Because community composition data are difficult to obtain on a routine basis (i.e., time consuming and taxonomic expertise required), temporal changes in inter-specific synchrony among zooplankton populations have been described in few studies (Keitt et al. 2006; Keitt 2008; Jochimsen et al. 2013; Vasseur et al. 2014). Two freshwater systems were in particular studied: the Constance lake (Switzerland) affected by a strong decrease in phosphate (Jochimsen et al. 2013) and the artificially acidified Little rock lake (Wisconsin, USA) (Keitt 2008). In both systems, higher synchrony was encountered as a primary effect after the identified perturbations. Interestingly, in the Keith study, the synchrony was driven mainly by winter tolerant species that drastically decreased after the perturbation, while in the present work all populations persisted. Jochimsen et al. (2013) hypothesized that the subsequent regime shift they observed was favored by the loss in compensatory dynamics. Our results may concur with their observations: the decoupling of the two community aggregated properties observed after the period of high synchrony (total zooplankton biomass increased while abundance decreased), gives some indications that structural changes have occurred within the community assembly.

Ecological implications

Downing et al. (2008) lamented that despite the advances in theory, relatively little empirical work existed to determine how populations oscillate within a community. Some studies have focused on the analysis of temporal patterns of plankton aiming to discern the type of population dynamics exhibited by these organisms: compensatory or synchronous dynamics (Vasseur et al. 2005; Houlahan et al. 2007; Keitt 2008). In the present work, we were able to quantify synchrony at the seasonal scale and to describe fluctuations in the degree of synchrony in natural marine communities, providing one of the first evidences that interspecific synchrony can fluctuate in relation to environmental forcing.

Temporal variability among populations (or compensatory dynamics) has been proposed to be an indicator of stability while synchrony has been linked to extinction probability (Pimm et al. 1988; Inchausti and Halley 2003) and especially to a decrease in food-web stability (Gonzalez and Loreau 2009). From the Constance lake observations, Jochimsen et al (2013) also hypothesized that the loss of compensatory dynamics facilitated the community shift to another stable state. Although in the present study we couldn’t describe changes in the community food-web, the decrease observed after 2005 in the zooplankton community abundance contrasted with the increase observed in the zooplankton community biomass, giving some indications that the loss of compensatory dynamics may have favored deep changes in the size structure of the community.

In the present work, we have tracked changes in zooplankton populations focusing on their seasonal dynamics. Some recent works suggested that while synchrony is the predominant dynamics at the annual scale, a compensatory
dynamics can occur simultaneously at other scales (Keitt et al. 2006; Vasseur and Gaedke 2007; Vasseur et al. 2014). The use of scale-specific methods, such as the wavelet analysis, and the increasing length of the marine zooplankton time series, as such obtained within the RADIALES program, will allow further assessments of the zooplankton community dynamics at multiple scales.

Conclusions

In the present work, we were able to: (1) discern the temporal patterns of zooplankton dynamics at different levels of the community assembly, (2) quantify the degree of synchrony among zooplankton functional groups and species of copepods at the annual scale and its variability trough time, and (3) highlight the predominant role of abiotic, weather-induced factors acting at multiple scales to drive zooplankton fluctuations and shape community dynamics.

We hypothesize that higher amplitude of the seasonal cycle (reinforced seasonality) of abiotic factors, upwelling index and river Miño outflow, as well as the reduction of the duration of upwelling events, drove the increases in zooplankton abundance and biomass observed in 2000. The development of the WIBP and downwelling enhanced retention in winter, whereas primary production on the shelf in summer was enhanced by frequent but short upwelling events that minimize offshore exportation. These environmental changes consisted in a long-term disturbance (2000–2004) that modulated not only the community aggregated properties, but also affected the stability of the zooplankton community. Indeed, accentuation of the inter-specific synchrony may have caused the community to step to another state and likely led to a reorganization of the community size structure.

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Conflict of Interest
None declared.