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Environmental variability and larval supply to wild and cultured shellfish populations

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ABSTRACT

Coastal upwelling ecosystems support some of the most productive fisheries of the planet together with a large shellfish aquaculture sector that depends on oceanographic processes to deliver planktonic larvae to replenish and feed the farmed stock. Coastal shellfish aquaculture operations in Chile and Perú have experienced large interannual fluctuations in larval supply over the past decade, yet the drivers of such variability remain unidentified. We focused on the effects of environmental variability on larval supply of the farmed Peruvian bay scallop *Argopecten purpuratus* in a bay in northern Chile (Tongoy Bay, 30°S) that accounts for over 90% of countrywide landings. We examined the hypothesis that the environmental processes governing larval supply were shared with wild benthic invertebrates with planktonic larval development and compared time series of larval abundance for the scallop with larval supply rates to benthic populations of two well-studied wild intertidal species: the Chthamalid barnacle *Jehlius cirratus* and the purple mussel *Perumytilus purpuratus*. To this end, we examined the cross-correlation of larval supply to environmental variability using MODIS satellite fields of sea surface temperature (SST) chlorophyll-a concentration (chl-a) and fluorescence line height (nFLH), together with three climate indices relevant for the south east Pacific sector: the Southern Oscillation index (SOI), the Pacific Decadal Oscillation (PDO) and the Antarctic Oscillation Index (AAO). Our results showed that over the five-year study period (2009–2013), patterns of larval supply to the scallop population were related to interannual variability in the environmental processes as captured by their Empirical Orthogonal Functions (EOFs), likely to adult condition before spawning. Surprisingly, larval supply for none of the wild species showed a clear association to the EOFs. In contrast, scallops and wild species showed significant association to lower frequency climate variability as captured by the SOI and the PDO, but not the AAO. Results suggest that larval supply patterns to Tongoy Bay may be modulated by regional patterns of climatic variability, particularly of tropical origin. Thus, changes in coastal oceanography associated with ongoing changes in global climate could have strong and lasting effects on the supply of seedstock for wild and cultivated species across this eastern boundary coastal system and argue for the establishment of long-term ocean observing and early warning systems along the region.

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1. Introduction

Aquaculture production currently matches the landings of all global fisheries combined; over a third of this production is carried out in marine coastal regions, with mollusks contributing up to a fifth of the tonnage (Béné et al., 2016; FAO, 2020). Eastern boundary upwelling ecosystems represent a tiny fraction of global coastlines yet the tight coupling between oceanographic processes and biological production support the largest fisheries worldwide and provide key services for society (Chavez and Messié, 2009; García-Reyes et al., 2015). Similarly, mollusk aquaculture along the coastlines of eastern boundary regions is fueled by the efficient transfer of pelagic primary productivity to farmed benthic adults. As such, aquaculture production on the coasts of Chile and Spain rank amongst the world's top producers of shellfish after China, in 3rd and 6th place, with productions of 400.000 and 287.000 thousands tons live weight, respectively (FAO, 2020). The Peruvian, or Calico bay scallop, *Argopecten purpuratus* is native to the Humboldt Upwelling ecosystem and found in sheltered bays from northern Perú to central Chile. It commands a high price in foreign markets, in contrast to other farmed shellfish exports such as Mytilid mussels. During 2020 *A. purpuratus* landings from aquaculture accounted for only 1% of fresh weight but for 3% of total shellfish by value (SubPesca, 2020), making it the most valuable cultivated mollusk in Chile, and also in neighbouring Perú (Von Brand et al., 2016; Kluger et al., 2019). Scallop farming in Chile is a well-established industrial aquaculture activity and is mainly developed in Tongoy Bay (Fig. 1), which accounted for about 98% of scallop landings in Chile during 2018. Current production accounts for 20% of annual landings between 2000 and 2010 (Von Brand et al., 2016).

Natural populations have declined over the past decades with potential causes ranging from biotic to abiotic (Lohrmann, 2009; Lagos et al., 2016). Scallop farming operations in Perú rely on the collection of juveniles from the wild to stock shallow bays, a process know as sea ranching (Kluger et al., 2019). On the other hand, operations in Chile depend on seedstock obtained through the passive collection of planktonic larvae that settle on collecting surfaces. The delivery of planktonic young to adult stocks is naturally subject to large interannual variation (Von Brand et al., 2016; FAO, 2020). Mechanistic linkages between environmental variability and temporal changes in seedstock supply remain tentative at best partly due to the dearth of long-term quantitative information of both processes (Flores-Valiente et al., 2019). The role of upwelling dynamics in the supply of larvae to adult populations of wild benthic invertebrates along eastern boundaries worldwide has received intense attention over the past decades (e.g. Roughgarden et al., 1988; Poulin et al., 2002; Pfaff et al., 2011; Shanks and Morgan, 2018). Studies along the coast of central Chile using satellite data on sea surface temperature (SST) and chlorophyll-a concentration have shown that larval arrival dynamics are strongly tied to environmental patterns over the annual cycle and longer time scales, chiefly through the changes in the phenology of primary production and SST variability (Navarrete et al., 2005; Lara et al., 2016). The role of oceanographic processes and climatic-scale variability on the delivery of larvae of coastal aquaculture species has only recently been addressed along the Pacific coast of south America and elsewhere (Lara et al., 2016; Fuentes-Santos and Labarta, 2015; Flores-Valiente et al., 2019). As upwelling dynamics across eastern boundaries are changing, coastal upwelling ecosystems will be exposed to changes in key ecological processes (Iles et al., 2012; Sydeman et al., 2014; García-Reyes et al., 2015). To this end, understanding the linkages between environmental variability and larval supply is key for the sustainability of shellfish

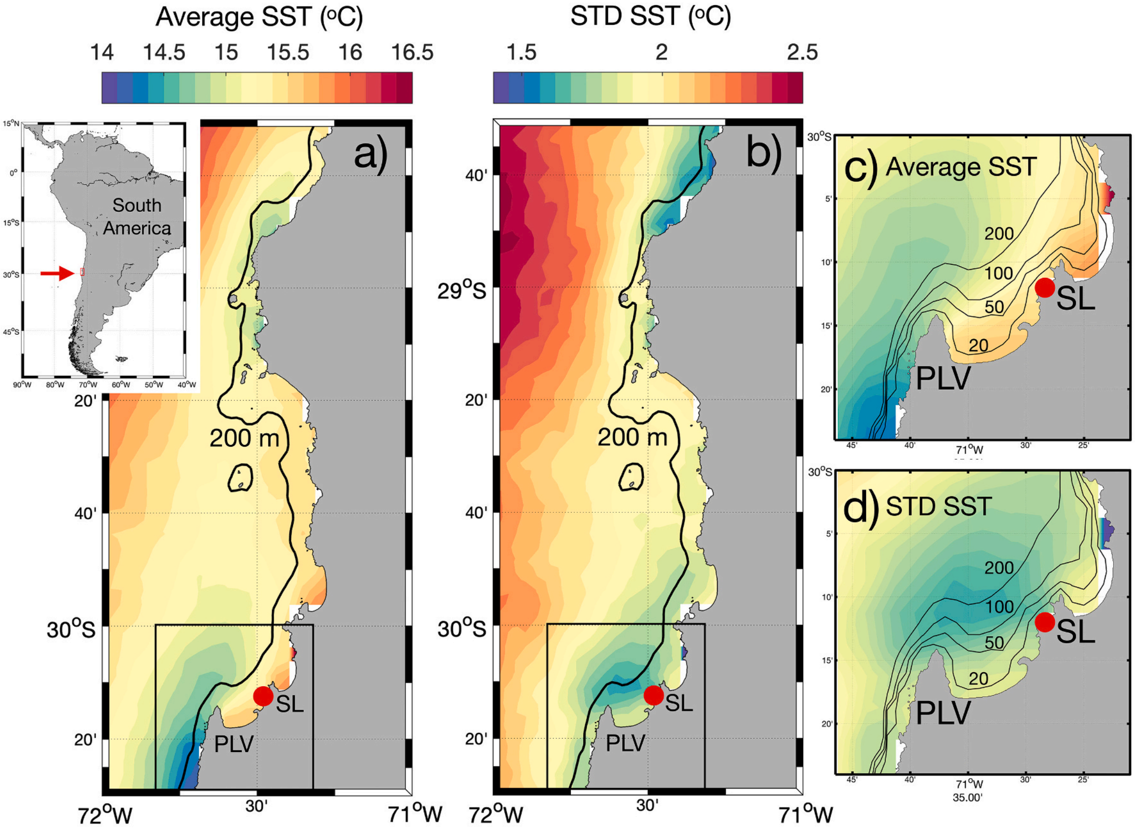

Fig. 1. Study area off central-northern Chile. (a) Average, and (b) Standard deviation of Sea Surface Temperature (SST; 2009–2013). The black box in (a) and (b) is shown enlarged in (c) and (d). The 200 m isobath is shown in a black contour in (a) and (b). Additional isobaths (20, 50, and 100 m) are also included in (c) and (d). Acronyms for Sampling Location and Punta Lengua de Vaca are indicated as SL and PLV, respectively. SL indicates the sampling region of wild species and the location of the temperature logger. Scallop were sampled all around the bay (shown in panels (c) and (d)).

aquaculture and global food security. Examining the role of low-frequency environmental variation on larval recruitment of commercially exploited populations is complicated by the alteration of the adult reproductive stock by the human activity, which can indeed drive future recruitment. We submit that much insight into the role and generality of environmental factors on the replenishment of exploited cultured and fished populations can be gained by comparisons to larval recruitment in co-occurring wild, non-exploited species.

In this study, we examine patterns of larval supply of *A. purpuratus* in Tongoy Bay and compare them with larval arrival rates to benthic populations of two wild non-commercial species: the Chthamalid barnacle *Jehlius cirratus* and the purple mussel *Perumytilus purpuratus*, common species along the coasts of Chile and Peru. We examine the hypothesis that larval supply of both farmed and wild species is influenced by similar low-frequency environmental patterns. To this end, we use time-lagged relationships between local and large-scale patterns of environmental variability and larval arrival records across all species in Tongoy Bay for the 2009-2013 period. Finally, we discuss the implications of shared patterns of environmentally-driven variability on wild and farmed species in the future.

2. Data and analysis

2.1. Study area

Oceanographic conditions along the coast of central-northern Chile are controlled by environmental processes over a range of different spatial and temporal scales. Large-scale processes are tightly linked to atmospheric forcing from decadal to interannual scales, namely the Pacific Decadal Oscillation (PDO) and El Niño-Southern Oscillation (ENSO) cycles, respectively. During the cold (warm) phases of ENSO events, the water column off northern Chile presents a shallower (deeper) thermocline, which generates negative (positive) temperature anomalies (Ulloa et al., 2001; Montecino and Lange, 2009). In contrast, the PDO is related to protracted temperature and wind anomalies in extra tropical regions and during warm (cold) phases, positive (negative) SST anomalies prevail along the coast of the temperate eastern Pacific (Mantua et al., 1997). Mesoscale processes are dominated by intraseasonal-to-seasonal variability, prominently by variation in upwelling-favorable wind forcing, which intensifies during austral Spring-Summer (Rutllant et al., 2004). Coastal upwelling is controlled by the alongshore equatorward wind field which is locally intensified by prominent topographic features, such as large capes and headlands (Aiken et al., 2008; Aguirre et al., 2012) and modulated by horizontal pressure gradients. In this way, local-scale circulation processes can be important along the region, particularly in shallow environments where tides and stratification can modulate variability of water properties (Bravo et al., 2013). In the case of Tongoy Bay (Fig. 1), which is located on the lee of Punta Lengua de Vaca (PLV), one of the largest upwelling centers of the south east Pacific, local and mesoscale processes can modulate variation of stratification and mixing conditions inside the bay (Bravo et al., 2013; Lagos et al., 2016).

2.2. Invertebrate life histories and larval sampling

The scallop *A. purpuratus* is a fast growing species reaching a commercial size of ca. 90 mm shell width in 18-20 months. In the wild, this species forms banks in wave protected environments, from 4 to 40 m depth (Stotz and Gonzalez, 1997). Spawning occurs during austral Spring-Summer with a secondary spawning period in late austral Winter (Avendaño and Le Pennec, 1997; Von Brand et al., 2016). The pelagic larval development of the planktotrophic trocophore larva is estimated to last around 16–25 days (Von Brand et al., 2016). The Chthamalid barnacle *J. cirratus* and the mytilid mussel *P. purpuratus* are the dominant sessile organisms in the upper and mid intertidal zones, respectively, along rocky shores of central and northern Chile (Navarrete et al., 2005). *Jehlius cirratus* undergoes several planktotrophic naupliar stages concluding with a lecitotrophic cyprid stage. The development is completed in about 30-35 days (Venegas et al., 2000). *Perumytilus purpuratus* larvae are facultative lecitotrophs and complete development in about 14–20 days. The arrival of barnacle and mussel larvae to shore takes place in two peaks, one during late austral Spring and another in early Autumn (Navarrete et al., 2008). Thus, there is variability in larval biological attributes among the species, although development times are comparatively similar and are likely to change under variable natural conditions.

Competent larvae (D-stage) of *A. purpuratus* were sampled every week during the recruitment season inside the farmed sector of Tongoy Bay using a vertically towed 1 m long net with a 30 cm opening and a 80 μm collector at 10 m depth and averaged over monthly scales prior to data analysis. On the other hand, we collected recently settled (post-metamorphic) larvae of *J. cirratus* and *P. purpuratus* using five replicates of passive samplers, plates and Tuffy pads, respectively, bolted to the mid (settlement pads) and mid-high (settlement plates) rocky intertidal zone, respectively. Mussel and barnacle larval collectors were installed at a long-term monitoring location (30.2°S, 71.48°W, Sampling location in Fig. 1) and were replaced approximately every month. Extensive details on the sampling procedure are provided in the literature (Navarrete et al., 2008). All samples were either frozen for later analysis or processed immediately in the laboratory where larvae were identified and counted using a dissecting microscope. Larval supply is expressed as larval density (individuals per m^3) for scallops or individuals per day for mussels and barnacles. It is important to note that longer temporal deployment of the rocky intertidal plates and tuffies estimate cumulative larval arrival, while the towed nets point out to instantaneous larval abundance. However, the post-settlement stage from tuffy pads and plates we utilize for analysis correspond only to individuals that have recently settled onto the larval collector and likely underestimate cumulative larval abundance due to post-settlement mortality of recruits between the deployment and replacement of the collectors (Navarrete et al., 2002, 2008).

2.3. Satellite and in situ data

We used MODIS Level-1 data obtained from NASA's ocean color website (http://oceancolor.gsfc.nasa.gov/). All Level-1 files were processed in the SeaWIFS Data Analysis System (SeaDAS) software to generate monthly 1-km resolution images of sea surface temperature (SST; °C), Chlorophyll-a concentration (chla; mg m^{-3}) and normalized fluorescence line height (nFLH; mW $cm^{-2} \mu m^{-1} sr^{-1}$) for the 2009–2013 period. We incorporated nFLH because of its enhanced performance as an indicator of phytoplankton fluorescence activity (see more details in Behrenfeld et al., 2009). In addition we used SST derived from subtidal temperature data loggers (HOBO U22; ONSET, Pocasset, Massachusetts, USA), moored approximately 1 m below sea level and adjacent to the larval collectors at the sampling location (Guanaqueros; specific location of the sampling location is shown in Fig. 1) (see more details in Piñones et al., 2007; Aravena et al., 2014; Tapia et al., 2014). To examine the effect of large-scale climatic variability on our study area, we used three global indices that are based on atmospheric pressure and SST over the Pacific Ocean: the Southern Oscillation Index (SOI), the Pacific Decadal Oscillation (PDO) and the Antarctic Oscillation (AAO) indices. The SOI quantifies the magnitude of El Niño-Southern Oscillation on inter-annual timescales and closely tracks temperature anomalies in central-southern Chile (Narváez et al., 2019). The PDO index is the dominant year-round pattern of SST variability and sea surface height over the north Pacific Ocean and captures a similar spatial pattern of temperature anomaly than the SOI, but over much longer (i.e. decadal) timescales (Mantua and Hare, 2002; Newman et al., 2016). Finally, we also examined the relationship between larval supply and the AAO. The AAO captures the distribution of atmospheric pressure over the Southern Hemisphere and represents the poleward intensification (positive values) of the mid-latitude westerly winds (Thompson and Wallace, 2000). Monthly data of SOI and AAO were obtained from the NOAA Climate Prediction Center (https://www.cpc.ncep.noaa.gov/). The PDO dataset was obtained from The Joint Institute for the Study of the Atmosphere and Ocean website (http://research.jisao.washington.edu/pdo/PDO.latest). It is important to note that the three indices are selected to represent variability in multi-parameter hydrographic and circulation conditions over different time scales (Halpin et al., 2004).

2.4. Data analysis

We used Empirical Orthogonal Function (EOF) analysis to characterize the dominant spatio-temporal variability patterns of monthly satellite SST and nFLH data. To remove the stationary contribution of the seasonal cycle from patterns of environmental variability, we subtracted the mean monthly values for each monthly observation of the time series and conducted EOF analyses on climatological anomaly time series, i.e. the principal modes of non-seasonal variability. The EOF for each satellite field were computed following the Singular Value Decomposition (SVD) approach to avoid a very large covariance matrix as result of the high resolution of the images (Emery and Thomson, 2004). To validate the use of a remote sensing approach in the shallow protected of Tongoy Bay, we compared the performance of the MODIS-derived SST fields with temperature data collected *in situ* by the temperature loggers. We extracted SST time series from the closest pixel to the location of the moored instrument and compared them using Pearson linear correlation analysis. Finally, we assessed the relationships between the two first EOF modes of the different environmental variables and the time series of larval supply separately for the three study species using temporal cross-correlation analyses. Since we wanted to focus on the trends in temporal variability between environmental forcing and biological response variables, without assuming linearity or other form of association in magnitudes of larval settlement (as Pearson and Spearman correlations do), we used Kendall's Tau (r_τ) for cross-correlations, which were calculated on first-order differenced time series (Broitman et al., 2008). Kendall-tau measures the level of synchrony in the temporal fluctuations between two time series, regardless of the magnitude of those fluctuations. We assumed that variation in magnitude of fluctuations were partly related to changes in spawning stock, besides variation in per capita larval output. We present all cross-correlation functions up to lags of 10 months for completeness, yet significant (r_τ over lags longer than 6–7 months (i.e. the period from gonad development to larval settlement for our study species) should be interpreted with caution.

3. Results

3.1. Larval supply patterns

The temporal variation in larval supply to benthic invertebrate populations in Tongoy Bay showed a clear seasonal pattern during the study period (Fig. 2). The chthamalid barnacle *J. cirratus* showed increased larval arrival rates from December to March and remained near zero for the rest of year (Fig. 2, blue line). The mytilid mussel *P. purpuratus* (Fig. 2, red line) exhibited a similar temporal pattern as the barnacle during our study period (2009-2013), with the exception of austral Spring-Summer 2009-2010. Non-zero larval arrival rates were more prolonged for the mussel than for the barnacle, from austral Spring to Summer (i.e. November to March). As expected from previous studies, we observed large temporal variation in the abundance of scallop larvae, which showed marked seasonal and interannual variations, with increased abundance during late Spring, Summer and Autumn and low abundance during Winter (Fig. 2, green line). The temporal coefficient of variation, however, was almost twice as large for the barnacle (2.869) when compared to the mussel (1.564) and the scallop (1.375), respectively. Following the strong seasonal variability observed in larval supply in all species, there were significant positive r_τ correlations between all raw (without removing the seasonal cycle) larval supply time series. Correlations between larval arrival rates of the wild barnacle and mussel species was highest ($r_\tau = 0.47$, $p < 0.01$) than the correlations of the cultivated *A. purpuratus* with either *J. cirratus* and *P. purpuratus* ($r_\tau = 0.42$ and $r_\tau = 0.32$, $p < 0.01$, respectively).

3.2. Oceanographic variability in and around Tongoy Bay

As shown in Fig. 3, we observed a good agreement between MODIS SST and *in situ* temperature. The single nearest-pixel reproduced well the temporal patterns and overall magnitude of the SST signal from the *in situ* logger. The seasonal cycle with well-defined warm (austral Summer and Autumn) and cool seasons (austral Winter and Spring) are clearly registered in the satellite and *in situ* records. We observed a strong correlation between the nearest pixel temperature time series derived from satellite and the *in situ* SST record over monthly scales ($R = 0.95$,

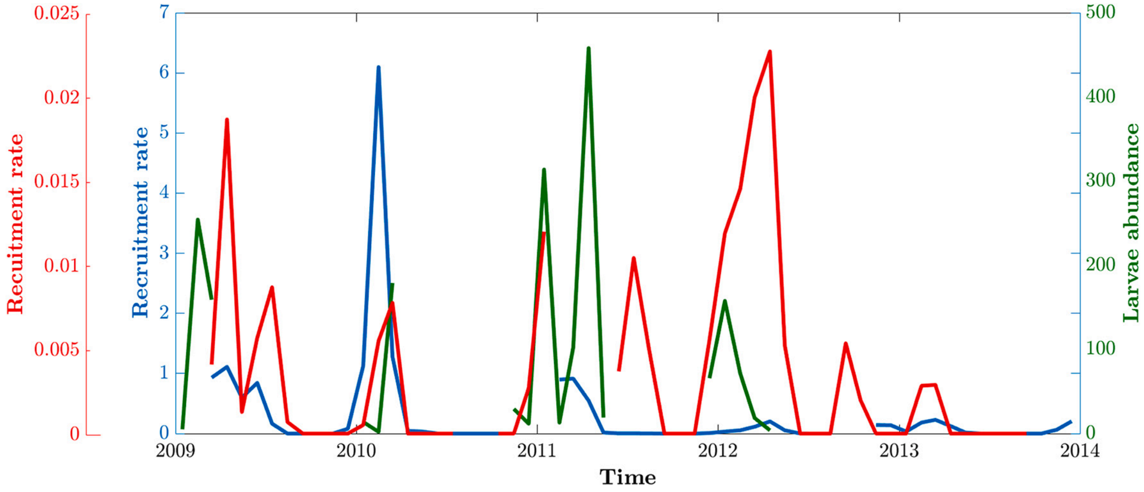

Fig. 2. Time series of larval supply expressed as daily recruitment rates (ind/day^1) for *Jhelius cirratus* (blue line), *Perumitylus purpuratus* (red line), and larvae abundance of *Argopecten purpuratus* (ind/m^3, green line), from January 2009 to December 2013. Sampling locations are presented in Fig. 1. Note the strong seasonal signal linked to the Austral spring-summer period (September to March).(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

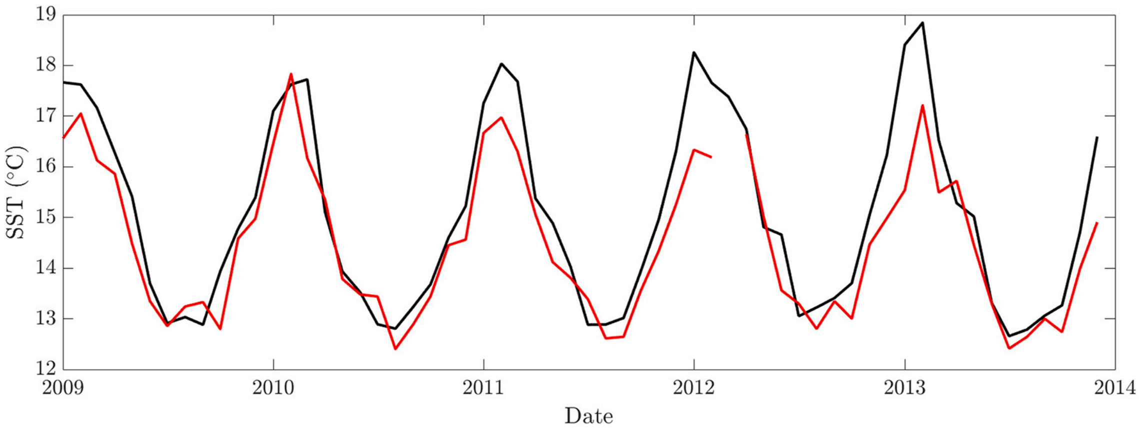

Fig. 3. Composite of Sea Surface Temperature (SST) derived from MODIS-Aqua from January 2009 to December 2013. The solid red line represents *in situ* measurements. The solid black line represents satellite-derived Sea Surface Temperature from the closest satellite pixel (1 km) respect to the location of the *in situ* measurements.

$RMSE_{1pix} = 0.84$ (C°). A high level of consistency between satellite and *in situ* data was observed throughout the cold seasons. However, SST showed a warm bias of 1–2°C during austral Summer.

The EOF analysis of SST and nFLH showed the main modes of environmental variability. As shown in Fig. 4, the first mode of the SST signal accounted for 87.6% of the total variance capturing the annual cycle in SST anomalies, where higher (warmer) temperature anomalies were observed during fall-winter months (i.e. 2009, 2012) and the lowest (cooler) temperature anomaly was observed during spring 2010 (Fig. 4a, b). The second mode of SST variability accounted for a very small fraction (5.8% of the total variance) (Fig. 4c, d) and is commonly associated to synoptic-scale temporal oscillations (Tapia et al., 2014), but in our analyses such fluctuations are masked by the use of monthly means (Valdivia et al., 2015). The EOF analysis of the nFLH fields during the five years considered in this study indicated a weaker partitioning of variance among temporal components than the SST field. The first mode explained 64% of the total variability and showed a marked seasonal pattern (Fig. 5a, b). The second nFLH mode explained 6.3% of the variability in nFLH within and around Tongoy Bay (Fig. 5c, d). The first two principal components of the chl-a surface fields explained about

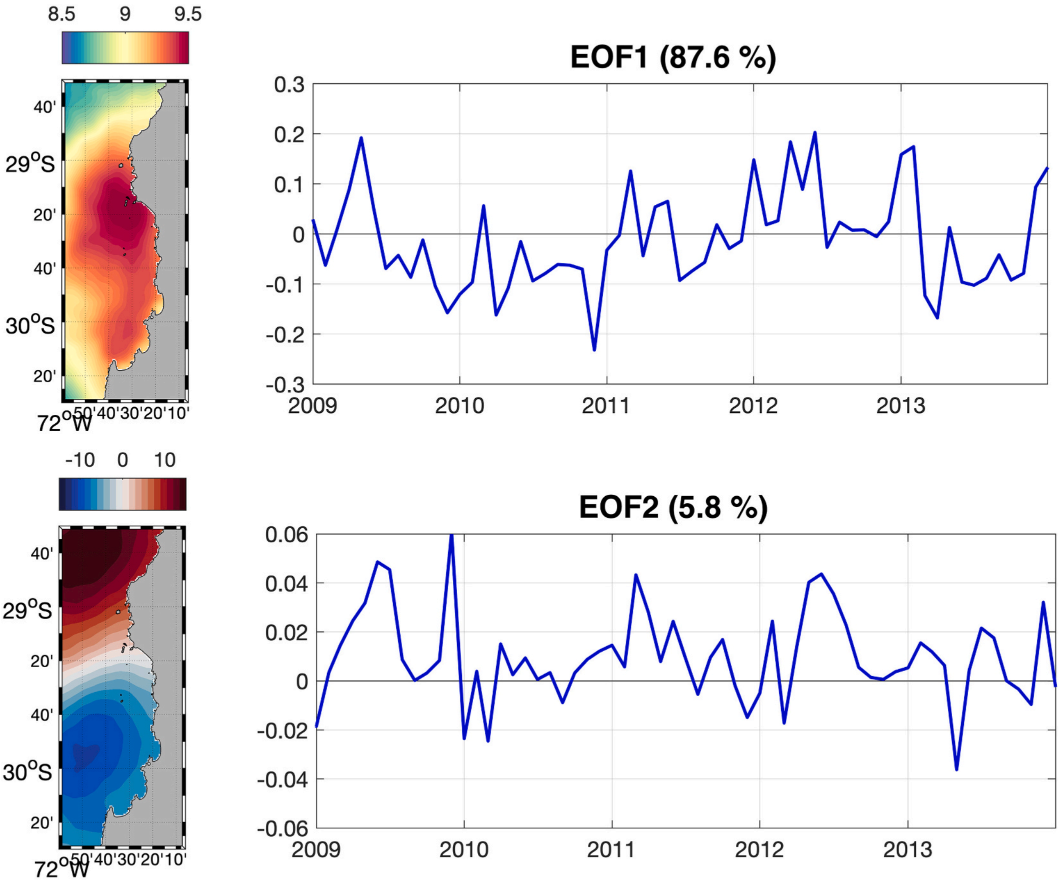

Fig. 4. Variability in SST during 2009–2013 over the study region as captured by EOF analysis. (Left panels) EOF spatial patterns and (right panels) corresponding EOF time series. The percentage of the total variance explained by each mode is indicated in parenthesis.

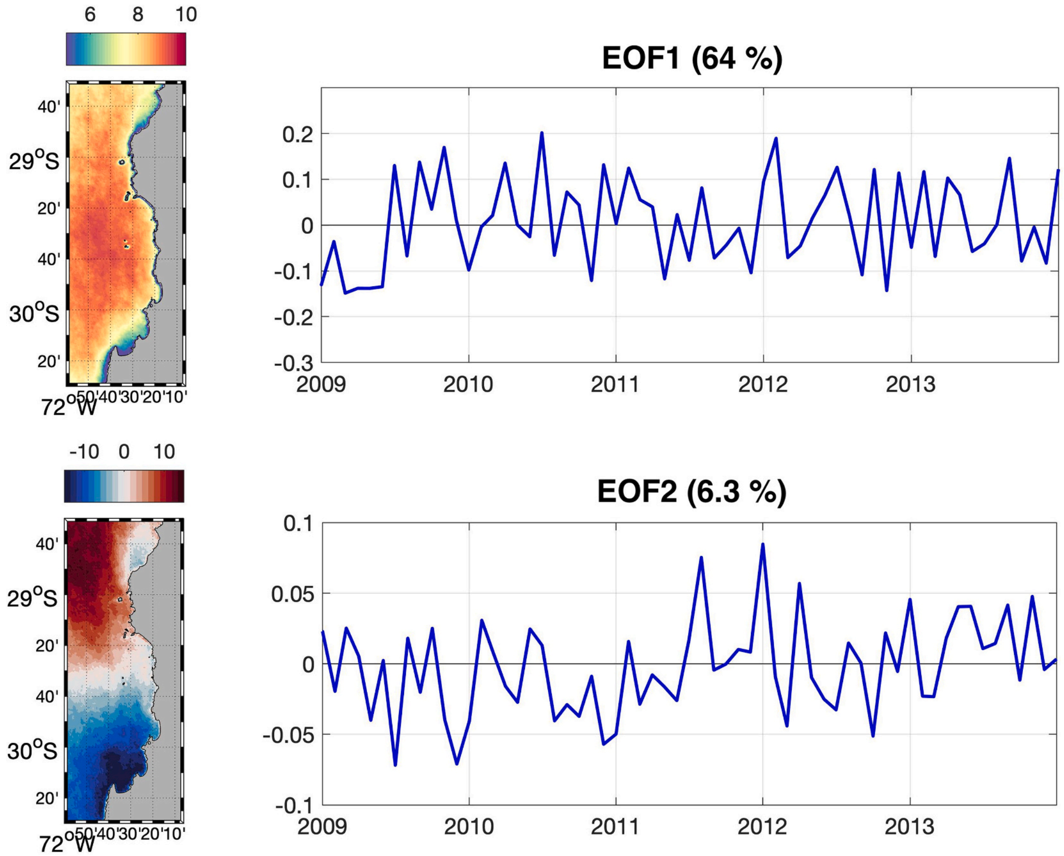

Fig. 5. Variability in nFLH during 2009–2013 along the study region as captured by EOF analysis. (Left panels) EOF spatial patterns and (right panels) corresponding EOF time series. The percentage of the total variance explained by each mode is indicated in parenthesis.

25.7% of the total variance. The first mode accounted for 17.8%, while the second mode explained the 7.9%. Both signals showed a similar seasonal variability. The EOFs evidenced the strong spatial structure in the dominant modes of temporal variability (Fig. 6a, b). The spatial structure of the dominant EOFs for SST and nFLH were clearly associated with coastal topography.

3.3. Larval supply and environmental variability

We observed significant lagged correlations between deseasoned larval supply time series and de-seasoned EOFs of environmental variables. In the case of the cultivated scallop *A. purpuratus*, we observed positive lagged correlations with a lag of 5 month with the first mode of SST, while a positive significant correlation at lag 1 and 8 were observed with second mode of SST (Fig. 7a, d). Negative and significant correlation for *J. cirratus* and the second mode of SST with 8–9 months lag were also evident. No significant correlations were observed between mussel larval arrival rates and the two SST modes. For the fist mode of the nFLH signal we observed significant positive cross-correlations with the larval concentration of *A. purpuratus* with 3 and 9 months of lag and significant negative cross-correlations with the larval arrival rates of the barnacle at 3–4 months of lag. Lagged correlations between the second mode of nFLH showed a positive association with *J. cirratus* with 7 months of lag, while for *A. purpuratus*, negative correlations were observed with 0, 3 and 8–10 months lags (Fig. 7b, e). Again, no significant correlations were observed between nFLH modes of variability and larval mussel arrival rates after removing the seasonal signal. In the case of chl-a modes of variability, *P. purpuratus* showed a positive and significant correlation for 2 month lags with the first mode of chl-a (Fig. S1 a) and *J. cirratus* showed a positive correlation for 2–3 moths lagged with the second mode of chl-a. Finally we observed a negative correlation at 3 and 6 month lags with *A. purpuratus* larval abundance and the second mode of chl-a (Fig. S1b).

Cross-correlation functions between deseasoned larval supply time series and the climate indices showed different temporal structures to those observed with satellite fields (Fig. 7c, f). Environmental variability over interannual scales showed a significant negative correlation between larval supply of *J. cirratus* and SOI at 0-month lag. On the other hand, *P. purpuratus* presented significant positive associations with SOI with a peak at 3-5 months of lag, while *A. purpuratus* showed strong significant positive correlations with SOI at 0-1 month lags (Fig. 7c). For decadal-scale variability, *J. cirratus* showed a positive correlation at 0–1 month lags with PDO whereas *P. purpuratus* exhibited significant negative correlations over a broad 2–6 month lag (Fig. 7f) and larval abundance of *A. purpuratus* showed no association with the decadal-scale pattern of variability. Finally, no clear temporal correlations were observed between any larval supply time series and AAO (Fig. S2).

4. Discussion

4.1. Environmental variability and larval supply

Mollusk aquaculture is heavily dependent on ecosystem services that range from food supply for farmed livestock to the delivery of young to replenish farmstock (Béné et al., 2016). Our results indicate that larval supply to benthic populations of wild and farmed species is synchronous over seasonal scales and that larval delivery patterns are impacted by similar environmental processes that change over inter-annual timescales. Larval arrival patterns between the wild and farmed species examined in our study share a phenological structure that has been noted before independently (Navarrete et al., 2008; Von Brand et al., 2016; Oyarzún et al., 2018). Despite the presence of a clear seasonal

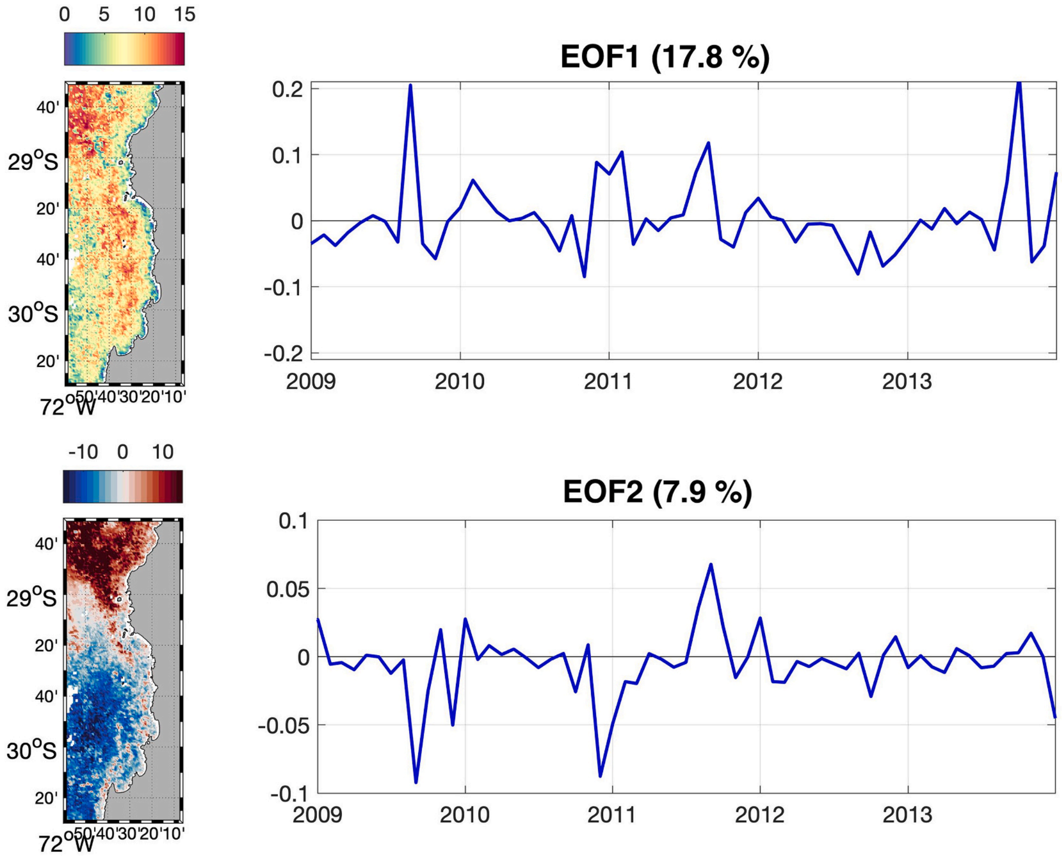

Fig. 6. Variability in Chl-a during 2009–2013 along the study region as captured by EOF analysis. (Left panels) EOF spatial patterns and (right panels) corresponding EOF time series. The percentage of the total variance explained by each mode is indicated in parenthesis.

pattern, larval supply for the barnacle was almost twice as variable than for the mussel and the scallop. On the other hand, the cross-correlation functions between larval arrival patterns and the dominant modes of non-seasonal environmental variability over monthly scales provided important insights into the processes controlling the availability of planktonic larvae to wild and farmed benthic species. Surprisingly, the first mode of SST, the leading mode of non-seasonal variation in our study, was unrelated to larval abundance of the wild species. Yet for the cultivated species we observed positive associations with the first and second modes of SST over either long and short lags (i.e. 5 and 1 months, respectively). In the case of nFLH, the cultivated species displayed a similar correlation structure but the significant association with the second mode of variability was negative and over shorter lags. This cross-correlation structure and the lack of a meaningful pattern for the wild species suggests that the influence of non-seasonal anomalies are more important for the cultivated species inside Tongoy Bay, which is likely influenced by events lasting one month or less. The seasonal-scale associations for *A. purpuratus*, after removing the seasonal component, – 0 to 6 months – suggests correlations may be due to conditions affecting larval production. A strengthening in larval output and larval provisioning are correlated with a favourable food environment for adults prior to spawning (Sinervo and McEdward, 1988), an effect that might be blurred in wild populations under multiple other sources of stress (McCabe and Navarrete, 2018). Given that the length of the larval development period of our study species is close to the timescale utilized in our analyses, we are not able to extend the previous inference to the known impact of food environment during larval development (Phillips, 2002; Pechenik, 2006). It is worth noting that the second EOF mode of nFLH seems related to seasonal fluorescence variability inside Tongoy Bay, which is likely driven by the strength of the spring phytoplankton bloom in this shallow bay. Nevertheless, raw primary productivity in coastal environments, which is dominated by large cells such as diatoms, is an equivocal proxy of food environment for planktonic larvae (Vargas et al., 2006). Moreover, satellite-derived Chl-a concentration is not necessarily an accurate measurement of *in situ* chl-a concentration in shallow coastal waters (Lara et al., 2017). This latter point is highlighted by the lack of clear associations and temporal structure of the cross-correlation between the main modes of chl-a variability and the larval arrival time series (Fig. S1a, b). Finally, the small fraction of variance accounted by the two leading EOF modes of nFLH suggests that monthly satellite data does not capture well the variability associated to temporal changes in food supply for both young and adult benthic filter feeders, at least over the 5-year period covered by our study (Vargas et al., 2006).

Relations with environmental variability over the longer time scales captured by the climate indices showed distinct relationships between species. Our study did not span a time period long enough to tease out long-term trends or the effects of event-scale disturbances, such as an ENSO event or a phase-shift of the PDO (Mantua et al., 1997; Iles et al., 2012). The 2009-2013 period covered by our study was marked by large-scale climatic instability that impacted ecosystem dynamics along the south eastern Pacific, which is well represented by the pattern of variation of the SOI and the PDO indices (Schneider et al., 2017; Lara et al., 2017; Narváez et al., 2019). In this context, it is interesting to note the quick temporal response of *A. purpuratus* and *J. cirratus* larval supply to thermal anomalies related to SOI (Fig. 7c, respectively). Increased larval supply following mass spawning after ENSO events had been reported for the scallop in northern Perú and Tongoy Bay in Chile (Von Brand et al., 2016; Flores-Valiente et al., 2019). This pattern is not consistent with the negative association of SOI and *J. cirratus* arrival rates registered in our study. Evidence for chthamaloid barnacles is mixed, however. Locations around central-northern Chile (Navarrete

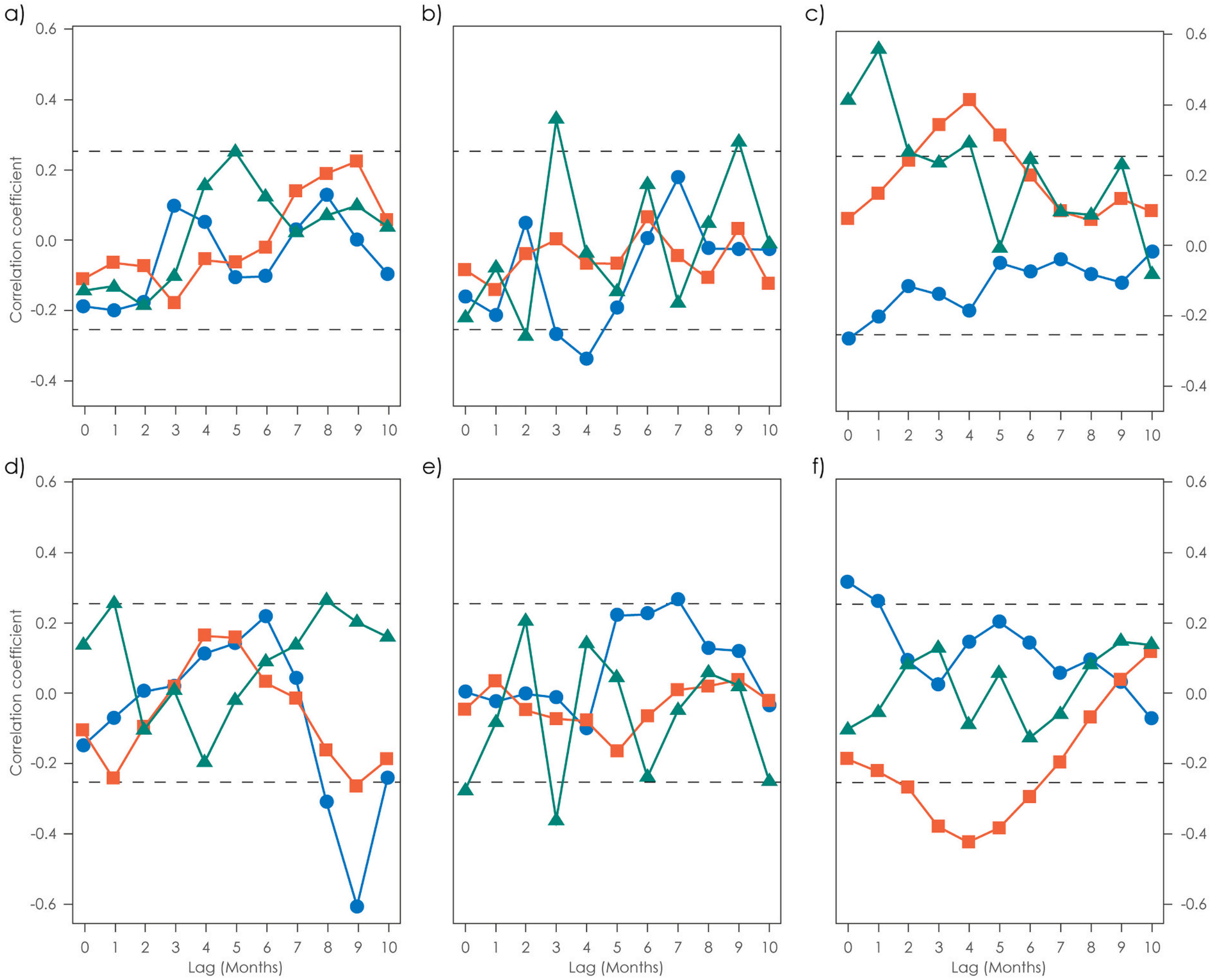

Fig. 7. Cross-correlations functions between two primary modes SST (a,d), nFLH (b,e) determined by EOF, SOI (c), PDO (f) and *J. cirratus* (circles), *P. purpuratus* (square) and *A. purpuratus* (triangle). Horizontal dotted gray line represent the 95% confidence intervals.

et al., 2002) and southern California have experienced either increased or decreased larval supply, depending on the particular ENSO event (Broitman et al., 2005, 2008; Pineda et al., 2018). In the case of mussel larvae, our results showing an increase in larval arrival rates after a long lag are consistent with an observed increase in larval arrival rates the years after the 1997–98 ENSO event (Navarrete et al., 2002). Changes in phytoplankton community composition during warm events are well suited to favour the development of larvae that feed on pico and nano-plankton, such as our study species (Iriarte and González, 2004). On the other hand, the persistent positive and negative lagged correlations between *P. purpuratus* and SOI and PDO, respectively, suggest different climate impacts on larval supply. While SOI is directly related to positive/negative SST anomalies in central Chile, which represents extremes of the ENSO cycle, positive correlations between larval supply over 3-4 month scales could also indicate a parental effect, for example through mild winter temperatures or a change in phenology across the study period (Oyarzún et al., 2018). In line with this argument, the 6-month negative relationship with PDO likely reflects the interannual trend observed for this decadal climate index over our study period, where a excursion to negative PDO values over the 2009–2013 period was mirrored by a similar oscillation in the strength of the seasonal pattern for this intertidal mussel (Fig. 6 f).

4.2. *Climate impacts and coastal ocean observation systems*

Our analysis of the impact of environmental variability on larval supply patterns has focused on SST and primary productivity as captured by SST and nFLH patterns. The seasonal cycle of SST is relevant as water temperature is a key factor in physiological responses, i.e., from protein damage to organ function (Harley et al., 2006), and also plays an important role in the spatial and temporal distributions of organisms in coastal marine ecosystems (Somero, 2005). In this sense, satellite SST appears as a useful indicator of larval supply pattern for the farmed species. On the other hand, biological productivity also stands out for its predictive strength. The nFLH field is a more accurate proxy of phytoplankton biomass or its physiological variability in coastal waters with high input of sediments and/or Colored Dissolved Organic Matter (Behrenfeld et al., 2009; Lara et al., 2017). However, validation of the nFLH product with *in situ* time series should remain the focus of future research. Other environmental processes not incorporated in our study are likely to be important for mollusk aquaculture and patterns of larval supply in shallow benthic environments under a changing climate: ocean acidification, warming and deoxygenation (Allison et al., 2011). As climate change proceeds, environmental drivers impacting aquaculture are bound to exacerbate (Allison et al., 2011). These concerns are supported by the direction and magnitude of changes predicted for most eastern boundary upwelling regions, where coastal upwelling is predicted to intensify, thus impacting the temperature, oxygen levels and pH of coastal waters (García-Reyes et al., 2015). Large scale climatic varibility attributable to global warming is already having observable effects on coastal circulation patterns along our study region (Weidberg et al., 2020). Mollusk aquaculture in the northern Chile takes place under conditions of the carbonate system parameters, temperature and oxygen that challenge the physiological limits of *A. purpuratus* (Lagos et al., 2016; Saavedra et al., 2020). Indeed, recent experiments evaluating the physiological response of juvenile and adult *A. purpuratus* to future environmental conditions (i.e. high/low temperature and high-pCO$_2$/low pH conditions) have found negative impacts in multiple biological responses (Lagos et al., 2016; Lardies et al., 2017; Ramajo et al., 2019). To this end, two important adaptation strategies emerge. The first is the use of hatcheries where high-quality broodstock can readily generate larvae in optimal conditions for field cultivation, and where research and breeding programs can be implemented, as was the case of Tongoy Bay at the dawn of the industry in Chile (Von Brand et al., 2016; Willer and Aldridge, 2020). Secondly, installing the capacity for operational monitoring of oceanographic parameters and their distribution to stakeholders can provide valuable information for the aquaculture community. A benchmark of this approach is provided by the US Integrated Ocean Observing System, where carbonate system parameters are monitored and distributed in real time and utilized by the Oyster industry to control carbonate chemistry in industrial hatcheries (Barton et al., 2015). As shown by our results, remote sensing products, near–real time observations and climate indices can be readily bundled for the public domain, as is currently done by the CEAZAMar initiative (http://www.ceazamar.cl/boletines-2021/) for central–northern Chile. Hence, establishing long-term observational capabilities along this eastern boundary can provide key information to develop adaptive capacity across the suite of stakeholders interested in sustaining aquaculture production (Froehlich et al., 2018; Todd et al., 2019).

5. Conclusions

Our results underline the association between larval supply to benthic populations and environmental variability over annual and interannual timescales - the annual cycle and ENSO-driven variability - in a protected bay heavily used for shellfish aquaculture production. Changes in coastal circulation can impact the supply of larvae to benthic population (Iles et al., 2012). Our comparative analyses highlighted the association between temporal fluctuations in temperature, and how the lagged response of the reproductive stock can consistently lead management decisions, providing insights into the role of environmental variables. Establishing capable coastal observing systems that can gather relevant observations on an operational basis seems an urgent task for all stakeholders involved in the multiple uses of the coastal zone under a changing climate (Hobday et al., 2018; Todd et al., 2019).

CRediT authorship contribution statement

Bernardo R. Broitman: Conceptualization, Methodology, Data curation, Writing – original draft, Supervision, Writing – review & editing. **Carlos Lara**: Conceptualization, Methodology, Data curation, Writing – original draft, Writing – review & editing. **Raúl P. Flores**: Visualization, Investigation. **Gonzalo S. Saldías**: Visualization, Investigation, Writing – review & editing. **Andrea Piñones**: Validation. **Andre Pinochet**: Visualization, Investigation. **Alexander Galán Mejía**: Visualization, Investigation. **Sergio A. Navarrete**: Data curation, Writing – original draft, Writing – review & editing.

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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