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Spatial heterogeneity in mussel larval abundance across fjord systems of northern Chilean Patagonia

Felipe I. Torres [a,b,*], Carlos Lara [c,d], Carlos Molinet [e,f], Nicole Castillo-Villagrán [b,g], Bernardo R. Broitman [b,h]

[a] *Programa de Doctorado en Ciencias Mención Biodiversidad y Biorecursos, Universidad Católica de la Santísima Concepción, Concepción, Chile*
[b] *Instituto Milenio en Socio-Ecología Costera (SECOS), Santiago, Chile*
[c] *Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Concepción, Chile*
[d] *Centro de Investigación en Recursos Naturales y Sustentabilidad, Universidad Bernardo O'Higgins, Santiago, Chile*
[e] *Programa de Investigación Pesquera, Instituto de Acuicultura, Universidad Austral de Chile, Puerto Montt, Chile*
[f] *Programa Integrativo, Centro Interdisciplinario para la Investigación Acuícola (INCAR), Concepción, Chile*
[g] *Coastal Ecosystems & Global Environmental Change Lab (ECCALab), Faculty of Environmental Sciences, Universidad de Concepción, Concepción, Chile*
[h] *Facultad de Artes Liberales, Universidad Adolfo Ibañez, Viña Del Mar, Chile*

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ABSTRACT

Climate change is reshaping marine ecosystems by altering the timing, intensity, and predictability of key biological processes. In northern Chilean Patagonia, where mussel aquaculture depends on wild seed collection, variability in oceanographic and climatic conditions may affect mussel larval abundance at local scales. Here, we analyze a decade of monthly data on mussel larvae collected at seven sites distributed across contrasting fjord and channel systems. We assess phenological patterns, extreme events, and long-term trends in larval abundance, and evaluate their associations with local hydrography and large-scale climate indices (ENSO, PDO, SAM) and local hydrographic variability. Larval peaks varied in timing and duration across sites, and we identified extreme positive and negative events. Extreme positive larval abundances were concentrated at mid-latitude sites and occurred during strong negative PDO phases, often combined with La Niña or positive SAM. In contrast, decreasing trends were detected at the southernmost sites, while a positive trend emerged at one mid-latitude site. These contrasting patterns suggest that larval dynamics are primarily shaped by large-scale climate forcing, with local hydrographic conditions modulating site-specific responses. These contrasting patterns highlight strong spatial heterogeneity in larval dynamics, suggesting that local hydrographic conditions and geomorphological setting play a key role in modulating the effects of large-scale climate variability. Our results emphasize that larval abundance cannot be generalized across the region and must be interpreted within the context of site-specific processes. Understanding these local dynamics is critical for predicting variability in seed availability and supporting the sustainability of mussel aquaculture under changing environmental conditions.

1. Introduction

Global environmental change is modifying marine ecosystems by altering regional phenological cycles, and local species composition and abundance (Doney et al., 2012; Tang et al., 2016; Maulu et al., 2021). Rising ocean temperatures, increased stratification, acidification, and deoxygenation have already triggered responses across multiple taxa, with species shifting their distributions towards higher latitudes or to deeper waters (Poloczanska et al., 2013). Responses to environmental change are not uniform across life stages or taxa: early developmental stages, such as the larvae of marine invertebrates, are often tightly coupled to environmental variability (Asch, 2015; Pandori and Sorte, 2019). The vast majority of benthic marine organisms display a complex life cycle and open population dynamics where planktonic larvae recruit to populations of sessile adults (Roughgarden et al., 1988). In this way, larval abundance is a fundamental ecological processes that control local adult abundance and, in turn, the structure and persistence of the regional populations (Roughgarden et al., 1988; Gaines and

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* Corresponding author at: Programa de Doctorado en Ciencias Mención Biodiversidad y Biorecursos, Universidad Católica de la Santísima Concepción, Concepción, Chile.

E-mail address: ftorres@doctorado.ucsc.cl (F.I. Torres).

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Roughgarden, 1985). The delivery of planktonic larval stages to adult benthic habitats largely depends on oceanographic processes controlling along and cross-shelf transport (Farrell et al., 1991). For different species of mussels, regional patterns of larval abundance (i.e. hundreds of kilometers) have been linked to chlorophyll availability, wave exposure, and changes in sea surface temperature (Arribas et al., 2015; Menge et al., 2009; Navarrete et al., 2005; Broitman et al., 2008; 2022). These studies have shown that beyond strong phenological cycles (i.e. purely seasonal patterns), thermal anomalies are associated with changes in larval abundance. Thus, understanding the underlying mechanisms behind how climate-driven changes in local-scale environmental variability affects larval abundance is essential to anticipate future impacts on marine biodiversity and ecosystem functioning.

Marine mussels play a crucial role in marine ecosystems as ecosystem engineers that enhance habitat complexity, promote biodiversity, and support nutrient cycling through their filter-feeding activity (Buschbaum et al., 2009; Strand and Ferreira, 2019). By forming dense beds, they create structurally complex habitats that offer refuge, feeding grounds, and nursery areas for benthic organisms, contributing to community structure and ecosystem functioning (Craeymeersch and Jansen, 2019). These beds also help stabilize sediments and improve water quality through suspension feeding and biodeposition (Cranford, 2019; Petersen et al., 2019). In southern Chile, native mussels such as *Mytilus chilensis, Aulacomya atra* and *Choromytilus chorus* dominate extensive intertidal and subtidal habitats (Molinet et al., 2021). Along the Pacific coast of northern Patagonia, chiefly around the interior sea of Chiloé (ISC), in southern Chile (Bagnara and Maltrain, 2008), a widespread aquaculture sector cultivates *M. chilensis*, accounting for 22% of global mussel production (FAO, 2025). This important social-ecological system is critically dependent on the collection of mussel larvae from the wild to stock adult on-growing aquaculture systems (Bagnara and Maltrain, 2008; Molinet et al., 2025). However, wild adult populations are increasingly exposed to altered regional environmental processes, including salinity changes driven by diminished precipitation and freshwater inputs from the andean catchments (León-Muñoz et al., 2018, 2021). These climate–driven environmental changes, together with increased industry–driven larval collection can threaten the persistence of adult mussel beds and, by extension, the ecosystem services they provide, chiefly larval production and supply of young for the wild and cultivated populations (Molinet et al., 2025). Hence, the resilience and functionality of this social-ecological system is critically dependent on the understanding of the open population dynamics of *M chilensis* and how environmental factors influence larval abundance and the vulnerability of its early life stages around the ISC.

Globally, the large-scale climate patterns, may influence larval abundance through their influence of oceanographic processes that control temperature, salinity, and food availability (Menge et al., 2009; Asch, 2015). In northern Patagonia and the ISC, spatial patterns of mussel larval abundance over periods of 2–3 years have been suggested to reflect the interplay between seasonal reproductive dynamics, productivity, coastal circulation, and large-scale climate oscillations like ENSO (El Niño Southern Oscillation), PDO (Pacific Decadal Oscilation) and SAM (Southern Annular Mode) (Barria et al., 2012; Avendaño et al., 2011; Lara et al., 2016). Similarly, studies using satellite imagery have showed that regions of strong temperature gradients, most frequent during spring and summer, are located in the northern ISC and off Chiloé Island, and coincide with peak productivity and the areas where aquaculture collects larvae (Lara et al., 2010; Saldías et al., 2019). On the other hand, large-scale climatic variability has been shown to influence phytoplankton productivity within the ISC over (Narváez et al., 2019; Lara et al., 2016). These earlier observations suggest that, over longer temporal scales, an interaction between climate and oceanographic processes may reflect patterns of larval supply across the larger ISC (Lara et al., 2016; Molinet et al., 2025).

The environmental conditions regulating mussel reproduction and larval abundance are changing in northern Patagonia and the ISC. The study region is characterized by a complex system of fjords, channels, and islands (Viviani, 1979; Narváez et al., 2019). Seasonal variations in freshwater discharge and solar radiation drive primary production and influence the composition of the pelagic community (León-Muñoz et al., 2018, 2021). On the other hand, local hydrographic conditions are influenced by large-scale climatic and oceanographic processes, including the poleward intensification and displacement of upwelling and downwelling-favorable winds (Narváez et al., 2019; Linford et al., 2024). During austral summer, upwelling favorable winds promote offshore advection and thinning of freshwater layers, thereby modifying stratification patterns and the extent of low-salinity surface layers in the ISC (Saldías et al., 2019). These dynamics, together with river discharge, snowmelt, tides, and wind forcing, influence the biogeochemical cycling, nutrient availability, and larval dispersal pathways, with potential implications for both, ecological processes and aquaculture operations in the region (Viviani, 1979; Aguayo et al., 2019). For instance, glacial melt in northern Patagonia reduces water alkalinity and alters the carbonate system, together with primary production and carbon cycling in fjord ecosystems (Vargas et al., 2018; Jahnsen-Guzmán et al., 2021), which might negatively impact mussels during early life stages, which are particularly sensitive to ocean acidification (Duarte et al., 2014; Jahnsen-Guzmán et al., 2021).

Despite the social-ecological importance of mussels, the relationships between climatic variability, environmental conditions and larval abundance in northern Patagonia remain poorly understood. Genetic studies indicated strong connectivity among *M. chilensis* populations in northern Patagonia. The connectivity pattern is underlined by low genetic differentiation, high genetic diversity and a lack of isolation by distance patterns indicate widespread larval dispersal and high gene flow across the region (Astorga et al., 2020; Haye and Segovia, 2023). Together, these findings reinforce the idea that mussel populations are part of a well-connected metapopulation, where local patterns of larval abundance may result from both nearby spawning and regional dispersal. Previous studies on larval abundance have described seasonal abundance and vertical distribution patterns for several locations over short time periods (Avendaño et al., 2011; Barria et al., 2012; Astorga et al., 2020; Molinet et al., 2017, 2021). However, long-term, large-scale assessments of how climatic and hydrographic variability influence larval abundance along this vast region have not been attempted. In this study, we analyze over 10 years of monthly larval abundance data from seven sites spread along northern Patagonia, Chile. Our aim was to identify temporal patterns and trends in mussel larval abundance and examine the influence of different environmental and climatic drivers on patterns of larval abundance to test the hypothesis of geographic differences in the relationship between larval abundance and environmental forcing along the region.

2. Methods

2.1. Data

We obtained over a decade of bimonthly records of mussel larval abundance (MLA) from a monitoring program by the Servicio Nacional de Pesca y Acuicultura (SERNAPESCA) and the Instituto de Fomento Pesquero (IFOP), titled “Monitoring and surveillance program on the larval availability of mussels for the sustainability of aquaculture activity in the southern zone of Chile”. We obtained data from 7 sites with contrasting geomorphologies, sampled at least twice per month between 2013 and 2024, totaling 1871 observations (Fig. 1). During the monitoring program, triplicate samples were taken by submerging a zooplankton net at a depth of 15 m and hauled to the surface. The samples were fixed in 70% ethanol for subsequent identification and quantification under a stereomicroscope. The D-stage mussel larvae (veliger larvae) were separated, identified and their average depth–integrated abundance recorded. Species–level identification by morphology alone is difficult at the D-stage (i.e. veliger larvae with a

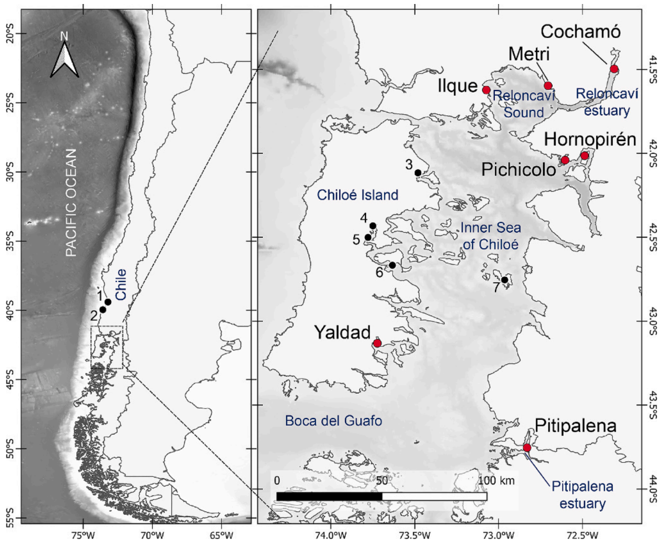

Fig. 1. Study region showing the location of the different larval abundance sampling sites (red dots) along the Interior Sea of Chiloé (ISC), northern Patagonia, Chile. Other locations mentioned in the Discussion are indicated by black dots: 1) Queule, 2) Chaihuín, 3) Tubildad, 4) Putemún, 5) Nercón, 6) Yal Bay, 7) Talcán island. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

straight hinge and a maximum length of <170 μm) since there are at least three co-occurring mussel species (Mollusca, Mytilidae): *Mytilus chilensis*, *Aulacomya atra* and *Choromytilus chorus*. From this point forward, we will refer to them as mussels or mytilids. Estimates of mussel larval density are presented as the monthly average, and expressed as number of larvae/m^{-3}.

Water temperature (°C) and salinity (PSU) were measured using a Sea-Bird CTD profiler during each larval sampling event. The CTD recorded data at 1-m intervals from the surface down to a maximum depth of 20 m. For each site and sampling date, we calculated a depth–integrated mean for temperature and salinity across all measurements taken between 0 and 15 m depth to match the depth of the zooplankton net.

The climatic indices used in this study were the Southern Annular Mode (SAM), Multivariate ENSO Index (MEI.v2), and Pacific Decadal Oscillation (PDO). These climatic oscillations are the dominant modes of variability in the Pacific basin. They modulate nutrient availability, primary production, and the retention or dispersion of mussel planktonic larvae in fjord ecosystems (Lara et al., 2016; Molinet et al., 2025). They have been shown to influence key oceanographic and atmospheric conditions in northern Patagonia, including precipitation, river discharge, and stratification of the water column (León-Muñoz et al., 2013; Iriarte, 2018; Pérez-Santos et al., 2021), and are thus relevant for understanding variability in MLA and recruitment success. Indices came from different sources and were retrieved through the rsoi package in the R statistical environment ver. 4.5.0 (R Core Team, 2021). This package accesses publicly available datasets hosted by NOAA (National Oceanic and atmospheric Administration) and other institutions, such as the PSL (Physical Sciences Laboratory) and the Climate Prediction Center (CPC), which provide the official records for each index. We retrieved these time series for 2013–2024 to match our study period.

2.2. *Larval abundance patterns*

Publicly–available larval abundance data were collected year–round mainly on a monthly schedule, yet sampling did not always occur on identical calendar days and some months lacked observations due to missing or unreported samples. To obtain a complete monthly time series for each site, missing values were estimated using linear interpolation (Broitman et al., 2008). Interpolation was performed only within the temporal range defined by the first and last observations for each site (Table S3). To assess the temporal and spatial variability of larval abundance across sites we estimated standardized anomalies using Eq. (1). Prior to anomaly estimation, larval abundances were were log-transformed ($\log_{10}(n+1)$) to reduce skewness and stabilize variance (Broitman et al., 2008). Monthly Standardized Anomalies were computed for each site by subtracting the long-term mean for each month and dividing by the corresponding monthly standard deviation. This approach removes the long-term seasonal component (Fig. S1) and facilitates comparisons across sites. For simplicity, we refer to these standardized values as mussel larval anomalies (MLA anomalies) hereafter:

$$\text{MLA Anomaly} = \frac{A_{\text{current}} - \mu_m}{\sigma_m} \tag{1}$$

Where A_{current} is the log-transformed larval abundance for a given site and calendar month, μ_m is the historical mean log-transformed larval abundance for that site and calendar month (averaged across all years), and σ_m is the standard deviation of log-transformed larval abundance for that site and calendar month (across all years).

In order to pinpoint and quantify anomalies in larval abundance, we established an annual phenological baseline of larval abundance in the water column using the npphen package in R. This package implements a non-parametric approach based on Kernel Density Estimation (KDE) to reconstruct the annual expected phenological cycle and quantify the seasonal variability around it (Chávez et al., 2022). Observed larval abundances were aligned by phenological day using July 1st as the start of the reproductive season (mid-winter for the Southern Hemisphere), and used to estimate a bivariate KDE in the time-abundance space. This KDE surface was then used to compute a Reference Frequency Distribution (RFD), representing the relative likelihood of observing a specific abundance values throughout the season. Anomalies were calculated as the deviation between observed abundances and the KDE-derived phenological expectation. Each observation was also assigned a percentile rank within the RFD, allowing us to identify extreme anomalies: above the 90th or below the 10th percentile. The approach provides a robust, data-driven identification of phenologically unusual larval abundance events.

2.3. *Mann-Kendall trend analyses*

To evaluate long-term trends in MLA, we applied the non-parametric Mann-Kendall (MK) test to the time series of larval abundance anomalies. To remove the seasonal component and account for differences in magnitude across the time series, we used the standardized larval abundance anomaly from [equation anomaly] instead of the raw time series. The MK test assesses the presence of monotonic trends over time without assuming a particular data distribution. The analysis was conducted using the Kendall package in R, using the MannKendall function to each anomaly time series. The test results provided Kendall's τ coefficient and associated p-values, which were used to determine the direction and significance of the trends. The sites were classified as showing a positive, negative, or non-significant trend based on a significance threshold of $p < 0.05$.

2.4. *Local environmental variability*

To analyze the temporal variability in local environmental conditions, we computed standardized anomalies for temperature and salinity at each sampling site. This standardization allowed for comparisons of anomalies across sites and months by accounting for seasonal and spatial variability. The anomalies were calculated using [equation anomaly] on raw data.

2.5. *Lagged correlation analyses*

To evaluate the relationship between environmental conditions and larval abundance, we performed a lagged Kendall's τ correlation analysis. This approach involved computing pairwise correlations between standardized larval anomalies and lagged values (0 to 6 months) of environmental variables and climatic indices, independently for each site (Broitman et al., 2008; Lara et al., 2016). The non-parametric Kendall's τ method is well suited for ecological time series, as it assesses non-linear relationships and handles tied values effectively (Zar, 2009). All correlations were computed using the cor.test function in R. To account for multiple comparisons, p-values were adjusted using the Bonferroni correction across all site-by-lag combinations for each environmental variable or climatic index, and significance was assessed at adjusted $p < 0.05$.

3. Results

3.1. *Larval abundance patterns*

We observed distinct seasonal trends across sites (Fig. 2A). The abundance of mussel D-larvae generally peaked during the late austral spring and summer, and with periods of low abundance during winter (Fig. 2A). Monthly anomalies of mussel larvae concentration varied between sites and in intensity over the study period, although temporal patterns were evident among distant sites (Fig. 2B). Three negative multi-site anomalies stood out. The first, during 2015–2016, then during 2017–2018 and then a protracted period after 2019. The two southernmost sites evidenced important negative anomalies during 2021 and then again during 2023. Positive anomalies on the other hand, were observed for several sites in the northern sites in 2016, but only in sites from Pichicolo southward. Then again during 2021 throughout 2023, but only in sites from Hornopirén northward. Long site-specific positive anomalies were detected in Cochamó during summer of 2017, in Pitipalena during all 2017, and in Ilque and Metri at the end of 2022. A region–wide climatology of larval abundance is shown in Supplementary 1 (Fig. S1).

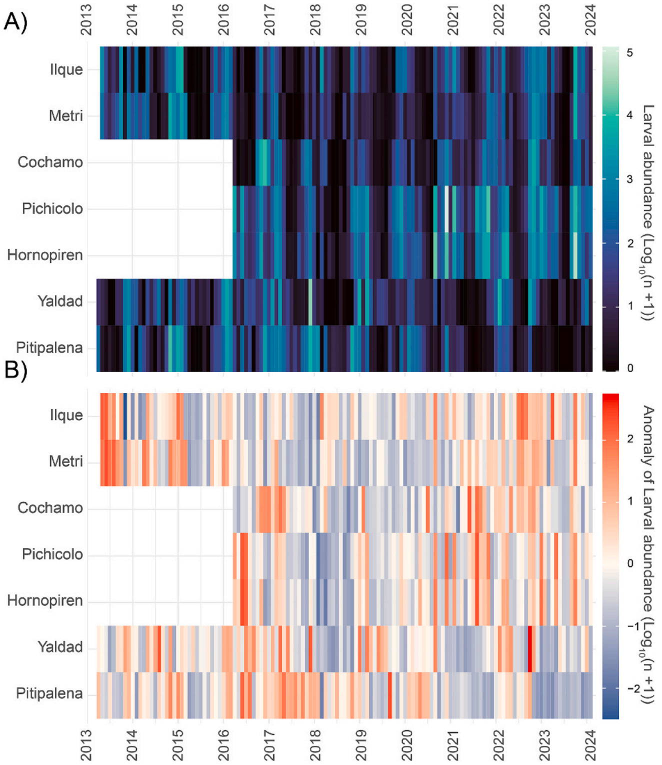

Fig. 2. Time series of mussel larval abundance across the studied sites. Each row in panel A represents the $\log_{10}$ average larval abundance for each site and month, while in panel B represents the normalized anomalies on larval abundance.

The analysis of positive extreme anomalies revealed that unusually high larval abundance were often concentrated between late spring and early summer. Several of the anomalous events were recorded between 2014 and 2017, however, the most extreme positive anomaly was observed at Hornopirén on October 4 of 2023, where larval abundance exceeded 795,000 larvae·m^{-3}, far surpassing other values in both magnitude and rarity (Table S1). High RFD percentiles ($\geq$92) were consistent across sites, indicating these events were exceptional relative to historical baselines.

Negative extreme anomalies (i.e. lower-than-expected larval abundance) were found across all sites, typically concentrated between May and July. These low-abundance events were most frequently observed in the years 2022 and 2023, suggesting the possibility of recent environmental stressors or mismatches between spawning cues and larval development conditions. The most extreme negative anomaly occurred at Hornopirén on March 10 of 2023, where abundance was around 1400 larvae·m^{-3} below the expected baseline, with a corresponding RFD of 7%. Several sites, including Yaldad and Pichicolo, registered anomalies with RFD values indicating larval abundances lower than any previously observed values for those dates. The complete list of anomalies per site is provided in the Supplementary 1 (Fig. S2-S8).

3.2. *Mann-Kendall trend analysis*

The Mann-Kendall test revealed differences in the long-term trends in MLA anomalies between regions (Table 1). Decreasing trends were detected at Yaldad ($\tau = -0.167, p < 0.01$) and Pitipalena ($\tau = -0.245$, $p < 0.001$), suggesting a consistent reduction in larval abundance at the polewardmost sites. Conversely, Pichicolo exhibited a significant increasing trend ($\tau = 0.143, p < 0.05$), hinting at an abundance increase at mid latitudes of the ISC. No significant trends were observed at Ilque, Metri, Cochamó, or Hornopirén. Conversely, we did not detect any trends in temperature or salinity anomalies (not shown).

3.3. *Oceanographic and climatic variability*

At all sites, temperature followed a consistent seasonal pattern (Fig. 3A), which was less evident for salinity (Fig. 4A). Temperatures were warmer at beginning and end of the calendar year (austral summer), and colder by mid-year. The equatorward sites, down to Hornopirén had overall higher temperatures, while poleward sites were colder (Fig. 3A). In recent years sites from Ilque to Hornopirén had warmer summers. Temperature anomalies exhibited a synchronized pattern throughout the study area, with changes occurring simultaneously even between distant sites (Fig. 3B). Throughout the study area we observed unusually high temperatures from 2015 to 2017. (Fig. 3B).

Table 1
Mann-Kendall test results for the trend of of mussel larvae abundance (MLA) anomaly across sites.

Site	τ Larvae
Ilque	0.05931
Metri	−0.06594
Cochamó	0.06140
Pichicolo	0.14291*
Hornopirén	0.11445
Yaldad	−0.16700**
Pitipalena	−0.24487***

Significance levels: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

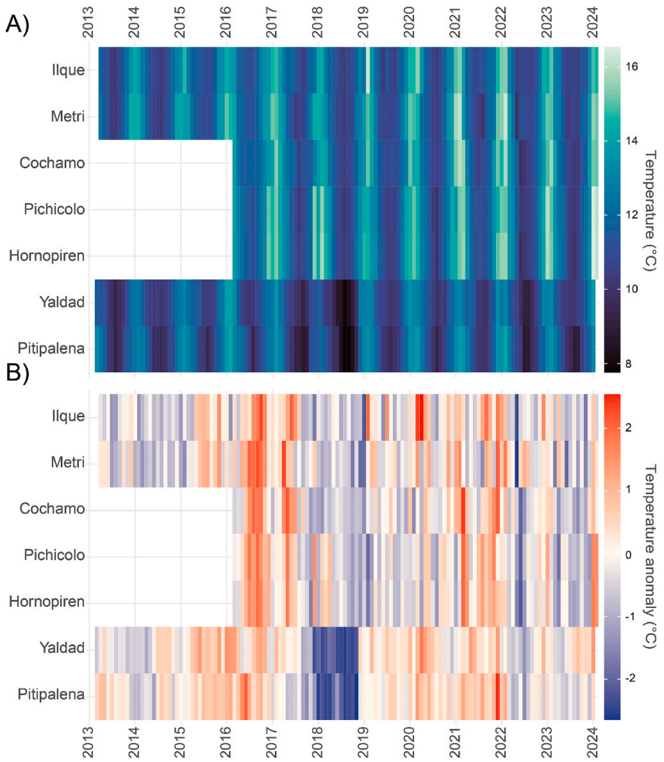

Fig. 3. Time series of seawater temperature across the studied sites. Each stripe in panel A represents the average water temperature for each site and month, while in panel B represents the normalized anomalies of temperature.

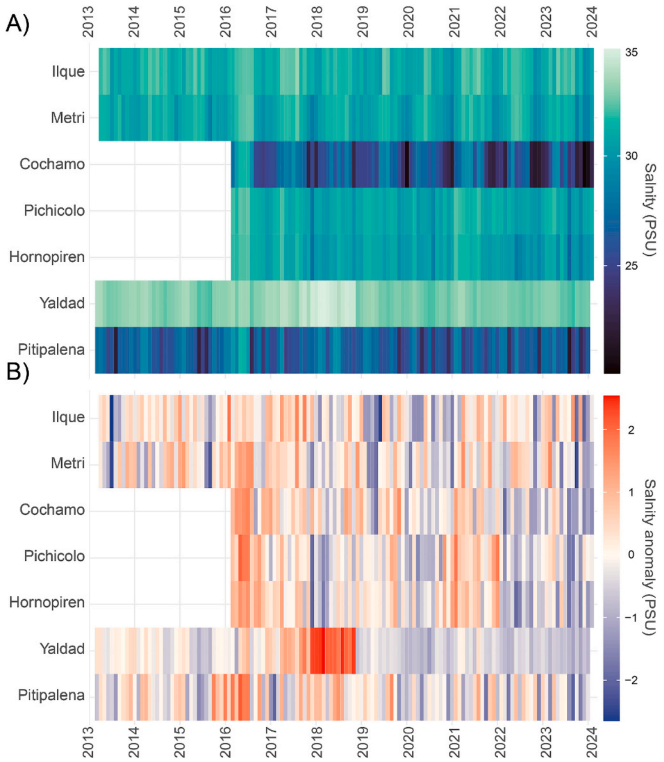

Fig. 4. Time series of seawater salinity across the studied sites. Each stripe in panel A represents the average water salinity for each site and month, while in panel B represents the normalized anomalies of salinity.

This was followed by a cold period up to 2019, which was particularly strong and sustained in the southernmost sites (i.e. Yaldad and Pitipalena). Salinity was relatively stable across sites. Exceptions were Cochamó (Reloncavi fjord) and Pitipalena (Pitipalena fjord) (Fig. 4A, 1), which showed lower and more variable salinities. Conversely, the site with higher salinity was Yaldad, the site adjacent to the Guafo mouth and the open ocean. The salinity anomaly displayed greater spatial variability, with changes occurring at different times even between close sites (Fig. 4B), likely influenced by the distinct geomorphological characteristics of each site, with different freshwater inputs and water mixing processes. Salinity in most sites was higher than usual during 2016 (Fig. 4B). During 2018 most northern sites (from Ilque to Dalcahue) had negative salinity anomalies, while the two southernmost sites (ie, Yaldad and Pitipalena) had a positive anomaly period. In Yaldad this positive anomaly was sustained up to the end of 2018, and has remained mostly negative since then.

Throughout the monitoring period, the climatic indices showed marked variability (Supplementary 1, Fig. S9). ENSO (MEI) fluctuated from La Niña conditions in 2013 to a strong El Niño (2014–2016), followed by alternating phases of varying duration, including a prolonged La Niña (2020−2023) and a return to El Niño in 2023. SAM also showed frequent shifts between phases, while PDO transitioned from positive at the start to negative around 2018–2020.

3.4. *Lagged correlation analysis*

The lagged correlation analysis between the MLA anomaly and local environmental variables and climatic indices, revealed spatially and temporally variable relationships (Fig. 5A, B). The lagged correlation analysis between MLA anomalies and local environmental variables (temperature and salinity) revealed no statistically significant associations after applying the Bonferroni correction across site-by-lag comparisons (Fig. 5A, B). Although some weak to moderate correlations were observed at specific sites and lags prior to correction, these did not remain significant after accounting for multiple testing. Overall, these results indicate that local temperature and salinity variability do not show consistent or robust temporal associations with larval abundance anomalies at the spatial and temporal scales examined. The analysis of climatic indices revealed a reduced number of statistically significant associations after applying the Bonferroni correction, with patterns that were highly site-specific (Fig. 5C–E). For the Multivariate ENSO Index (MEI), significant correlations were limited to only two sites. A strong negative association was detected at Cochamó at lag 0 ($\tau = -0.31, p < 0.001$), while Pitipalena showed positive correlations at lags of 1 and 2 months ($\tau = 0.25$ and 0.21, respectively; $p < 0.01$ and < 0.05), indicating contrasting responses to ENSO-related variability across locations. In contrast, no statistically significant correlations were detected between MLA anomalies and the Southern Annular Mode (SAM) after correction. The Pacific Decadal Oscillation (PDO) showed the clearest and most persistent associations among the indices examined. Significant positive correlations were observed at Pitipalena across all lags (0–6 months; $\tau = 0.26$–$0.30, p < 0.001$), with the strongest at lag 6 ($\tau = 0.30, p < 0.0001$). Additionally, a significant negative correlation was detected at Metri at lag 6 ($\tau = -0.21, p < 0.05$).

Lagged correlations between temperature anomalies and climatic indices revealed a reduced number of statistically significant associations after applying the Bonferroni correction, with MEI being the only index showing consistent relationships (Fig. 6A–C). For MEI, significant correlations were detected at a limited number of sites, showing both positive and negative responses. A positive association was observed at Yaldad at lag 0 ($\tau = 0.22, p < 0.01$). In contrast, negative correlations were found at Cochamó (lags 3 and 4; $\tau = -0.22$ and $-0.25, p < 0.05$ and < 0.01, respectively), as well as at Hornopirén and Pichicolo at lag 4 ($\tau = -0.22$ and -0.23; $p < 0.05$ and < 0.01, respectively). In contrast, no statistically significant correlations were detected between temperature anomalies and either SAM or PDO after correction.

Lagged correlations between salinity anomalies and climatic indices

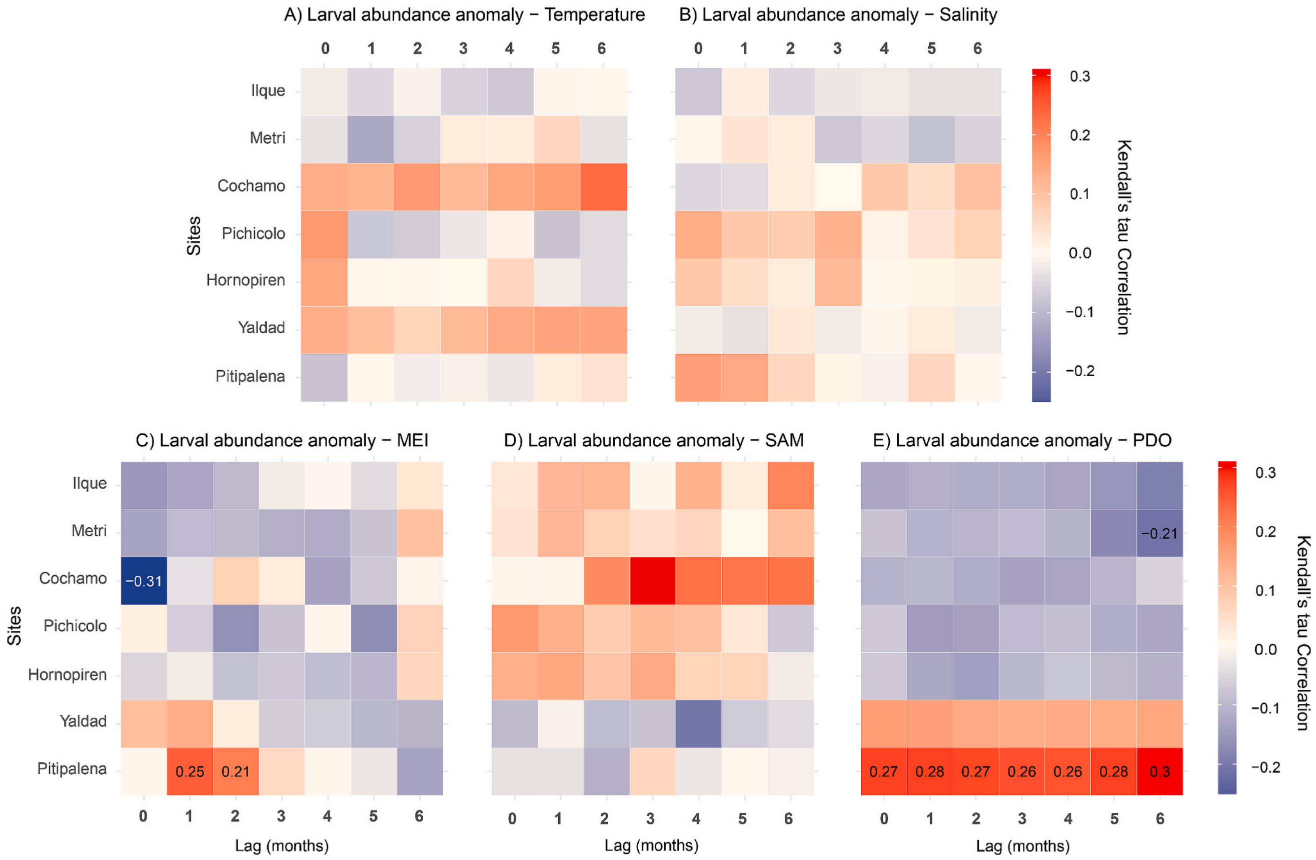

Fig. 5. Lagged Kendall's τ correlations between the MLA anomaly water parameters and climatic indices. The plots represent correlations between Larval anomaly and: A) water temperature, B) water salinity, C) Multivariate ENSO Index (MEI), D) Southern Annular Mode (SAM), and Pacific Decadal Oscillation (PDO). Colors represent the correlation coefficients: red indicates positive correlations, blue indicates negative correlations, and white indicates values near zero. Colour scale is consistent throughout plots. The numbers in each cell correspond to the Kendall's τ correlation coefficient for the respective lag (0–6 months) and site. Blank cells indicate correlations that are not statistically significant after Bonferroni correction (($p_{adj} \geq 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

revealed clear spatial patterns, with MEI and PDO showing significant associations after Bonferroni correction (Fig. 6D–F). For MEI, significant correlations were observed at several sites, displaying a consistent shift from positive associations at short lags to negative associations at longer lags. Positive correlations were detected at Yaldad at lag 2 ($\tau = 0.30, p < 0.001$), Cochamó at lags 0 and 1 ($\tau = 0.19$ and 0.30; $p < 0.05$ and < 0.001, respectively), and Hornopirén at lags 0 and 1 ($\tau = 0.21$ and 0.31; $p < 0.05$ and < 0.001). Similarly, Pichicolo showed a positive correlation at lag 1 ($\tau = 0.23, p < 0.01$). At longer lags, negative correlations became dominant, particularly at Hornopirén and Pichicolo. The strongest negative associations were observed at lag 4 in both sites ($\tau = -0.34$ and -0.36, respectively; $p < 0.001$), with additional significant negative correlations at intermediate lags. In contrast, no statistically significant correlations were detected between salinity anomalies and the Southern Annular Mode (SAM) after correction. The Pacific Decadal Oscillation (PDO) exhibited the most consistent and widespread positive correlations with salinity anomalies across sites from Cochamó to Yaldad, with significant associations detected across nearly all lags. The strongest correlations were observed at Cochamó and Hornopirén (e.g., $\tau = 0.36$ at lag 3 in Cochamó, $p < 0.001$), while similarly strong and persistent relationships were found at Pichicolo ($\tau \approx 0.27$–$0.28, p < 0.001$) and Yaldad ($\tau \approx 0.22$–$0.27, p < 0.05$–0.001).

4. Discussion

The present study reveals pronounced spatial heterogeneity in mussel larval abundance across northern Chilean Patagonia, with contrasting dynamics among fjord systems that highlight the dominant role of local hydrographic and geomorphological conditions (Iriarte et al., 2014). Our analyses were based on veliger mussel larvae, which cannot be easily distinguished at the species level using morphological criteria alone between the three closely related mussel species co-occuring in the study region. Importantly, interpolation represented a small fraction of the dataset (2–5% across sites; Table S1) and was restricted to short gaps within each station's sampling range, minimizing the risk of artificially smoothing temporal patterns. Accordingly, our results should be interpreted as representing a composite signal of co-occurring mytilid larvae, rather than a strictly species-specific response. Therefore, while we will focus our discussion on *M. chilensis*, which has been the subject of the majority of published ecological and physiological studies in the region (e.g., Santa-Cruz and Lozada, 1979; Avendaño et al., 2011; Oyarzún et al., 2011; Barria et al., 2012; Duarte et al., 2014; Molinet et al., 2015; 2017, 2021; Astorga et al., 2020; Jahnsen-Guzmán et al., 2021), and consistently dominates larval assemblages in most monitored sited in Northern Patagonia (Segura et al., 2024). However, we cannot exclude the possibility that part of the observed variability reflects shifts in the relative contribution of coexisting mytilid species, rather than changes in the abundance of a single species. Nevertheless, independent evidence supports the interpretation that the larval signal is largely driven by *M. chilensis*, and to a lesser extent *Aulacomya atra*. Extensive natural beds of both species have been documented in fjord systems such as Reloncaví and Hualaihué, including areas connected to some sampling sites (Molinet et al., 2015; 2025). In addition, the large-scale aquaculture production of *M. chilensis*

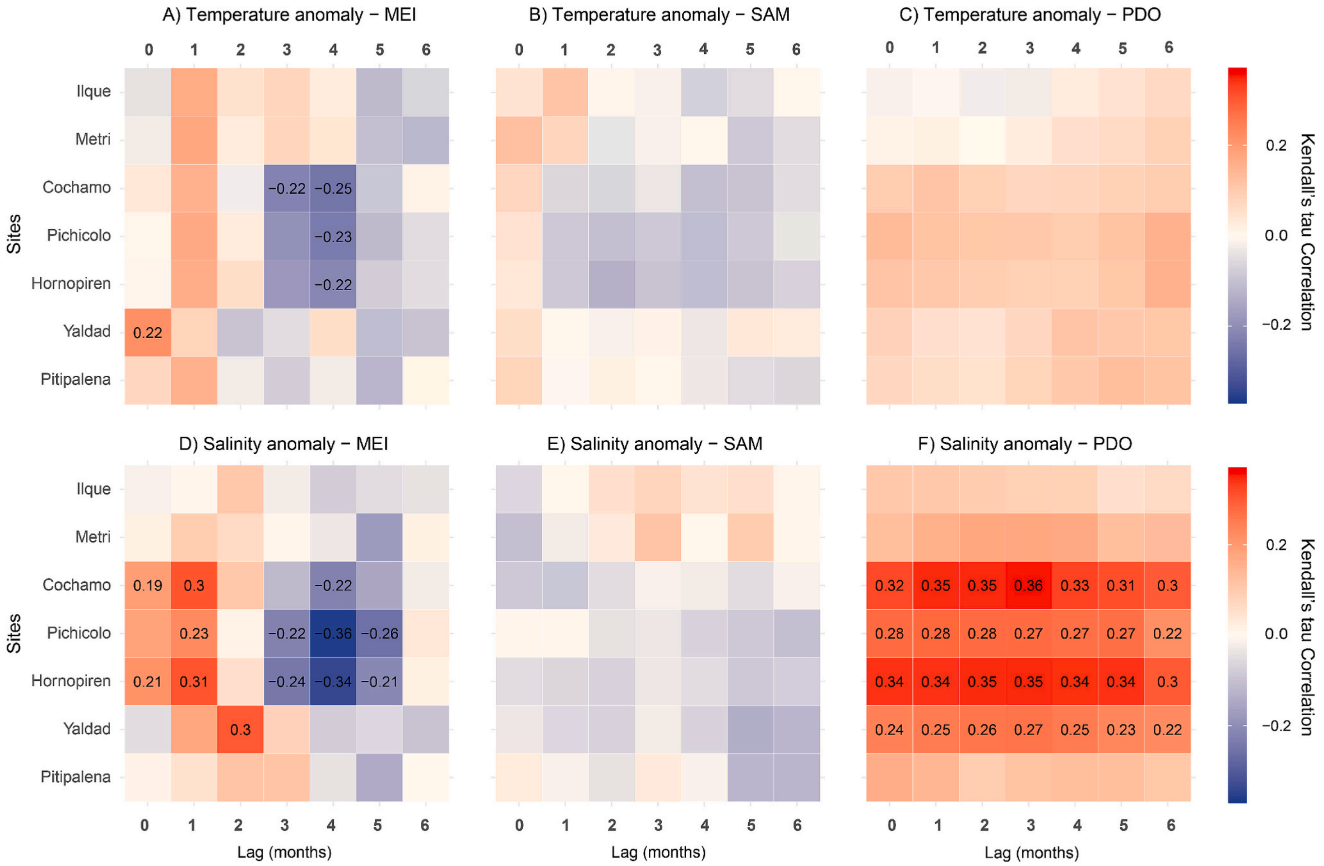

Fig. 6. Lagged Kendall'sτ lagged correlations between temperature and salinity anomaly and two climatic indices. A) Temperature anomaly and Multivariate ENSO Index (MEI), B) Temperature anomaly and Southern Annular Oscillation (SAM), C) Temperature anomaly and Pacific Decadal Oscillation (PDO), E) Salinity anomaly and MEI, D) Salinity anomaly and SAM, F) Salinity anomaly and PDO. Colors represent the correlation coefficients: red indicates positive correlations, blue indicates negative correlations, and white indicates values near zero. Colour scale is consistent throughout plots. The numbers in each cell correspond to the Kendall'sτ correlation coefficient for the respective lag (0–6 months) and site. Blank cells indicate correlations that are not statistically significant after Bonferroni correction (($p_{adj} \geq 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in southern Chile (400,000 tons annually; SERNAPESCA) implies a substantial reproductive output likely contributing to regional larval abundance. In contrast, combined landings of *A. atra* and *C. chorus* remain comparatively low (<10,000 tons annually), suggesting a more limited contribution. Although *C. chorus* can be locally abundant (Molinet et al., 2025), its overall biomass is unlikely to dominate larval dynamics at the regional scale. It is also important to note that larval abundance anomalies likely result from an increase in larval abundance, or lack of them, due to the overlap of multiple factors, such as regional spawning patterns, larval transport from distant sources, and water column conditions (Navarrete et al., 2005; Menge et al., 2009; Broitman et al., 2008, 2022). For example, when local spawning is low, larvae can be delivered from sites where spawning was successful, boosting larval supply. In the Reloncaví Fjord, estuarine circulation plays a key role in this process, as the highly stratified surface layer can transport particles from the fjord's head to its mouth in approximately two weeks (Valle-Levinson et al., 2007). This interpretation is consistent with previous observations of elevated larval abundance before the start of local spawning (Avendaño et al., 2011), and with evidence of a high larval abundance is independent of post-recruitment survival (Molinet et al., 2017, 2021). The opposite can also apply, as successful local spawning need not translate into elevated local larval abundance. Together, these findings highlight the complex physical and biological processes shaping larval abundance along this extensive region.

All sites exhibited seasonal peaks in larval abundance during austral spring and summer months, although the onset and intensity of these peaks varied considerably between sites (Fig. 2, S1). This coincides with the different timing on spawning events reported in the literature for different mussel species in the study regions. The onset of the reproductive season of *M. chilensis* was first reported during the late 1960s, between September and February in Nercón, Estero de Castro (42.5°S), highlighting the strong relationship between spawning and rising temperatures (Lozada, 1967; Santa-Cruz and Lozada, 1979). Later, in the 1970s, studies showed a strong correspondence between the condition index and extreme water temperatures, which aligned with two distinct spawning periods observed across several sites throughout Chiloé island (Tubildad, Yaldad) and the ISC (Talcán) (Hernández and González, 1975). Additionally, mussels translocated from Putemún (42°26′S) to Caleta Leandro (36°38′S) in the early 1970s, exhibited asynchronous partial spawning events from spring through February, followed by total spawning in February and April (Cifuentes, 1977). In the Reloncaví Sound and Fjord it started later, during November and January, respectively (Avendaño et al., 2011; Barria et al., 2012). The peaks of larval abundance were also consistent with the variable number of spawning events recorded for the same species. Between 2007 and 2008 there were two spawning events in Chaihuín (39°S), while in Yal Bay (42.6° S) four (from March to June) (Oyarzún et al., 2011). On the other hand, *Choromytilus chorus* also has been reported to have variable timing and duration of its reproductive period, with a spawning season in late spring, from October to November in Queule (39.4°S), while further south in Putemún (42.4°S) the spawning was longer, from September to January (Chanley and Chanley, 1991). Overall, the strongly seasonal pattern described in the literature, together with our synthesis of long-term observations, suggests an earlier seasonal peak in larval abundance equatorward. On the other hand, a more protracted high-abundance season –with a clear peak during early summer– appeared for the locations on center of the study area, on the continental coast. Finally, a later and more curtailed season was observed southward, particularly on the open-ocean poleward part of the Chiloé island coast. The spatial and temporal climatological patterns in larval abundance suggest a strong correlation of the seasonal cycle in SST, where the earlier onset of summer equatorward is related to an earlier spawning season, the shorter warm season limits the peak in abundance southward and more complex processes modulate local abundance patterns in the continental fjords.

Positive and negative anomalies in larval abundance were observed at all sites over the 10-year period, with the most extreme positive events recorded at mid-latitude stations, particularly in Pichicolo (December 2020, October 2023) and Hornopirén (December 2022, October 2023) (Table S1, S2). These events consistently occurred under strong negative PDO conditions (PDO < -1.0), with two of them coinciding with moderate La Niña phases (MEI between -1.0 and -1.5), and one (October 2023) occurring during neutral ENSO and moderate positive SAM (SAM $> +0.5$) (Fig. S9). Notably, no extreme positive anomalies were detected during months with even stronger negative PDO values, suggesting that PDO alone is not a sufficient driver. Instead, the combination of negative PDO with La Niña or positive SAM appears particularly favorable for larval abundance at mid-latitude sites. In contrast, no such extreme events were recorded at the northern stations (Metri, Ilque, Cochamó) or southern stations (Yaldad, Pitipalena) during these periods, suggesting that local oceanographic features such as stratification, fjord geometry, and freshwater input may mediate site-specific responses to large-scale climate forcing.

Beyond correlations with environmental and climatic variables, our analyses also revealed site-specific temporal trends of MLA (Table 1). We detected a decreasing trend in Yaldad, which is adjacent to the Boca del Guafo (Fig. 1), where the inner sea opens to the southern Pacific ocean, and it is more influenced by oceanic intrusions and upwelling events (Pérez-Santos et al., 2021; Linford et al., 2024). This observation is consistent with the findings of (Padin et al., 2024), who reported a long-term decline in *Mytilus galloprovincialis* seed abundance, associated with intensified coastal upwelling in Galicia (Northwest Spain). In contrast, Pitipalena is a semi-enclosed fjord with a shallow sill and strong internal recirculation (Díaz et al., 2011), and the mechanisms behind its decreasing larval abundance remain less clear. By comparison, the northern sites, sheltered within the Reloncavi sound and fjord, did not show significant trends, yet one location (Pichicolo), at the center of our study area did show a significant positive trend (Table 1). Although we do not have a clear mechanism, it is possible that local oceanographic conditions or site-specific interactions between climatic forcing and hydrographic structure may have favored increased larval retention or reproductive success at this mid-latitude location.

Climatic oscillation showed the most consistent influence on larval abundance, showing stronger and more spatially consistent associations than local hydrographic parameters such as temperature and salinity (Fig. 5). Large-scale climate indices integrate multiple environmental variables (e.g. temperature, precipitation, wind) over extended periods and regions, capturing delayed and cumulative effects on ecological processes more effectively than local measurements (Stenseth et al., 2002; Hallett et al., 2004). Similar associations have been reported for other benthic invertebrates in central Chile, where PDO and SOI were linked to larval delivery in scallop *Argopecten purpuratus*, barnacle *Jehlius cirratus* and mussel *Perumytilus purpuratus* (Broitman et al., 2022). These effects likely reflect how climate-driven changes in SST, stratification, and food availability influence both adult reproductive condition and larval development. In northern Patagonia, ENSO and SAM influence rainfall and freshwater input, which in turn affect stratification and nutrient dynamics within fjords (Iriarte, 2018). Negative ENSO (La Niña) and negative PDO phases enhance river discharge and stratification, which favors phytoplankton productivity and larval retention (León-Muñoz et al., 2013), while positive ENSO (El Niño) and positive SAM reduce freshwater input and promote oceanic intrusions, which can inhibit larval survival and increase harmful algae blooms (León-Muñoz et al., 2018; Crawford et al., 2021). Our anomaly analysis revealed considerable interannual variability in water properties (Figs. 3, 4). In 2016, most sites exhibited warm and salty anomalies following the strong El Niño and positive PDO phase (Fig. S9). This ENSO event was associated with shifts in genetic composition of mussel populations in northern Patagonia, suggesting that it may have influenced reproductive success and larval connectivity across the region (Haye and Segovia, 2023). In 2018, a cold temperature anomaly was recorded (Fig. 3), especially in Yaldad and Pitipalena, during La Niña and neutral PDO, and Yaldad showed a persistent shift from saltier to fresher conditions through the study period (Fig. 4). These hydrographic shifts likely influence not only larval development and settlement, but also the vertical and horizontal distribution of mussel beds, as shown in recent studies (Molinet et al., 2025).

The decrease in freshwater input and the increase in salinity change the vertical distribution of *M. chilensis* mussel beds in the Reloncavi fjord (Molinet et al., 2025). This species prefers superficial and fresher waters, and it is being replaced at shallower depths by the more salinity-tolerant mussel *Aulacomya atra*, increasing competition and predation risk (Molinet et al., 2025). Consistent patterns were observed on the horizontal contraction of *M. chilensis* beds in relation to salinity gradients (Molinet et al., 2015), and also regarding the larvae of *M. chilensis* that primarily settle above 7 m depth, while *A. atra* dominates below (Molinet et al., 2021). Moreover, experiments showed that juvenile *M. chilensis* had better growth and calcification at 4 m depth than near the surface, likely due to more stable salinity and carbonate conditions (Jahnsen-Guzmán et al., 2021). Other studies have also indicated that temperature influences larval growth and development in *M. chilensis*, with evidence of different responses between populations from distinct latitudes, highlighting the role of thermal history (Lagos et al., 2012). Likewise, low salinity negatively affects feeding and energy balance in native mussels like *C. chorus*, reinforcing the idea that estuarine salinity plays a key role in the performance of mussel species (Navarro, 1988). Interestingly, recent studies in extreme environments, such as those that exposed *M. chilensis* to near-freezing Antarctic winter temperatures (Navarro et al., 2024), revealed that while this species can survive suboptimal thermal conditions, the associated energy deficits and physiological stress may limit its ecological niche expansion. Considering that all these mussel species have different times of development and sexual maturation (Chanley and Chanley, 1991), these fluctuations in species composition and abundance might translate into pronounced fluctuations in larval abundance, which ultimately may influence MLA in northern Patagonia.

Overall, our analyses revealed a contrasting ecological response to environmental and climatic forcing between northern and southern sites (Figs. 5, 6), likely reflecting local differences reported in fjord morphology, river influence, and snowmelt patterns between sites (Sepúlveda et al., 2009; León-Muñoz et al., 2013). Studies in other mussel species worldwide have highlighted the role of hydrography and sea bottom topography on the spatio-temporal variability of larval abundance (McQuaid and Lawrie, 2005; Porri et al., 2006). These results suggest that mussel larval dynamics are not only driven by climatic variability, but rather by the ways in which climate influences the physical and chemical properties of the coastal ecosystem. Larval seed abundance patterns varied across sites, with the strongest coupling between Pichicolo and Hornopirén, while other site relationships were weak, possibly due to differences in local hydrography or larval retention (Fig. S10).

Understanding the mechanisms that regulate MLA is critical, as the livelihoods of thousands of families in southern Chile depend on the availability of wild-collected seed. Mussel aquaculture plays a central role in Chile's coastal economy, providing income, employment, and food security for thousands of families. Unlike hatchery-based systems, most mussel farming in Chile depends entirely on wild seed collection, relying on the natural arrival and settlement of larvae in collectors deployed in coastal waters (Kamermans and Capelle, 2019). This low-cost practice is economically accessible but leaves the industry highly vulnerable to fluctuations in larval abundance driven by environmental variability (Avendaño et al., 2011; Barria et al., 2012). Climate-related stressors (e.g. temperature anomalies, ocean acidification, and changes in salinity) can directly affect the viability, development, and transport of mussel larvae, compromising seed availability (Pandori and Sorte, 2019) and, in turn, aquaculture productivity (B. R. Broitman et al., 2022). Declines in seed abundance have already been reported in several regions and have raised concerns among producers (San Martin et al., 2020). As global demand for aquatic food continues to increase, future growth is expected to come primarily from aquaculture, not capture fisheries (Stead, 2019). Understanding the environmental drivers that control larval abundance is essential not only to ensure the long-term sustainability of mussel farming in Chile, but also to better anticipate how fluctuations in larval availability may impact the livelihoods that depend on it. While our analysis focused on total veliger abundance, future studies should distinguish among larval stages (e.g., D-veliger, umbonate, competent), as each stage may exhibit different responses to environmental variability. This distinction is particularly important for aquaculture, since only competent larvae are capable of settlement and thus directly influence seed collection success. Incorporating larval stage differentiation would improve our understanding of reproductive timing, recruitment dynamics, and the mechanisms linking climate variability to aquaculture outcomes.

5. Conclusions

This study analyzed seasonal and interannual variability in MLA across multiple sites in northern Chilean Patagonia, integrating long-term time series with environmental and climatic data. All sites exhibited larval peaks during the austral spring and summer, but the timing, duration, and intensity of these peaks varied markedly across the region. Extreme positive anomalies were concentrated at mid-latitude sites (Pichicolo and Hornopirén) and consistently associated with strong negative PDO phases, in combination with La Niña or positive SAM. In contrast, northern and southern sites showed no such anomalies during the same periods, suggesting that local hydrography may modulate the biological response to climatic forcing. Long-term trends revealed a decline in larval as climate change is reshaping marine ecosystems by altering the timing, intensity, and predictability of key biological processes. In northern Chilean Patagonia, where mussel aquaculture depends on wild seed collection, variability in oceanographic and climatic conditions may affect mussel larval abundance at local scales. Here, we analyze a decade of monthly data on mussel larvae collected at seven sites distributed across contrasting fjord and channel systems. We assess phenological patterns, extreme events, and long-term trends in larval abundance, and evaluate their associations with local hydrography and large-scale climate indices (ENSO, PDO, SAM) and local hydrographic variability. Larval peaks varied in timing and duration across sites, and we identified extreme positive and negative events. Extreme positive larval abundances were concentrated at mid-latitude sites and occurred during strong negative PDO phases, often combined with La Niña or positive SAM. In contrast, decreasing trends were detected at the southernmost sites, while a positive trend emerged at one mid-latitude site. These contrasting patterns suggest that larval dynamics are primarily shaped by large-scale climate forcing, with local hydrographic conditions modulating site-specific responses. These contrasting patterns highlight strong spatial heterogeneity in larval dynamics, suggesting that local hydrographic conditions and geomorphological setting play a key role in modulating the effects of large-scale climate variability. Our results emphasize that larval abundance cannot be generalized across the region and must be interpreted within the context of site-specific processes. Understanding these local dynamics is critical for predicting variability in seed availability and supporting the sustainability of mussel aquaculture under changing environmental conditions. Abundance at southern sites and a positive trend at Pichicolo. These results indicate that mussel larval dynamics are not solely driven by broad-scale climate variability, but emerge from its interaction with site-specific environmental conditions. This complexity underscores the importance of identifying the local mechanisms controlling larval abundance, particularly in regions where mussel aquaculture depends entirely on natural seed availability and remains vulnerable to climate-driven fluctuations.

CRediT authorship contribution statement

Felipe I. Torres: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Carlos Lara:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Conceptualization. **Carlos Molinet:** Writing – review & editing, Validation. **Nicole Castillo-Villagrán:** Writing – review & editing, Validation. **Bernardo R. Broitman:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jmarsys.2026.104227.

Data availability

Data will be made available on request.

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