



Interannual variability in temporal patterns of Chlorophyll-a and their potential influence on the supply of mussel larvae to inner waters in northern Patagonia (41–44°S)



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ABSTRACT

Environmental forcing of biophysical processes can have deep influences on patterns of supply of planktonic larvae to benthic communities in coastal marine ecosystems. We investigated the role of environmental forcing following a recent interannual decrease in larval supply in the Inner Sea of Chiloé (41–45°S) using direct observations and environmental time series over the period 2003–2014. To examine the temporal structure of larval supply and potential associations with environmental forcing (approximated using satellite chlorophyll-a and sea surface temperature), we used wavelet analysis and lagged correlations to test the hypothesis of an association between larval availability and changes in the seasonal cycle of chlorophyll-a concentration, sea surface temperature, and relevant climate variability (Pacific Decadal Oscillation, El Niño–Southern Oscillation and Southern Annular Mode). Our results indicate that a weakening in the annual cycle of chlorophyll-a concentration and abnormally cold sea surface temperature during 2009–2010 can be related to the observed disruption in larval supply to the Inner Sea of Chiloé starting during the 2010–2011 season. The potential influence of climate variability is further discussed as the spatial extent and temporal persistence observed suggest that other ecological processes might have also been affected, and consequently, we suggest a link to transient large-scale climatic forcing.

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1. Introduction

Coastal marine ecosystems depend on the flow of energy from primary producers to higher trophic levels. Energy flows follow a complex network of biological, physical and chemical interactions that directly modulate biological productivity (Chavez et al., 2008; Boyce et al., 2010). Coastal regions are characterized by their high biodiversity, biological productivity (Benazzouz et al., 2014; Sydeman et al., 2014), the large fraction of the global human population inhabiting the shorelines and the benefits derived from its multiple uses (Lakshmi and Rajagopalan, 2000; Islam and Tanaka, 2004). To this end, aquaculture in coastal ecosystems relies to a large extent on the integrity of different ecological and biophysical processes, which are subject to multiple sources of variability (Pineda, 2000; Barria et al., 2012), including environmental and anthropogenic disturbances (Goldburg et al., 2001). As aquaculture provides an increasing share of the protein consumed

globally, improving our understanding of how different drivers act as sources of variability in coastal ecosystems is of paramount importance (Merino et al., 2012).

Spatial and temporal variability of oceanographic processes has been shown to influence the supply of planktonic larvae to coastal waters, which is crucial for the replenishment of marine invertebrate populations with broadcast spawning. Larval supply to benthic habitats is often coupled to ocean circulation patterns linked to regional-scale phenomena (Gaines et al., 1985; Connolly et al., 2001; Broitman et al., 2005). However, local factors such as abiotic conditions, habitat complexity, and biological interactions can play an important role modulating temporal and spatial patterns of larval settlement to benthic communities (Whitman and Reidenbach, 2012).

Mussel farming is largely based on the collection of planktonic larvae produced by benthic populations. Competent larvae are collected with suspended artificial substrates deployed in areas of high larval availability. Settlers are then reared until they reach commercial size (7–10 cm) and harvested before they spawn (Camacho et al., 1995). Most of the Chilean mussel farming industry is clustered around the Inner Sea of

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Chiloé (ISC: 41–45°S), and is focused on the production of *Mytilus chilensis*. This region is characterized by high primary productivity linked to a strong annual cycle in seawater temperature (Iriarte et al., 2007; Tello and Rodríguez-Benito, 2009). Reproduction of *M. chilensis* is predominantly seasonal and spawning takes place during spring–summer. At the ocean temperatures prevailing in the ISC, the planktotrophic larval stage can last up to 45 days in the water column prior to settlement (Toro et al., 2004; Toupout et al., 2012). The collection of competent planktonic larvae (shell length 80 μm) takes place in summer–fall over a small region adjacent to the Reloncaví Sound and Reloncaví Fjord (Fig. 1). Strings that hang from moored buoys and arranged at different depths in the water column are used as larval collectors (Avendaño et al., 2011). The strings stocked with wild larvae are then transferred to different areas around the ISC to grow, and adults are harvested after ca. 12–18 months or before the spawning season in order to maximize the gonad weight. By relying on the provisioning and support from these different ecosystem services, the mussel aquaculture industry in the ISC has experienced an explosive growth over the past decade with a total production of about 2 million tons per year (Duarte et al., 2014) and among the top ten producers of mussel meat worldwide (Avendaño et al., 2011).

The ISC is a highly dynamic environment, where the paucity of systematic environmental observations poses a major obstacle to a deeper understanding of environmental variability patterns and their main drivers (e.g. Lara et al., 2010; Aiken et al., 2011). In this information-poor context and in the absence of an evident region-wide environmental driver, mussel farmers reported that the density of larvae at the collection areas started declining abruptly during the 2010–2011 larval collection period. The curtailed larval supply led to a drop the adult stock during 2011–2012 period and also coincided with lower growth rates of cultured adult individuals. This regional change in the ecosystem services that the mussel farming industry depended on, translated

into a 30% drop in mussel production after the 2011–2012 period, with widespread social and economic consequences.

The supply of planktonic larvae is affected by a number of endogenous (e.g. nutrient reserves, genotype) and exogenous (e.g. environmental variability) factors, in which temporal patterns of chlorophyll concentration and sea surface temperature are crucial for the physiology, survival, and duration of the planktonic phase (Peteiro et al., 2007). Understanding the physical and biological processes that could interact to set or alter periodic ecosystem processes such as spawning and larval settlement would allow us to assess potential effects on the structure and functioning of this important socio-ecological system. Thus, the aim of this study is to examine all relevant and publicly available climatic, oceanographic and biological information for the ISC between 2003 and 2014, in order to assess potential causes of the sudden decrease in larval supply. To this end, we test a simple hypothesis: larval availability in the larval collection areas is related to the patterns of temporal variability of chlorophyll-a concentration (Chl-a), surface temperature (SST) and climatic variability in the broader ISC region.

2. Methodology

2.1. Study area

The Inner Sea of Chiloé (Fig. 1) on the eastern South Pacific Ocean comprises a variety of semi-enclosed basins such as inlets, fjords, and estuaries that form the northernmost sector of the Patagonian fjords (Silva et al., 2009; González et al., 2010; Pavés et al., 2013). The West Wind Drift (WWD) reaches the southern coast of Chile at ca. 42°S (Dávila et al., 2002), promoting a strong interaction between Sub-Antarctic and continental waters and generates pronounced horizontal density gradients in the upper water column (Garreaud et al., 2013).

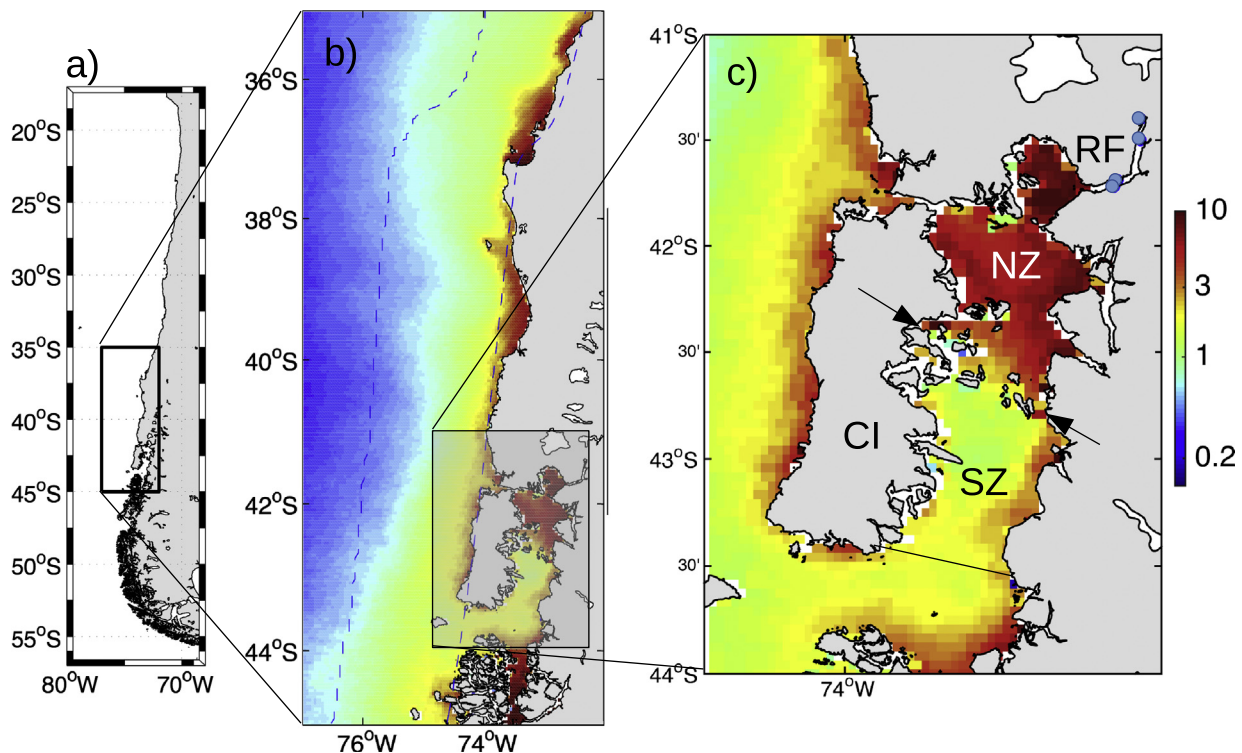


Fig. 1. (a) Study area showing its location along the coast of Chile. (b) Chlorophyll-a distribution off central Chile and northern Patagonia, and (c) detailed view of the Inner Sea of Chiloé. The dashed blue lines in (b) correspond to smoothed versions of the coastline and the corresponding 150 km offshore, which were used in the computation of coastal SST anomalies in Fig. 6. Blue dots in (c) represent the location of the sampling stations of mussel larvae in and around Reloncaví Fjord (RF). Also the main axis of Desertores Islands, separating the northern and southern ISC, are denoted by the black arrows. The black line represents the southern limit of the southern zone. Labels are CI (Chiloé Island), NZ (Northern Zone), SZ (Southern Zone) and RF (Reloncaví Fjord). Color bar shows the average values of MODIS chlorophyll (mg m^{-3}) for 11 years (2003–2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

This pattern of ocean circulation sets the stage for the mixing of Sub-Antarctic Water (SAAW) and freshwater from Patagonian rivers (Montecino et al., 2006; Iriarte et al., 2007), generating Sub-Antarctic Modified Water (SAMW) bearing high loads of macronutrients from the adjacent Pacific Ocean as well as from terrestrial origin (Iriarte et al., 2007). Topographic and bathymetric complexity in the region determines patterns of circulation in the ISC, that ultimately produce sub-regions with distinct regimes of environmental variability and, apparently, substantially different food supply for mussel larvae. To explore the spatio-temporal patterns in mussel larval density and phytoplankton biomass based on satellite chlorophyll-*a* data, we separated the ISC into two sub-regions based on their bathymetry and distinct environmental regimes in terms of SST and Chl-*a* (see Tello and Rodríguez-Benito, 2009; Lara et al., 2010): north and south of 42.6°S (Fig. 1). These two main basins are interconnected by narrow passages between islands, where the Deseriores Islands is the main bathymetric constriction (Silva et al., 2009).

2.2. Mussel time series

Samples were collected between October 2009 and April 2014 in Ralun (41.5°, 72.32°W), Cochamo (41.2°, 72.31°W), Sotomo (41.69°, 72.45°W) and Yates (41.72°, 72.47°W), all located in the northern ISC (Fig. 1), in order to assess the density and temporal variability of *M. chilensis* larvae in the water column. Monthly, three plankton samples were collected in each station, consisting of vertical tows from 15 to 0 m using a net with a 42 cm mouth diameter and 55 µm mesh. The samples were preserved in 70% ethanol until their identification and quantification in the laboratory, using a stereomicroscope. The identification of different larval stages of *M. chilensis* was performed by morphological and morphometric analysis according to Avendaño et al. (2011). For brevity we consider all three larval stages that can be found in the plankton: straight-hinged veliger, umbonate veliger, and eye-spot larva (Ruiz et al., 2008). Estimates of larval density are presented as the monthly average across the four sites and expressed as number of larvae per m³ (see Results).

2.3. Satellite and climate data

Eight-day composites (2003–2013) of MODIS Chl-*a* and SST data were analyzed to evaluate spatial differences between the northern and southern ISC. MODIS-Aqua Level 3 data at 4 km spatial resolution were acquired from NASA web site (<http://oceancolor.gsfc.nasa.gov/>). NASA uses the standard OC3 (O'Reilly, 2000) algorithm for Chl-*a* estimations from MODIS. This is a fourth degree polynomial algorithm that uses a maximum band ratio of 443 or 490 nm to 547 nm wavelengths (Sauer et al., 2012). The data were processed using ENVI/IDL 4.8 software and converted into monthly time series of spatially averaged Chl-*a* and SST over the northern and southern ISC.

Monthly composites of satellite-derived Sea Surface Temperatures Anomalies (SSTA) were calculated from GOES (Geostationary Operational Environmental Satellites) infrared satellite data. We used GOES imagery instead of other commonly used products (e.g. Pathfinder) as the percent of data available for the region is considerable higher because of the geostationary orbits (Wu et al., 1999). To further inspect the cooling event of 2010 and examine patterns of interannual variability, Latitude-Time plots of SSTA were computed for the period 2003–2013.

We considered three climatic indices, the Pacific Decadal Oscillation, the Multivariate ENSO Index and the Southern Annular Mode (PDO, MEI and SAM, respectively). PDO data were downloaded from the University of Washington – Joint Institute for the Study of the Atmosphere and Ocean website (<http://research.jisao.washington.edu/pdo>), MEI data were obtained from NOAA Earth System Research Laboratory (<ftp://www.esrl.noaa.gov/psd/ens/>

<http://www.cpc.noaa.gov>) and the SAM index from the NOAA Climate Prediction Center (<http://www.cpc.noaa.gov>).

2.4. Statistical analysis

To examine differences between years across sites, we used Repeated Measures Analysis of Variance (rep-ANOVA). To meet the normality and homoscedascity assumptions of rep-ANOVA, abundance data was Log₁₀ transformed. We considered two independent factors, site and year in our model, where year was included as a fixed factor and site nested within year as a random variable to explain changes in larval abundance. A Tukey's pos-hoc test was used to asses for differences among treatment levels for those factors that showed significant differences in larval abundance. We used wavelet analysis to detect temporal changes in the principal modes of Chl-*a*, SST and in the climatic indices (PDO, MEI and SAM) variability. The wavelet analysis allows a quantification of temporal evolution in time series made up of various harmonic constituents (Cazelles et al., 2007). Through this analysis it is possible to detect temporal changes in the contribution of different periods to non-stationary time series (e.g. Rouyer et al., 2008; Iles et al., 2012), and to associate them with changes in external variables (Cazelles et al., 2007). We used a Morlet wavelet that is defined as the product of a complex sinusoidal by a Gaussian envelope, which is the central angular frequency of the wavelet and allows extracting both time-dependent period and phase of a time series (Cazelles et al., 2007). Wavelet analysis was performed using the MATLAB algorithms developed by B. Cazelles (<http://www.biologie.ens.fr/cazelles/bernard/Research.html>).

To examine associations between monthly changes in the abundance of mussel larvae and monthly variability of SST and Chl-*a*, a proxy for phytoplankton abundance, we used lagged cross-correlation (Legendre and Legendre, 2012) to determine whether variations in the local abundance of mussel larvae in the northern ISC were driven by earlier changes in SST or Chl-*a* concentration concentration in the north and south ISC region. Similarly, we examined if monthly variation in larval abundance in the ISC were driven by large scale circulation patterns calculating cross-correlations with PDO, MEI and SAM. Monthly larval abundance anomalies and SST and Chl-*a* anomalies were calculated by subtracting from each monthly value the corresponding climatological monthly average. All cross-correlation analyses were carried out between anomalies (i.e. larval abundance, Chl-*a* and SST).

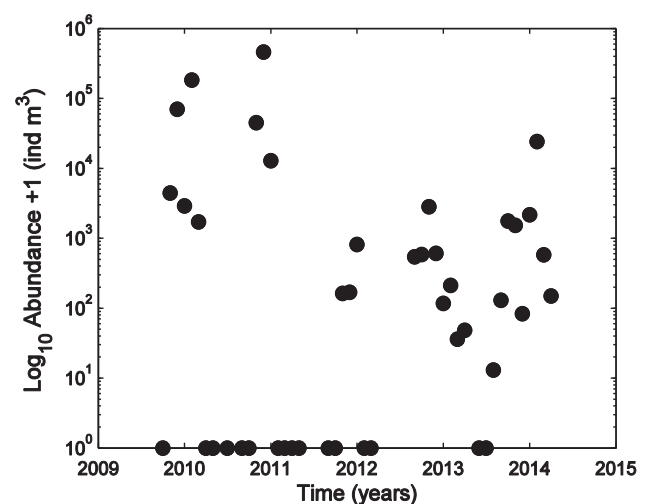


Fig. 2. Monthly time series of abundance of *Mytilus chilensis* larvae (ind/m³) averaged across the four sampling sites. See locations and sampling strategy in Methods: Mussel time series.

3. Results

We observed large interannual variability in the abundance of mussel larvae (Fig. 2) across the ISC over the study period. Overall, larval abundance showed a clear seasonal pattern with high values during the austral reproductive (October–March) seasons than in the rest of reproductive periods (Fig. 3). There were no significant differences in larval densities in space (i.e. across sites), but we observed significant differences between years (Table 1). The Tukey test revealed a significant difference between abundance during the reproductive season of 2009–2010, when abundances were higher than over the rest of the reproductive periods (Figs. 2 and 3). Although high values of larval density were observed at the end of 2010, this reproductive period was marked by near-zero larval densities during 2011 and limited abundances onward (Figs. 2 and 3), coinciding with field observations reported by the mussel aquaculture industry. Satellite Chl-a exhibited a marked seasonal pattern, with higher concentration in austral spring (September–December) and early autumn (March), and lower values during winter (June–August) (Fig. 8a). The local Wavelet Power Spectrum showed the main modes of temporal oscillation of Chl-a and SST for each sub-region (Fig. 4). In the northern ISC Chl-a variability revealed the presence of a significant six-month periodic mode extending from 2004 to mid-2008 and disappearing later, while the annual dominant mode remains significant until early 2009 (Fig. 4a). In the southern ISC the wavelet analysis shows that this temporal pattern is dominated by the annual mode (i.e. 12-months) extending from 2004 into 2008 (Fig. 4c). For SST, the wavelet showed a significant annual period for the whole extent of the time series in both northern and southern zones (Fig. 4e, g). The global wavelet power spectrum shows the statistical significant of each mode for each variable in each region (Fig. 4b, d, f and h, respectively). The wavelet analysis of PDO shows significant 12-month periodicity during 2004–2005 and 2011–2012, a temporal pattern that is highlighted in the global power spectrum and a minor significant cycle (4-months) during 2005 (Fig. 5a, b). The MEI index revealed significant 6 to 12-months modes between 2008 and mid-2012, with greater intensity for 2010–2011 period, minor clusters of 3- and 6-months modes took place between 2004 and 2011 (Fig. 5c). The wavelet analysis of SAM shows significant annual fluctuations during 2007 and spring 2011–summer 2012 seasons (Fig. 5e).

The cross-correlation function between time series of larval abundance anomalies revealed significant negative correlations with 2–3 (Northern Zone) and 3 (Southern Zone) months of lag with satellite Chl-a concentration anomalies (Fig. 6a). Cross-correlations between

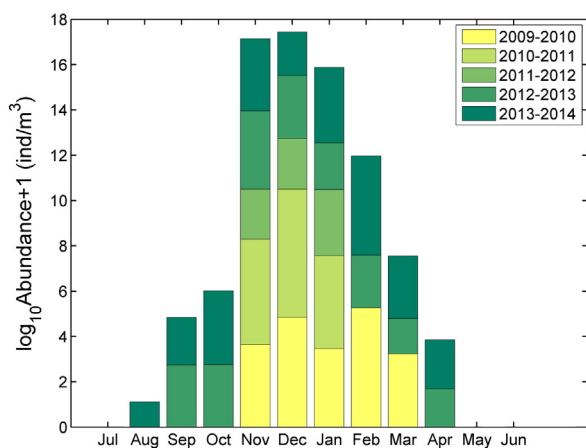


Fig. 3. Cumulative climatology of monthly averages of larval abundance (\log_{10} ind/ m^3) of *Mytilus chilensis* sorted by season and centered around December–January (i.e. austral summer). Note that the larval abundance of each month for a particular season (e.g. 2009–2010) corresponds to the height of a specific color in the bars. Larval abundance in the water for the seasons 2010–2011 and 2011–2012 were only recorded during the months of November to January.

Table 1

Repeated-measures ANOVA of variations in abundance of larvae between sites and across years using four sampling locations in the ISC. See Section 2.4 for details.

SOURCE	DF	SS	MS	F	P
Site	3	1.095	0.3650	1.717	0.216
Year	4	15.6087	3.9032	18.340	0.00004 *
Error	12	2.5532	0.2128		

larval abundance anomalies and SST anomalies showed significant negative relationships with lags between 0–3 months for Northern Zone and 0–1 month for the Southern Zone of ISC (Fig. 6b). Cross-correlation coefficients between climatic indices and larvae anomalies show a significant positive correlation with 2–4 (PDO), 4–5 (MEI) and 5 (SAM) months of lag, respectively (Fig. 6c).

The abrupt decline in larval abundance took place following cold anomalies in SST throughout the ISC in the 2010–2011 period (Fig. 7a). The negative anomaly observed for the surface waters of the ISC differed from the adjacent ocean waters west of Chiloé Island, as well as from off central-southern Chile (Fig. 7b). Overall, warm and cold phases coincide between the ISC and along central-southern Chile. A prolonged warm period from 2003 to early 2005 and during most 2006 transitioned to a cold phase starting in 2007, with some intermittent changes in 2008–2009 (Fig. 7). The onset of the cold period in December 2009–January 2010 was more marked in the ISC, which showed the lowest SST of the 11-year satellite record (Fig. 7a). This colder period appears to be finishing, particularly for the ISC, where near-neutral SST conditions were observed in late 2013. Note that the

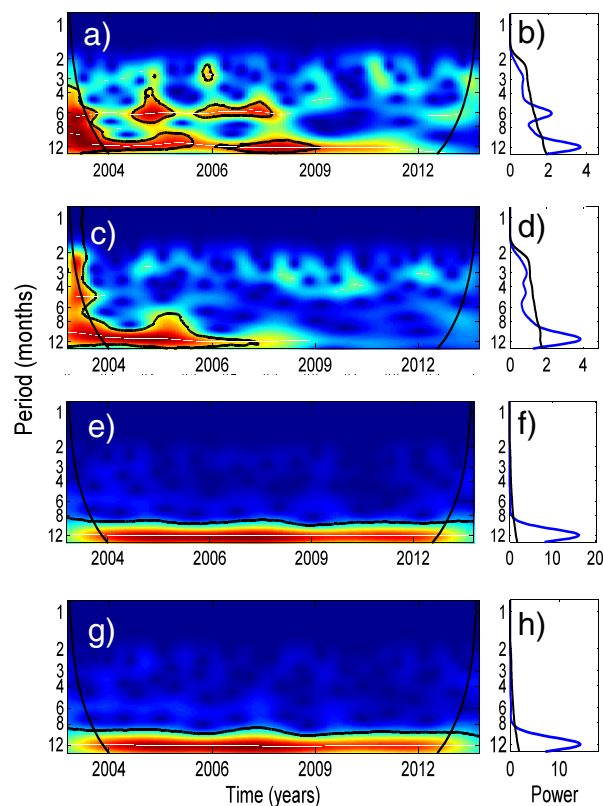


Fig. 4. Wavelet analysis of periodicity 2003–2013. Wavelet Power Spectrum of the aggregate monthly chlorophyll time series in (a) Chlorophyll in Northern Zone, (c) Chlorophyll in Southern Zone, (e) SST in Northern Zone and (g) SST in Southern Zone. The cone of influence (black lines) indicates the region not influenced by edge effects (threshold of 95% CI). Only patterns within the cone are considered reliable. The colors are coded from dark red (high-power values) to dark blue (low-power values). Right panels are the corresponding global wavelet power spectra (b, d, f and h). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

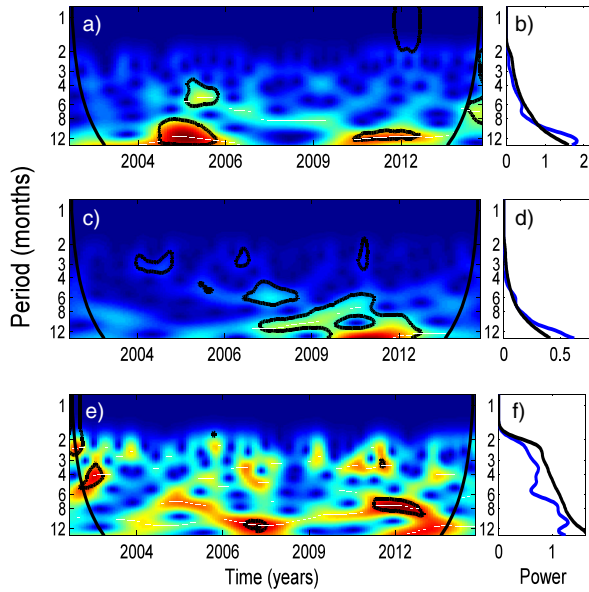


Fig. 5. Wavelet analysis of climatic indices periodicity, 2003–2013. Wavelet Power Spectrum of monthly (a) Pacific Decadal Oscillation (PDO). (c) Multivariate ENSO Index (MEI), and (e) Southern Annular Mode (SAM). The cone of influence (black lines) indicates the region not influenced by edge effects (threshold of 95% CI). Only patterns within the cone are considered reliable. The colours are coded from dark red (high-power values) to dark blue (low-power values). Right panels are the corresponding global wavelet power spectra (b, d and f). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cold SST anomalies along most central-southern Chile are computed from a band ca. 150 km from the coastline (Fig. 7b), and consequently, warm coastal features are masked in the averaging process.

4. Discussion

Temporal variability in primary production and supply of larvae are key drivers for population dynamics of many coastal species. Our study evaluated associations between the abundance of planktonic mussel larvae and different patterns of environmental variability in the ISC using satellite-derived time series of Chl-a, SST and key basin-scale climatic indices. Our test of hypothesis is strongly suggestive of links between the interannual variability in larval abundance, fluctuations in

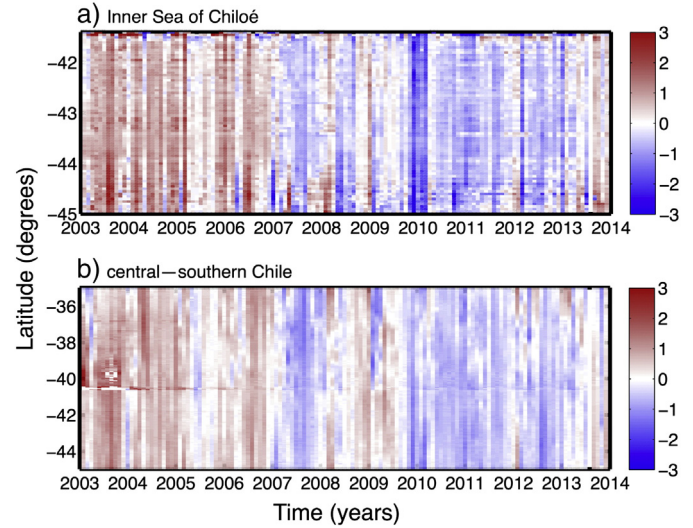


Fig. 7. Latitude-Time plot of SST anomalies (°C). Latitude-Plot anomalies SST for (a) whole ISC and (b) 150 km coastal band along central-southern Chile as specified in Fig. 1.

Chl-a and SST in the ISC and climate processes over larger scales. Larval abundance is a markedly seasonal process and our analysis detected a disruption of Chl-a seasonality across the ISC preceded by interannual changes in SST across the South Eastern Pacific (see Figs. 7 and 8). Then, our results provide a useful basis to understand how the supply of larvae for the mussel farming industry in the ISC is influenced by environmental variability, even though the effects of the extreme cooling event during the austral summer of 2010 (Fig. 9) and its possible effects on the ISC are not completely clear yet.

As noted before, larval availability in the water column of the ISC peaks between September and February, coinciding with periods of increased sea surface temperature ($>11^{\circ}\text{C}$; see Avendaño et al., 2011; Barria et al., 2012), whereas low abundances are observed during the austral Fall–Winter. We found that mussel larvae were significantly more abundant in reproductive season 2009–2010 than across subsequent reproductive periods (e.g., 2010–2011; 2011–2012). Overall, the significant inter-annual differences in planktonic larval abundance we observed in the northern ISC may be driven by changes in the larvae production, survival and/or dispersal of different larval stages. Therefore, identifying the factors and events that may affect survival

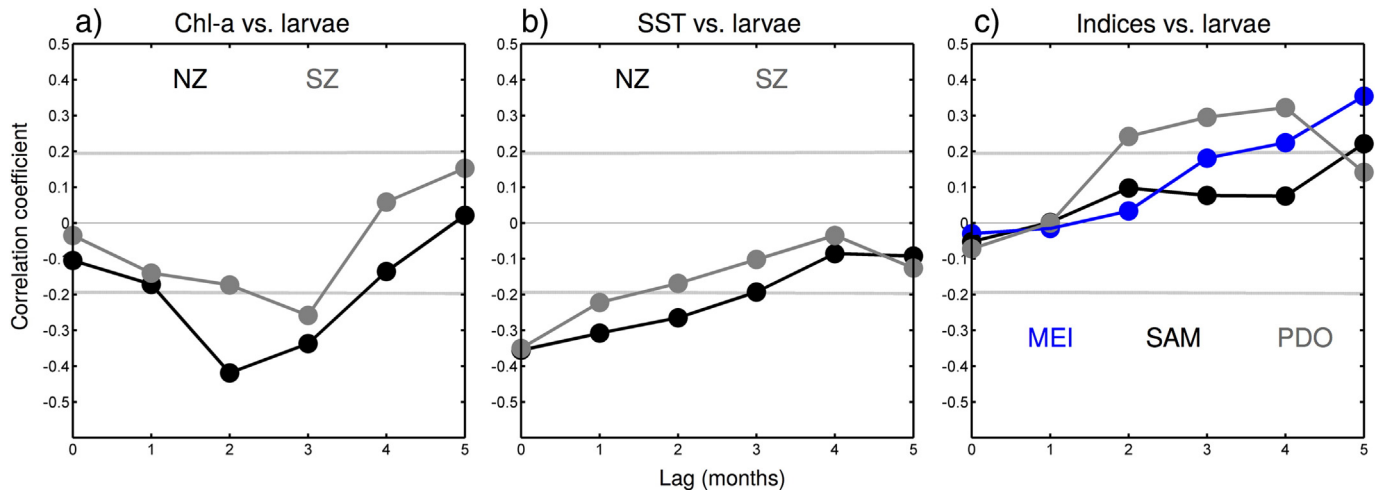


Fig. 6. Cross-correlation function between larval abundance anomalies and (a) Chl-a, (b) SST anomalies, and (c) climate indices. Correlations in (a) and (b) are presented for both northern (black lines) and southern (grey lines) zone. Climate indices considered in (c) correspond to MEI (blue line), SAM (black line), and PDO (grey line). Horizontal dotted lines represent the 95% confidence intervals. Lags indicate that changes in anomalies of Chl-a, SST, or climate indices precede those in larval abundance anomalies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

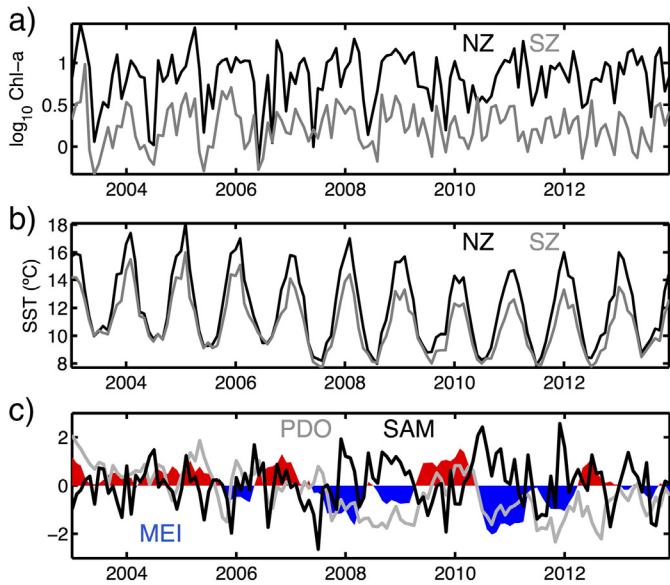


Fig. 8. Time series of (a) Chl-a concentration and (b) SST in Northern Zone (NZ; solid black line) and Southern Zone (SZ; dashed black line) of the ISC. (c) Climate indices of Multivariate ENSO Index (MEI; red/blue), Southern Annular Mode (SAM; black line), and Pacific Decadal Oscillation (PDO; grey line).

and distribution of planktonic larvae in the ISC is critical to understand interannual variability in larval abundance.

Although larval dispersal is a major source of variability for local larval abundance (Siegel et al., 2008), few studies have focused on the dispersal of invertebrate larvae in the region. Genetic information derived from a recent study in the northern ISC, indicates that dispersal patterns from local populations are influenced by the Reloncavi fjord (Perez, 2010), which is the area where the larval abundance data used in our analysis was collected (see Fig. 1). It has been suggested that this fjord is the main supplier of mussel larvae for the entire ISC region, although larvae collected from semi-isolated locations in the region (e.g. Ilque

Bay, 41.62°S) have a high degree of genetic dissimilarity with other locations (Perez, 2010).

Larval mussels may spend several weeks in the plankton (Toro et al., 2004) before reaching a competent stage (pre-metamorphic) and finding a suitable substrate for settlement. Over this time, the main sources of mortality in the plankton are predation (Allen and McAlister, 2007; Troost et al., 2009), starvation (White et al., 2014), genetic factors (Toro et al., 2004) and acidification (Gazeau et al., 2007). Although we were not able to assess the occurrence and relative importance of these sources of mortality, water temperature and food availability are critical factors (Caley et al., 1996). Pre-competent mussel larvae are omnivorous and feed directly on particles in the water column, mainly of organic matter in the seston (bacteria, cyanobacteria, phytoplankton). The duration of this omnivorous phase has been shown to be timed with the availability of food that is adequate for successful settlement (Toupoint et al., 2012). The cumulative climatology of larval abundance during reproductive period (Fig. 3) shows that larval abundance in the water column is tightly coupled to the seasonal cycle in Chl-a concentration and SST (see Fig. 8a, b). The significant negative cross-correlations between larval anomalies and anomalies in Chl-a concentration and SST in both the northern and southern sectors (Figs. 6a, b) highlight the unusual nature of the seasonal (annual) cycle across most of the study period. The damped seasonal cycle in SST is coupled to off-season Chl-a concentration peaks (Fig. 8a). This out of phase environmental pattern generates the negative cross-correlations, with positive chlorophyll concentration anomalies taking place 2–3 months before the November–January negative anomalies in larval concentrations over most of the study period. A similar pattern, of cold summer SST anomalies concomitant (e.g., 0–3 month lags) with the seasonal anomaly in larval concentration provides further support to this interpretation. The simultaneous and persistent changes in the climate indices (Fig. 8c) and the region-wide SST anomalies (Fig. 7) suggest a remotely-forced disruption of the seasonal cycle in the ISC as the lead causal agent behind the curtailed larval abundance during the study period. Hence, the proof of a link between larval abundance in the study area and local and large-scale environmental drivers warrants further attention.

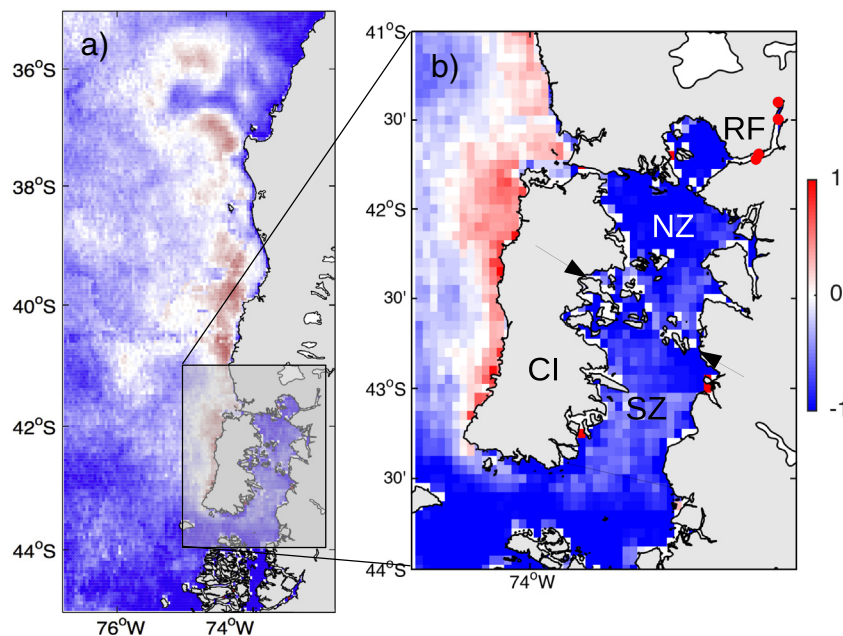


Fig. 9. Satellite image showing the widespread SST anomalies for January 2010 in (a) the coastal region off central-southern Chile. A zoomed-in version of the Inner Sea of Chiloé (ISC) and adjacent coastal ocean is presented in (b). Labels are presented for Chiloé Island (CI), Northern Zone (NZ), Southern Zone (SZ) and RF (Reloncavi Fjord). The black arrows denote the main axis of Desertoires Islands separating the NZ and SZ. Finally, purple dots show the location of the sampling stations of mussel larvae. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The change in larval abundance starting during the reproductive season of 2010–2011 onwards seems to be related to changes in environmental conditions over larger spatial and temporal scales. Changes in the rate of mussel recruitment associated with large-scale climatic variability as indicated by indices like ENSO, PDO or NPGO, have been observed in intertidal systems along the Pacific coast of North America (Menge et al., 2009). The negative anomalies found in SSTA from 2010 onward point to a change in advective conditions that may have affected the reproduction and/or the patterns of larval dispersal into the ISC. The spin-up of the Southeast Pacific Subtropical Anticyclone gyre is strongly related to the cooling of the South East Pacific ocean (Roemmich et al., 2007; Schneider et al., 2007). The possibility for such dynamic coupling has been analyzed for pelagic fisheries and environmental forcing in the SE Pacific during 2000–2008 by Cubillos et al. (2014), who suggested that low frequency variability in SSTA may induce large changes in the pelagic ecosystems off southern Patagonia. During austral summer 2010, the Southern Annular Mode (SAM) developed a considerable negative anomaly (Giesecke et al., 2014) in association with a poleward intensification of the Westerlies (Belmadani et al., 2014; Giesecke et al., 2014). These anomalous flow patterns could explain the intrusion of oceanic waters, proliferation of salps and subsequent decrease in phytoplankton abundance in the ISC during some months (February, March, October, November) of 2010 (Giesecke et al., 2014). SST anomalies during this extreme event is presented in Fig. 9 for evidencing the consistent low-SST pattern through the ISC and its contrast with the coastal ocean along central-southern Chile. The weakening of the annual cycle of Chl-a in the 2009–2010 season also coincides with a positive phase of MEI and PDO, which has been shown to influence Chl-a variability towards the study region (Thomas et al., 2009). During this period (2011) one of the greatest La Niña events of the last decade took place (Boening et al., 2012), which was associated with a phase change of the SAM during the 2010–2011 season (Fig. 8c). A synergistic effect of this climatic pattern may have resulted in the concomitant weakening of the semi-annual and annual cycle of Chl-a variability we report from 2009 onward. Indeed, a cross-correlation analysis of PDO, MEI and SAM, reported to influence biophysical variability in our study region (see above), are significantly and positively correlated to the larval anomaly time series with long lags (see Fig. 6c). Thus, these basin-scale patterns of climatic variability provide a potential link between oceanographic processes and the environmental drivers of larval abundance we observed in the ISC.

Our results highlight the need to improve our understanding of larval production, dispersal, and connectivity patterns in the region, with an emphasis on the sub-regions where most larval collection is conducted. This should be achieved by combining biological and environmental monitoring with hydrodynamic modeling of the coastal ocean. Ideally, these efforts should be paired with *in situ* measurements that aid in the validation of satellite algorithms used to derive estimates of Chl-a concentrations in the optically complex and time-varying surface waters of the ISC. We suggest that drops in the supply of larvae to the ISC can be linked to remote processes that disrupted the seasonal cycle in surface conditions and cascaded into the larval production capacity of the natural stocks. In this way, enhancing our capacity to establish causal links between multiple environmental drivers and patterns of larval production and abundance could contribute to forecast and dampen the future impacts on productive activities that rely on fragile ecosystem processes, such as the supply of competent planktonic larvae to the mussel aquaculture industry.

5. Conclusions

Analysis of long-term satellite Chl-a data revealed a sharp break of the annual cycle of Chl-a concentration in the northern ISC. This change was probably forced by changes in oceanographic conditions at the regional scale, which can be inferred from interannual changes in SST-anomaly fields and large-scale climate indices. A perturbation in the

seasonal cycle of Chl-a co-occurred with a marked cooling of surface temperatures and foreshadowed a posterior abrupt drop in mussel larval abundance in 2010–2011 reproductive season in ISC. The spatial extent and temporal persistence of changes in Chl-a concentration and abundance of mussel larvae suggest that other ecological processes may have been affected. Our results highlight the current need for more extensive and periodic biophysical observations in the ISC, and the supporting role that satellite-derived data can play in this complex and logistically challenging region.

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