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Original Article

Carbonate chemistry dynamics in shellfish farming areas along the Chilean coast: natural ranges and biological implications

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The increasing shellfish aquaculture requires knowledge about nearshore environmental variability to manage sustainably and create climate change adaptation strategies. We used data from mooring time series and *in situ* sampling to characterize oceanographic and carbonate system variability in three bivalve aquaculture areas located along a latitudinal gradient off the Humboldt Current System. Our results showed $pH_T < 8$ in most coastal sites and occasionally below 7.5 during austral spring–summer in the lower (−30°S) and central (−37°S) latitudes, related to upwelling. Farmed mussels were exposed to undersaturated ($\Omega_{arag} < 1$) and hypoxic ($< 2\,\mathrm{ml\ l^{-1}}$) waters during warm seasons at −37°S, while in the higher latitude (43°S) undersaturated waters were only detected during colder seasons, associated with freshwater runoff. We suggest that both *Argopecten purpuratus* farmed at −30°S and *Mytilus chilensis* farmed at −43°S may enhance their growth during summer due to higher temperatures, lower pCO_2, and oversaturated waters. In contrast, *Mytilus galloprovincialis* farmed at 37°S grows better during spring–summer, following higher temperatures and high pCO_2. This knowledge is relevant for aquaculture, but it must be improved using high-resolution time series and *in situ* experimentation with farmed species to aid their adaptation to climate change and ocean acidification.

Keywords: bivalve aquaculture, carbonate system, climate change, nearshore, variability

Introduction

In the future, aquaculture is set to become the largest source of marine protein worldwide; it currently provides nearly half of the seafood intended for human consumption (Gentry *et al.*, 2017; FAO, 2018). This explosive growth is fuelled by the aquaculture of non-feed animals, chiefly shellfish bivalves such as mussels, scallops, and clams, which has grown exponentially around the world over the past three decades (FAO, 2018). This type of growth is based on the low technical barriers for shellfish farming and the increasing need for healthy and low-cost protein sources (Lovatelli *et al.*, 2008). Chile is among the top 5 global producers of shellfish, a trend that has been bolstered by the rapid development of bivalve aquaculture since the 1990s (FAO, 2018). The main farmed species include the northern scallop *Argopecten* *purpuratus*, which is farmed in protected embayments along the arid-semiarid northern coast of Chile (Thiel *et al.*, 2007), and the Chilean mussel *Mytilus chilensis* in the southern fjord systems (Fernández *et al.*, 2018; San Martín *et al.*, 2019). A small-scale mussel farming area is also present along the wave-exposed central coastline (Mesas and Tarifeño, 2015), where the main cultured species is *Mytilus galloprovincialis* (Ruiz *et al.*, 2008).

Until 2017 Chilean aquaculture was based mostly on salmonid production, corresponding to 54% of the total weight, yet molluscs also played an important role with 31% of the total production (Fernández *et al.*, 2018; Sernapesca, 2018). Chile has become one of the largest producers of farmed mussels around the world and number one in exportation, with ~300 000 tonnes of mussels produced in 2017 (FAO, 2018; Fernández et al., 2018). The rapid development of mussel aquaculture is reflected by the increase from 24 000 to 300 000 tonnes in the last 10 years, while scallop production has decreased from 19 000 to 3500 tonnes, recovering slightly after the 2016 El Niño event (Sernapesca, 2000–2016, see inset of Figure 1). Mussel aquaculture production currently relies on the collection of wild larvae in nearshore areas located close to shellfish farming areas; thus, they are highly sensitive to changes in seawater conditions and other environmental processes, which have affected production in the past (Lara *et al.*, 2016). In contrast, scallop aquaculture can supplement seed stock with larvae produced in hatcheries, where environmental conditions are more controlled; later juveniles are grown in nearshore rafts (Von Brand *et al.*, 2016).

Bivalve aquaculture is carried out at specific locations spanning different ocean conditions that may shift as global and climate change proceeds, thus impairing the expansion of sustainable aquaculture (Broitman *et al.*, 2017; Froehlich *et al.*, 2018). Coastal regions extending along broad latitudinal gradients such as the Chilean coastal system exhibit environmental variation (Montecino *et al.*, 2002; Wieters et al., 2003; Iriarte *et al.*, 2007; Lara *et al.*, 2016; Vargas *et al.*, 2017; Narváez *et al.*, 2019). For instance, major changes in salinity and pH/pCO$_2$ are observed in river plumes and/or river-influenced coastal areas due to variable freshwater influx (Pérez *et al.*, 2015; Vargas *et al.*, 2016), whereas

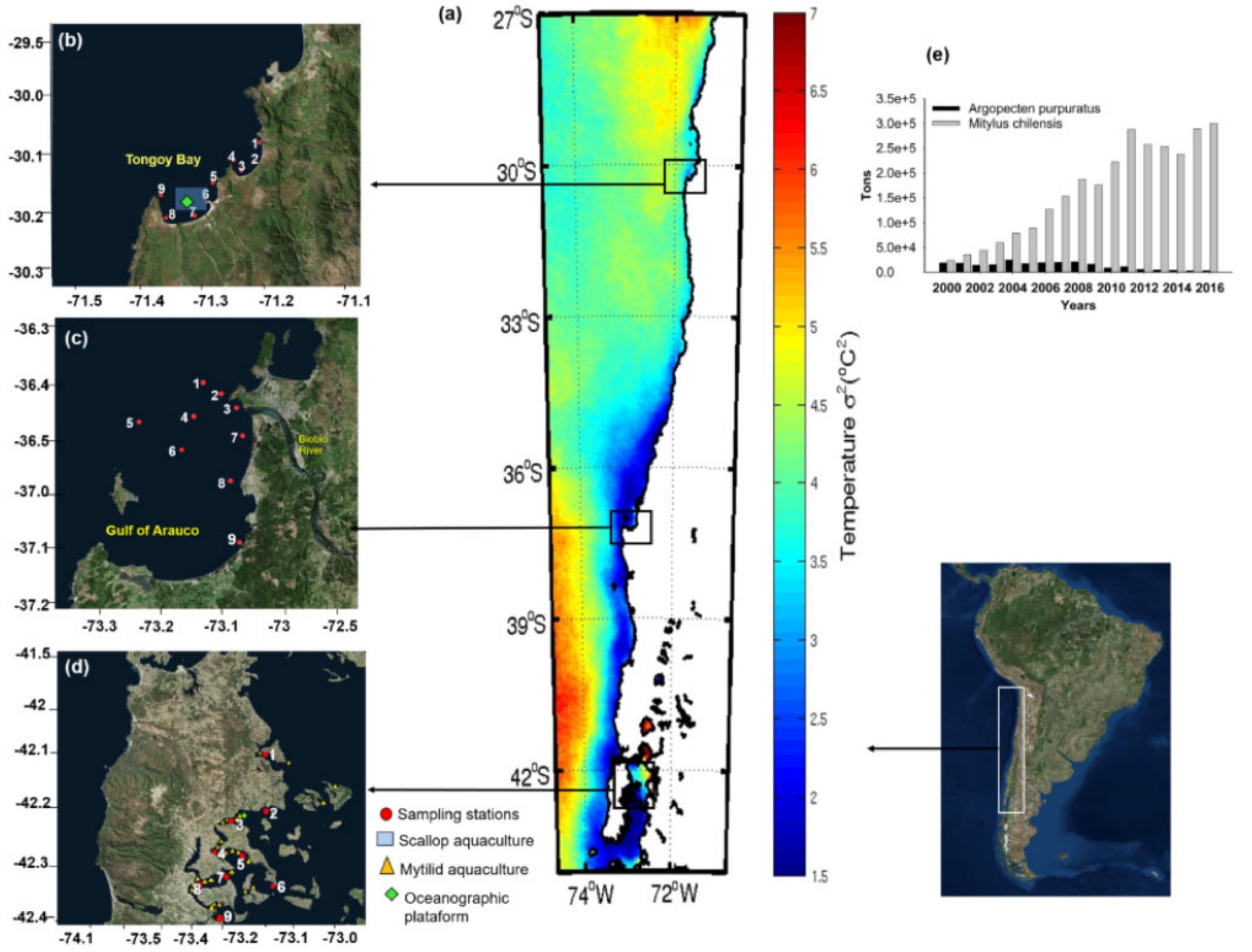


Figure 1. Geographic location of study areas along the Chilean coast, showing (a) variation of sea surface temperature and the locations of sampling stations for (b) Tongoy and Guanaqueros Bay (northern area); (c) Arauco Gulf (central area); and (d) Chiloe island (southern area). Sampling sites are shown by red dots, while scallop aquaculture areas are marked with a light blue square and mytilid aquaculture centres are shown by yellow triangles. The locations of the oceanographic platforms are marked with green diamonds in (b) and (d). The last decade trends in scallop (*A. purpuratus*) and Chilean mussel (*Mytilus edulis chilensis*) production are shown in (e) and were obtained from the national aquaculture production data (Sernapesca, 2000–2016).

temperature, oxygen, total chlorophyll and pH/pCO_2 can vary dramatically during episodic events of coastal upwelling (Torres and Ampuero, 2009; Vargas *et al.*, 2016; Vargas *et al.*, 2017). Consequently, shellfish farming areas along the Chilean coast will be affected by intensified environmental conditions of both the average and variability of environmental conditions, especially in carbonate chemistry (i.e. pH, pCO_2 and the saturation state of calcium carbonate Ω_{arag}) (Yáñez et al., 2017; Ramajo *et al.*, 2019).

Adequate characterization of coastal carbonate system variability is challenging, mostly due to the complex spatial and temporal variability and multiple physical, chemical, and biological drivers occurring in this coastal domain (Vargas *et al.*, 2016). It is also critically important due to the well-known effects on shellfish physiology and their implications for aquaculture production (Gazeau *et al.*, 2013; Barton *et al.*, 2015; Waldbusser *et al.*, 2015b; Navarro *et al.*, 2016; Clements and Chopin, 2017; Fitzer *et al.*, 2018). This is especially relevant in upwelling regions such as California and north-central Chile, where more acidic upwelling waters may affect bivalve larvae growth and development (Barton *et al.*, 2015; Vargas *et al.*, 2017); the low carbonate saturation state ($\Omega_{arag} < 1$) is mainly responsible for these effects (Waldbusser *et al.*, 2015b). Recent studies in Chile reported the impact of low pH/high pCO_2 levels on mussel and scallop physiology. Lagos *et al.* (2016) shows that low pH/pCO_2 conditions may increase shell dissolution, thus compromising scallop growth. Nevertheless, some marine calcifiers exhibit mechanisms to cope with low pH/high pCO_2 conditions (Thomsen and Melzner, 2010; Thomsen *et al.*, 2010), and recent evidence shows that factors such as high food availability and temperature can mitigate the negative effects of low pH conditions on different physiological traits (Thomsen *et al.*, 2013; Ramajo *et al.*, 2016). Thus, the impact of ocean acidification (OA) on the shellfish industry is modulated by other environmental variables, such as temperature, oxygen, and food supply; in high productive upwelling regions, many stressors may be present at the same time, such as hypoxia and low pH due to increased pCO_2 from respiration (Melzner *et al.*, 2013). However, local adaptation of shellfish may occur in this coastal zone as demonstrated recently by Ramajo *et al.* (2019), who show that *A. purpuratus* could be acclimated to short-term colder, acidic and hypoxic conditions in northern Chile.

The temporal persistence of spatially structured patterns of environmental variability is a key driver for potential adaptation through the selection of genotypes that are resilient to the local combinations of multiple stressors (Ramajo *et al.*, 2013; Lardies *et al.*, 2014; Duarte *et al.*, 2015; Osores *et al.*, 2017; Vargas *et al.*, 2017; Fitzer *et al.*, 2018). Comprehensive characterization of the natural temporal variability in the carbonate chemistry of shellfish farming areas is necessary to link OA experiments with aquaculture species in present and potential future organismal performance. Here, we established the patterns of temporal variability in environmental conditions (temperature, salinity, oxygen and food supply) and changes in the carbonate system chemistry along a wide latitudinal range characterized by contrasting oceanographic drivers (e.g. river plumes, tidal inlets, coastal upwelling areas) where the main cluster of shellfish aquaculture is carried out in southern Chile. Based on these comprehensive analyses, we also discuss the potential implications of natural environmental variability in local adaptation processes and the increasing resilience of farmed species to future environmental change.

Methodology

Study areas

The present study focused on three main geographic areas (spanning a 1500-km latitudinal gradient) that concentrate most of the Chilean shellfish aquaculture. Scallop aquaculture (*A. purpuratus*) is mostly carried out in Tongoy Bay, located on the coast of northern-central Chile (30°12′S, 71°34′W, Figure 1b). This embayment is sheltered by Punta Lengua de Vaca, a major upwelling centre with high coastal productivity (Bravo *et al.*, 2016). It is typically characterized by cold, CO_2-saturated, and poorly oxygenated waters, particularly during spring and summer (Thiel *et al.*, 2007; Torres and Ampuero, 2009). Upwelling waters are transported towards the inner shelf during austral spring and summer in response to the anticyclonic wind stress curl caused by seasonally weaker trade winds off the coast (Torres *et al.*, 2011; Gallardo *et al.*, 2017; Aguilera *et al.*, 2018). Monitoring was performed through 1- or 2-day shipboard campaigns per season, including two depths, spread over nine nearshore stations (Figure 1), and hourly automatic measurements from oceanographic sensors on a moored buoy placed in Tongoy Bay (Figure 1 and Table 1).

The Arauco Gulf in south-central Chile is a second shellfish farming area where a small-scale mussel farming industry is currently being developed. It is mostly based on the mussel *M. galloprovincialis*, located in a river-influenced upwelling area inside the Arauco Gulf (37°10′–36°45′S, 73°W, Figure 1c). The Arauco Gulf is a large, sheltered embayment (ca. 40 km) characterized by a marked change in the general orientation of the coastline from N–S to E–W, with a relatively smooth bathymetry and the presence of the Biobío River Canyon (Sobarzo *et al.*, 2016). The open coastal zone adjacent to the gulf, on the left of Punta Lavapié, is exposed to intense seasonal upwelling events, mostly during spring/summer (Sobarzo and Djurfeldt, 2004), when low pH/high pCO_2 waters prevail over the continental shelf driven by both upwelling and freshwater discharge from the Biobío River, which drains into the northern edge of the gulf (Vargas *et al.*, 2016). During winter months the Biobío River plume typically flows south into the Arauco Gulf (Saldías *et al.*, 2012). Monitoring in this coastal zone consisted of bi-monthly shipboard sampling (15 days each) of one nearshore station (St 9, Figure 1 and Table 1) adjacent to a small-scale mussel aquaculture operation. We also included two daily field campaigns involving nine nearshore stations during spring and summer (Figure 1 and Table 1).

Finally, the main cluster of the mussel farming industry in Chile is located in the southern region, mainly in the Inner Sea of Chiloé, and is focused on *M. chilensis* (Fernández *et al.*, 2018; San Martín *et al.*, 2019). The Inner Sea of Chiloé (42–44°S) is characterized by high seasonality with higher temperatures during summer (∼18°C) and minimal values during winter (9°C). A clear vertical salinity distribution is generated over its eastern side due to the freshwater runoff from small rivers during summer (Iriarte *et al.*, 2007). Surface waters in the southern portion of the coastline (>37°S) are relatively brackish and more oxygenated because of the influence of large freshwater runoff from snowmelt and icefields, with lower levels of inorganic carbon; they are strongly undersaturated in CO_2 and depleted in nitrate (Torres *et al.*, 2011). Despite our knowledge of undersaturation of CO_2 in southern coastal waters, there is no information about the carbonate system parameters (Omega aragonite and calcite) in the Inner Sea of Chiloé to date. Monitoring of this nearshore zone was carried out through seasonal daily shipboard campaigns including two depths at nine stations and hourly automatic measurements from a moored buoy located at one of the mussel farming sites (near St 3, Figure 1 and Table 1).

Table 1. Summary of oceanographic observations including time series from buoys and conventional shipboard sampling.

Location	Coordinates	Period		Type	Frequency	Stations (*n*)	Depth (m)	Measurements	Sensors
		Start	Finish						
Tongoy Bay	$-30°16'30.27''$, $-71°33'41.7''$	15 July 2015	12 March 2018	Buoy	Hourly	1	8–10	T°, Sal, O_2, Chl-total, pHT	WQM and SeaFet
		10 December 2014	22 May 2016	Shipboard sampling	Seasonally[a]	9	2 and 8	T°, Sal, O_2, Chl-total, pH, A_T	CTD, water samples
Arauco Gulf	$-37°09'32.4''$, $-73°11'32.5''$	8 April 2015	4 April 2017	Shipboard sampling	Bi-monthly	1	2, 5, and 10	T°, Sal, O_2, Chl-total, pH, A_T	CTD, water samples
		14 September 2015 20 January 2016	14 September 2015 20 January 2016	Shipboard sampling	daily	9	2 and 10	T°, Sal, O_2, Chl-total, pH, A_T	CTD, water samples
Inner Sea of Chiloé	$-42°21'55.8''$S, $-73°34'59.8''$	11 August 2015	22 October 2017	Buoy	hourly	1	4	T°, Sal, O_2, Chl-total, pHT	WQM and SeaFet
		8 July 2014	28 April 2016	Shipboard sampling	Seasonally[a]	9	2 and 8	T°, Sal, O_2, Chl-total, pH, A_T	CTD, water samples

[a] Seasonal sampling corresponds to a 1-day campaign per season. The field work involved nine stations where water samples were taken at two depths (with a replicate at each depth level).

Water sampling and hydrography

The hydrographic and chemical seawater characterization was performed using two methodological approaches: (i) manual sampling campaigns at different stations in the three major shellfish farming sites and nearby areas and (ii) automatic high-frequency records using oceanographic buoys in two coastal zones (Tongoy Bay and the Inner Sea of Chiloé, Chiloé hereafter). The details of the dates of each campaigns are presented in Table 1.

Temperature, salinity, and oxygen concentration were measured in shipboard sampling campaigns using a SeaBird SBE-19plus conductivity–temperature–depth (CTD) profiler equipped with a Westar fluorimeter. Water samples for total chlorophyll, total alkalinity (A_T), pH_T and nutrients [silicic acid ($Si(OH)_4$), nitrate (NO_3^-), nitrite (NO_2^-) and orthophosphate (PO_4^{3-})] were collected in surface and subsurface waters using 5 l Niskin bottles. Samples for nutrient analyses were filtered through GF/F glass fibre filters (47 mm diameter) and frozen at −20°C until analysis in the laboratory. Depth levels were selected based on the arrangement of aquaculture systems in shellfish farming areas of each region (Table 1).

In addition to seasonal characterization of the carbonate system through field sampling campaigns (Figure 1b and d), we used information from 3-year time series obtained from oceanographic buoys deployed in two of the major shellfish aquaculture areas: Tongoy Bay (Figure 1b) and Chiloé (Figure 1d). Time series were available from August 2015 to November 2017. These oceanographic buoys are specifically designed to collect information for the shellfish farming industry (CEAZA and MUSELS Research Centre). As a consequence, the oceanographic buoy arrangements and sensor depths were based on the vertical distribution of shellfish culture systems: 8–10 m in Tongoy and 4 m in Chiloé. Continuous records of temperature, salinity, total chlorophyll fluorescence, dissolved oxygen (DO), and pH were obtained with a Seabird Water Quality Monitor (WQM) and a Satlantic SeaFET (Figure 1d). The SeaFET pH (ISFET pH sensor) measurements were corrected by temperature (both recorded by the WQM) using the equations from Martz *et al.* (2010). This correction indicated differences no greater than 10^{-13} between corrected and uncorrected pH data.

Chemical analyses and estimation of other carbonate system parameters

Subsamples for total chlorophyll concentration estimates were extracted in the dark with 95% acetone (Parsons *et al.*, 1984) and measured in a Turner Design TD-700 fluorimeter. NO_3^-, NO_4^-, and PO_4^{3-} concentrations were determined via spectrophotometry following Parsons *et al.* (1984) and Murphy and Riley (1962). $Si(OH)_4$ concentrations were determined following Koroleff (1972). The protocols for A_T and pH_T estimates were conducted following the Guide for Best Practices for Ocean pCO_2 Measurements (Dickson *et al.*, 2007) and EPOCA Guide (Riebesell *et al.*, 2010). pH_T samples were collected in 50-ml syringes, immediately transferred to a 25-ml thermostatted cell at

25.0 ± 0.1°C for standardization with a Metrohm® pH meter using a glass combined double junction Aquatrode plus Pt 1000, and measured at total scale (pH_T) using a calibrated Tris buffer at 25 ± 0.1°C (pH = 8.089).

Samples for A_T were poisoned with 50 μl of saturated $HgCl_2$ solution and stored in 250-ml borosilicate BOD bottles with ground-glass stoppers lightly coated with Apiezon L® grease and kept in darkness at room temperature. A_T was determined using the open-cell titration method (Dickson *et al.*, 2007), with an automated Alkalinity Tritrator (Model AS-ALK2 Apollo SciTech). The AS-ALK2 system is equipped with a combination of pH electrode (8102BNUWP; Thermo Scientific, USA) and temperature probe for temperature control (Star ATC probe; Thermo Scientific) connected to a pH meter (Orion Star A211 pH meter; Thermo Scientific). All samples were analysed at 25°C (±0.1°C) with temperature regulation using a water bath (Lab Companion CW-05G). The accuracy was controlled against a certified reference material (supplied by Andrew Dickson; Scripps Institution of Oceanography, San Diego, CA, USA); A_T repeatability averaged 2–3 μmol kg^{-1}. Temperature and salinity data were used to calculate the remaining carbonate system parameters (pCO_2, CO_3^{2-}) and the Aragonite saturation state (Ω_{arag}). Analyses were performed using CO_2SYS software for MS Excel (Pierrot *et al.*, 2006) set with Mehrbach solubility constants (Mehrbach *et al.*, 1973), refitted by Dickson and Millero (1987). The $KHSO_4$ equilibrium constant determined by Dickson (1990) was used for all calculations.

To estimate the parameters of the carbonate system from the oceanographic buoys deployed in Tongoy and Chiloé, we established an empirical relationship between A_T and discrete salinity to create an estimated total alkalinity (e A_T) time series (Jiang *et al.*, 2014; Fassbender *et al.*, 2017). The relationship for the Chiloé oceanographic buoy was built using monthly parallel samples of A_T and salinity in the same place as the buoy, from which a strong statistical relationship was obtained [A_T (μmol/kg) = 43.9 SAL + 799.7, $R^2 = 0.97$, $p < 0.05$]. This is in accordance with the linear regression described by Alarcón et al. (2015) in a nearby area. For Tongoy Bay, we used the carbonate system parameters published by Vargas *et al.* (2017). Time series of temperature, pH_T and e A_T, together with inorganic nutrient data, were used in the CO_2SYS programme to calculate partial pressure of CO_2 (pCO_2) and aragonite saturation state (Ω_{Arar}), using the methodology described above.

A time series analysis of wind intensity and direction was also included in addition to hydrographic data and chemical analysis. Wind data were obtained from meteorological stations located near two of our study sites: Tongoy Bay (Punta Lengua de Vaca upwelling centre) and the Arauco Gulf (Punta Lavapie upwelling centre). Time series involved a period ranging from August 2015 to March 2017 in Punta Lengua de Vaca and between June 2015 and February 2016 in Punta Lavapié.

Data analysis

We tested for differences in average seasonal conditions and carbonate system parameters between the three locations using two-way ANOVA and Tukey's test for multiple comparisons to assess differences between aquaculture areas. To examine the dominant cycles of the temporal variability in environmental variables, a power spectral density (PSD) analysis was performed using the Fast Fourier Transform approach (Emery and Thomson, 2004) with the hourly time series of Tongoy Bay and Chiloé. The time series were previously filtered to remove low-frequency fluctuations (cycles >6 months) and to enhance the high-frequency variability shown in Figure 3. Spectral analysis is commonly used to separate or partition the variance of a time series at different frequencies. It is a powerful data analysis method to identify dominant frequencies and periods of variability in a time series. The quantification of the variance is expressed in the *y*-axis with units of variance (squares of the variable being analysed) over units of frequency (e.g. cycles per hour), which defines the PSD. For further details about PSD analysis, see Chapter 5.6 of Emery and Thomson (2004). From the wind time series at Tongoy Bay and the Arauco Gulf, Ekman Transport was calculated as an indicator of upwelling-favourable conditions.

Results

Sub-annual variability in shellfish farming areas

High-frequency variability was observed for temperature and oxygen in the northern site. All variables seemed to covary in phase over seasonal scales (Figure 2), and high-frequency variability was enhanced during spring–summer (Figure 2a and c). A PSD analysis of the hourly time series in Tongoy Bay and Chiloé showed energetic environmental variability taking place from a few days to ~30 days (Figure 3). There were common variability cycles over shorter periods for both locations, such as the diurnal and semidiurnal cycles (Figure 3b and d), which are associated with the dominant tidal regimes. A 6–8-h variability pattern appeared in the pH in Chiloé; however, there is no clear evidence of a real process promoting such a cycle. At longer temporal scales, fluctuations ~7, 15, and 28–32 days appeared to dominate the intraseasonal variability (Figure 3a and c), although other periods might also be important. The cycles of ~15 and 28–32 days were most likely associated with the spring-neap and apogee-perigee tidal cycles in Chiloé (Figure 3c).

Seasonal variability in shellfish farming areas

The seasonal pattern across the study areas showed a clear latitudinal temperature gradient, with the highest mean temperature values in Tongoy Bay during summer and the lowest in Chiloé during winter (15.7 and 10.5°C, respectively, Table 2 and Figure 4a). Well-oxygenated waters (>4 ml l^{-1}) were observed during the entire study period at the Chiloé site, whereas almost hypoxic waters (oxygen <2 ml l^{-1}) (Díaz and Rosenberg, 1995) were observed in the Arauco Gulf and Tongoy Bay during spring–summer and winter–spring periods, respectively (Figure 4c). Maximum food availability for shellfish (represented by total chlorophyll concentration) was observed during the spring–summer periods at all sites; the highest chlorophyll concentration (>5 μg l^{-1}) was observed in the Arauco Gulf (Figure 4b). Food availability was greater during the warm seasons (upwelling period) in Tongoy Bay and the Arauco Gulf and lower year-round in Chiloé (Tukey *post hoc* test, $p < 0.001$, Table 3 and Figure 4b).

Based on our time series, we observed clear differences in carbonate system parameters among the three shellfish farming areas (Table 3). pH_T and oxygen showed a similar seasonal trend among sites (Figure 4d), and as expected, pCO_2 showed the opposite trend from pH_T. Low pH/high pCO_2 waters occurred in northern Chile mainly during spring (Tukey *post hoc* test, $p < 0.001$), when nearshore waters reached maximum pCO_2 levels

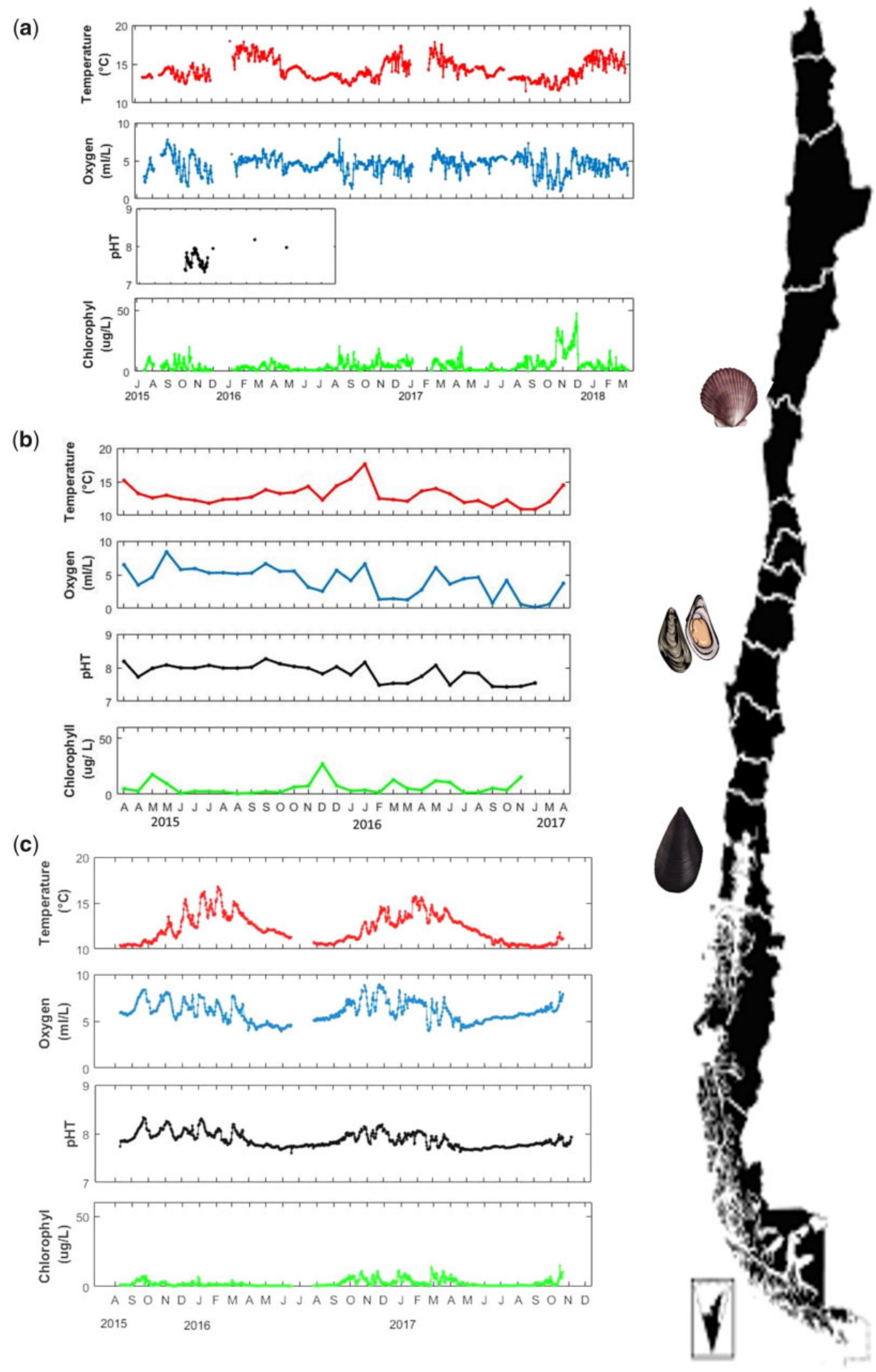


Figure 2. Time series of temperature, DO, pH_{total}, and total chlorophyll for (a) Tongoy Bay; (b) Arauco Gulf; and (c) Chiloé aquaculture zones off the Chilean coast. Time series were obtained by oceanographic buoys installed in the Tongoy Bay and Chiloé study areas, while data were obtained through shipboard bi-monthly sampling (more details in Methodology section) in the Arauco Gulf.

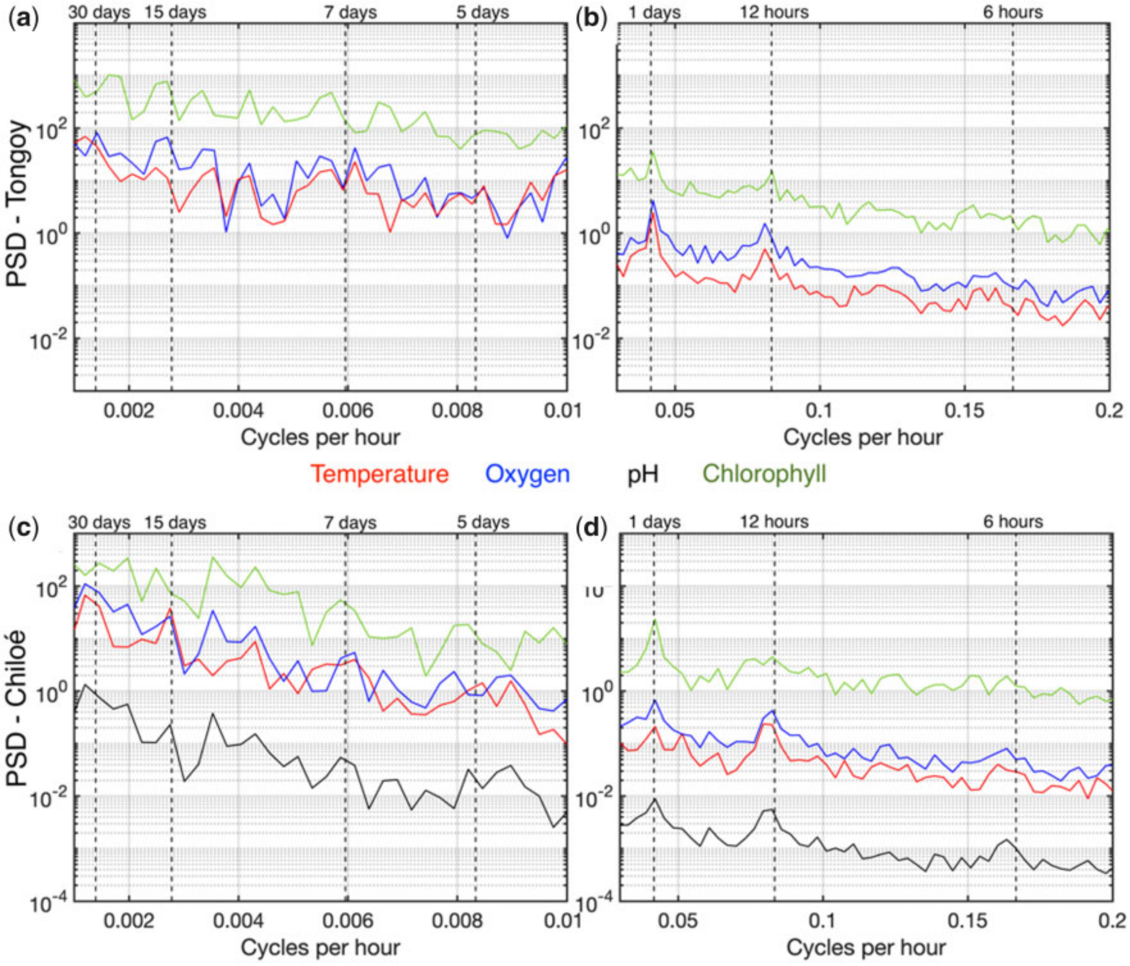


Figure 3. PSD analysis of the time series of temperature (red), oxygen (blue), pH (black), and chlorophyll (green) from (a and b) Tongoy Bay and (c and d) Chiloé. Vertical dashed lines are included to specify the period of some peaks in spectral energy, and as references for better visualization.

of 1726 μatm and undersaturated conditions (Table 2). However, pCO$_2$ showed the highest variability during spring, with daily alternation between high and low levels. Shellfish farming areas in Tongoy Bay were also subject to hypoxic waters ($<$2 ml l^{-1}) during coastal upwelling conditions, typically during spring. During these periods, DO reached values as low as 1 ml l^{-1} (Figure 2a), while normoxic ($>$4 ml l^{-1}) conditions occurred during the remaining part of the year (Figure 4c). In agreement with our observations, the Ekman transport analyses suggest upwelling-favourable conditions almost year-round off Punta Lengua de Vaca, with increased intensity from August and maximum transport during austral spring (September to November) (Supplementary material).

The Arauco Gulf site showed the lowest seasonal mean pH (pH$_T$ $\sim$ 7.78) and the highest mean pCO$_2$ ($>$800 μatm) values, which were observed during austral spring and summer (Table 2 and Figure 4d). The lowest pH$_T$ values of 7.410 and maximum pCO$_2$ of 1923 μatm were reached during some summer days (Figure 2b). The amplitude in the range of carbonate system parameters (pCO$_2$, pH and Omega aragonite) was higher than in the other study sites, which is apparent from the high standard deviation (SD) in the selected parameters (Figure 4d–f and Table 2). Our study site in the Arauco Gulf shellfish farming area was also subject to hypoxic waters ($<$2 ml l^{-1}), reaching values $<$0.5 ml l^{-1} during some days in spring and summer (Figures 2b and 4c), especially in deeper waters (10 m). Total chlorophyll values also reached the highest levels during spring and lowest during winter (Figure 4b). Ekman transport estimates at Punta Lavapie suggest more upwelling-favourable conditions during spring and summer, but the analyses show that upwelling events typically had short pulses ($<$5 days) (Figure 1 and Supplementary material).

pH$_T$ followed a seasonal trend similar to both oxygen and total chlorophyll concentrations in Chiloé. In this mussel farming area, the lowest pH$_T$ values were observed during autumn, reaching values $<$7.7, while pCO$_2$ reached 1100 μatm (Figure 4d and e). The clear seasonality of oceanographic parameters in the southern shellfish farming area was reflected by lower temperatures, oxygen and pH during the cold seasons (Figure 2c), and almost undersaturated waters during some days of winter and autumn ($\Omega < 1.5$). In contrast to the sites located at lower latitude, shellfish cultured in this coastal zone were exposed to normoxic ($>$4 ml l^{-1}) conditions throughout the study period (Table 2 and Figures 2c and 4c), yet total chlorophyll concentrations were comparably lower

Table 2. Seasonal variability in temperature, salinity, oxygen, chlorophyll, pCO_2, A_T, and pH_T (mean ± SD) in the three coastal study zones: Tongoy (30°S), Gulf of Arauco (37°S), and Chiloé (42°S).

		Tongoy	Arauco	Chiloé
Winter	*n*	234	35	236
	Temperature (°C)	13.37 ± 0.6	12.45 ± 0.3	10.4 ± 0.3
	Salinity	34.3 ± 2.2	31.5 ± 2.7	32.6 ± 0.3
	Oxygen (mg l^{-1})	4.8 ± 1.3	5.03 ± 1.2	5.7 ± 0.6
	Chlorophyll (mg C l^{-1})	4.5 ± 3.7	3 ± 2.7	1.3 ± 1.2
	n	9	23	144
	pCO_2 (µatm)	530 ± 176	605 ± 406	609 ± 192
	A_T (µmol/kg)	2 248 ± 6.3	2 118 ± 147	2 238 ± 18.6
	pH	7.95 ± 0.1	7.92 ± 0.19	7.85 ± 0.1
	Ωarag	1.87 ± 0.4	1.57 ± 0.5	1.3 ± 0.3
Spring	*n*	270	25	211
	Temperature (°C)	13.8 ± 1.1	12.8 ± 1.83	12 ± 1.2
	Salinity	34.5 ± 0.2	31.9 ± 3.5	32.5 ± 0.2
	Oxygen (mg l^{-1})	4.2 ± 1.3	4.1 ± 2.2	6.9 ± 0.9
	Chlorophyll (mg C l^{-1})	8.18 ± 8.6	6.7 ± 7.5	3.3 ± 2.5
	n	74	25	158
	pCO_2 (µatm)	696 ± 376	878 ± 698	461 ± 134
	A_T (µmol/kg)	2 280 ± 29	2 156 ± 228	2 231.3 ± 11
	pH	7.88 ± 0.2	7.85 ± 0.3	8.0 ± 0.1
	Ω_{arag}	1.8 ± 0.8	1.54 ± 0.8	1.9 ± 0.5
Summer	*n*	213	23	193
	Temperature (°C)	15.8 ± 0.9	13.4 ± 1.8	14 ± 1
	Salinity	34.3 ± 0.3	34.3 ± 0.3	32.8 ± 0.2
	Oxygen (mg l^{-1})	4.7 ± 0.8	2.3 ± 1.7	6.3 ± 1
	Chlorophyll (mg C l^{-1})	4.07 ± 2.9	6.7 ± 6.1	3 ± 2.8
	n	9	20	103
	pCO_2 (µatm)	317 ± 41	1 134 ± 535	490 ± 167
	A_T (µmol/kg)	2 298 ± 23	2 281.7 ± 33	2 235 ± 8
	pH	8.13 ± 0.05	7.68 ± 0.2	7.98 ± 0.13
	Ω_{arag}	2.9 ± 0.3	1.22 ± 0.7	1.92 ± 0.5
Autumn	*n*	183	14	196
	Temperature (°C)	14.5 ± 0.8	14.1 ± 1.2	12.2 ± 0.7
	Salinity	34.3 ± 0.1	33.3 ± 0.7	33 ± 0.2
	Oxygen (mg l^{-1})	4.63 ± 0.7	5.6 ± 1.8	4.8 ± 0.6
	Chlorophyll (mg C l^{-1})	2.95 ± 3	8.4 ± 5.5	1.5 ± 1.5
	n	9	14	104
	pCO_2 (µatm)	572 ± 129	422 ± 250	889 ± 114.5
	A_T (µmol/kg)	2 302 ± 10	2 200 ± 34	2 254 ± 5
	pH	7.92 ± 0.07	8.05 ± 0.2	7.70 ± 0.08
	Ω_{arag}	1.87 ± 0.24	2.36 ± 0.79	1.1 ± 0.2

throughout the year, fluctuating between 1.8 and 2.5 mg l^{-1} (Figure 4b).

Aragonite saturation state in shellfish farming areas

The physicochemical properties of the main oceanographic (e.g. upwelling, river discharge) and biological (photosynthesis: respiration) processes, or the combination of both, produced different patterns of temporal and spatial variability in the aragonite saturation state (Ω_{arag}) across shellfish farming areas. The lowest Ω_{ara} was observed in the Arauco Gulf ($\Omega_{arag} = 0.595$), especially during the warmer seasons (spring and summer) (Figure 4f), whereas Tongoy Bay was affected by low Ω_{arag} conditions during spring. In contrast, Chiloé was affected by undersaturated conditions only during the colder seasons (winter and autumn). Therefore, significant differences in carbonate saturation states were observed between Chiloé and the lower latitude areas only during winter and autumn, while Tongoy Bay showed oversaturated waters compared to higher latitude sites during summer (Tukey *post hoc* test, $p < 0.001$, Table 2).

Carbonate system drivers

To evaluate the interplay between dominant biological processes that control carbon chemistry in the coastal ocean (e.g. respiration, photosynthesis) and other drivers such as river runoff and/or changing temperature, all pH_T data obtained through continuous measurements (buoys) and seasonal spatial sampling from the three coastal zones were correlated with temperature, chlorophyll concentration and DO. A significant positive relationship was found between DO and pH_T across all coastal zones ($R^2 > 0.6$; $p < 0.001$, Figure 5). A positive relationship was also observed for temperature and pH_T; however, it explained <50% of pH_T variability in the three nearshore sites (Figure 5). Chlorophyll *a* concentrations were not related to pH_T levels, but a seasonal coupling with pH_T was evident in Chiloé, where low total chlorophyll

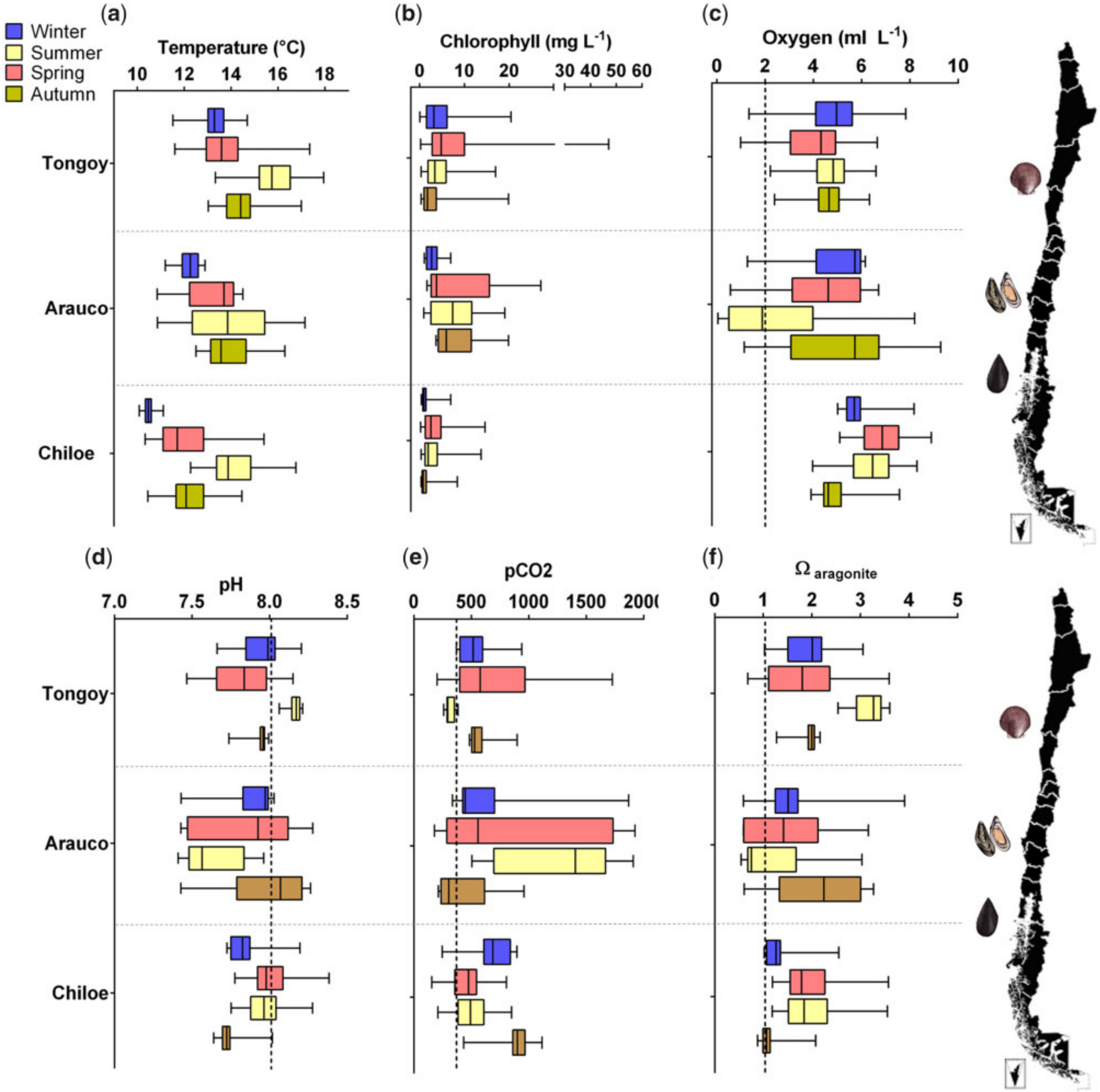


Figure 4. Seasonal mean and range of (a) subsurface temperature, (b) total chlorophyll, (c) DO, (d) pH_{total}, (e) pCO_2, and (f) Omega aragonite in three nearshore zones along the Chilean coast. Oceanographic parameters of Tongoy Bay come from a moored CTD, while carbonate system was obtained from both shipboard sampling and using data included in Vargas *et al.* (2017). Oceanographic and carbonate system parameters in Arauco Gulf come from manual bi-monthly sampling; while these data were obtained from a buoy located in one station of Chiloe. Ranges of the carbonate system parameters for Tongoy Bay represent differences between sampling stations in summer, winter, and autumn and spring of an instrumental time series obtained at the moored location.

concentrations were observed mainly during the winter months (Figure 2c).

Discussion

Bivalve aquaculture is concentrated in coastal areas exposed to multiple drivers that lead to highly variable environmental conditions, especially in seawater chemistry. The extreme range of variation documented among shellfish aquaculture areas in the present study is most likely related to the large latitudinal gradient, ranging from persistent to strong seasonal upwelling along an exposed eastern boundary coastline, to a cyclical seasonal pattern within a semi-enclosed cold-temperate basin (Sobarzo *et al.*, 2007; Calvete and Sobarzo, 2011; Bravo *et al.*, 2016; Narváez et al., 2019; Pérez-Santos et al., 2019). The marked seasonality observed in Chiloé is explained mainly by the annual variation in solar heat flux and light availability across the area (Iriarte *et al.*, 2007; Garreaud *et al.*, 2013; Narváez et al., 2019). Our temperature measurements at the lower latitude site

Table 3. Evaluation of significant differences for oceanographic and carbonate system parameters among seasons and study regions.

Response	Source	df (source, error)	MS (mean square)	*F*	*p*-Value	Tukey *post hoc*
pH	Region	2	0.259	10.31	<0.0001	Winter: Tongoy = Arauco > Chiloe
	Season	3	0.2035	8.1	<0.0001	Spring: Chiloe > Tongoy = Arauco
	Interaction	6	0.8264	32.89	<0.0001	Summer: Tongoy > Arauco = Chiloe
						Autumn: Tongoy = Arauco > Chiloé
Temperature	Region	2	915	1050	<0.0001	Winter: Tongoy>Arauco > Chiloe
	Season	3	227.7	261.2	<0.0001	Spring: Tongoy =Arauco > Chiloe
	Interaction	6	22.42	25.71	<0.0001	Summer: Tongoy > Arauco = Chiloé
						Autumn: Tongoy = Arauco > Chiloé
Oxygen	Region	2	449.8	423.4	<0.0001	Winter: Chiloe > Tongoy = Arauco
	Season	3	4.163	70.38	0.0084	Spring: Chiloe > Tongoy = Arauco
	Interaction	6	74.75	3.92	<0.0001	Summer: Chiloe > Tongoy = Arauco
						Autumn: Chiloe > Tongoy > Arauco
*p*CO2	Region	2	743 943	11.46	<0.0001	Winter: Tongoy = Arauco < Chiloe
	Season	3	309 929	4.776	0.0027	Spring: Arauco > Tongoy > Chiloé
	Interaction	6	1.98E+06	30.54	<0.0001	Summer: Arauco > Chiloe > Tongoy
						Autumn: Chiloé > Tongoy = Arauco
Chlorophyll	Region	2	1 784	95.26	<0.0001	Winter: Tongoy > Chiloe
	Season	3	355.5	18.99	<0.0001	Spring: Arauco > Tongoy > Chiloé
	Interaction	6	223.1	11.92	<0.0001	Summer: Arauco > Chiloe = Tongoy
						Autumn: Arauco > Tongoy > Chiloé
Omega Aragonite	Region	2	12.1	48.18	<0.0001	Winter: Arauco = Tongoy > Chiloe
	Season	3	1.49	5.94	<0.0005	Spring: Tongoy = Chiloé = Arauco
	Interaction	6	2.839	11.31	<0.0001	Summer: Tongoy > Arauco = Chiloe
						Autumn: Arauco = Tongoy > Chiloé

(Tongoy Bay) showed more energetic variability than at the southern site (Chiloé) across all temporal scales, in agreement with the year-round upwelling-favourable conditions found in this study (see also Rutllant and Montecino, 2002; Aguirre *et al.*, 2012). This also complements the upwelling dynamics reported for this area (Bravo *et al.*, 2016). However, temperature is not the main driver of the carbonate system variability, which was reflected by its weak linear relation with pH$_T$.

Unlike offshore oceanic waters, where pH$_T$ ranges between 8 and 8.3, the pH$_T$ of the nearshore areas where bivalve aquaculture takes place is normally lower than that observed in the open ocean, reaching values $<$7.8 during spring and summer in the lower latitude areas due to the incidence of more acidic upwelling waters (Vargas *et al.*, 2017). Minimum pH$_T$ values as low as 7.40 observed in the Arauco Gulf during upwelling-favourable conditions (summer 2017) are among the lowest levels reported to date for the surface ocean (Hofmann *et al.*, 2011; Melzner *et al.*, 2013; Chan *et al.*, 2017). Despite the well-known occurrence of upwelling events in Tongoy Bay (reviewed by Aguilera *et al.*, 2018), our short time series were not able to detect high pCO$_2$ levels in this area. However, values of pH$_T$ $<$7.4 were also recorded during some spring days, which are not uncommon for the area (Figure 2a, see Lagos *et al.*, 2016). In Chiloé (43°S), lower pH$_T$ ($\sim$7.6) and higher pCO$_2$ values were only detected during the cold seasons, coinciding with freshwater input. No relationship was found between salinity and pH$_T$, supporting that, in coastal regions, the pH is controlled by the balance between photosynthesis and respiration (Vargas *et al.*, 2017; Narváez et al., 2019).

The wide range of variability in the carbonate system parameters in the Arauco Gulf appears to be linked to two dominant environmental drivers—coastal upwelling during summer and spring and river discharges during winter and autumn (Vargas *et al.*, 2016). This zone is considered as one of the most productive river-influenced upwelling areas in the South Pacific coast (Daneri *et al.*, 2000), with very low Ω_{arag} levels ($\sim$1) during upwelling conditions in spring and summer, while the freshwater discharge during the cold season affects the alkalinity/salinity, and therefore Ω_{arag} levels. The low Ω_{arag}, low pH, and high pCO$_2$ conditions observed during upwelling periods are combined with the presence of nearly anoxic waters ($<$0.5 ml O$_2$ l^{-1}), as suggested by Melzner *et al.* (2013) for highly productive coastal zones. However, chlorophyll concentration reached its highest levels during spring months, meaning that more phytoplankton is available at this site during warmer seasons. We also observed inter-annual differences in pH$_T$ and oxygen (mainly during spring and summer months), which might be related to the influence of the strong El Niño event that affected the Chilean coast during the summer of 2016 (Santoso *et al.*, 2017). In higher latitudes (Chiloé), Ω_{arag} is low ($<$1.5) only during colder seasons due to the influence of freshwater discharges, but oxygen levels were always near normoxic levels ($>$4 ml l^{-1}, Figure 4c) and, therefore, this should not be a relevant stressor for the farmed mussels.

The analysis of the frequency components between our low and high latitude sites highlights that an important fraction of the environmental variability was spread over a wide range of frequencies. High energy was mostly associated with the dominant semi-diurnal and diurnal tidal regimes .However, longer periods related to synoptic variability can be associated with the frequent favourable upwelling conditions produced throughout the year, but especially during summer and spring at the Tongoy Bay site (Bravo *et al.*, 2016) and the passage of weather systems in the Chiloé area (Pérez-Santos *et al.*, 2019). Patterns of temporal variability also differed between parameters; temperature and oxygen covaried, and while total chlorophyll showed higher variability in both localities, pH showed less variability compared to the other parameters in the Chiloé site. Given the short time scale of this time series, it is difficult to find an explanation for these between-

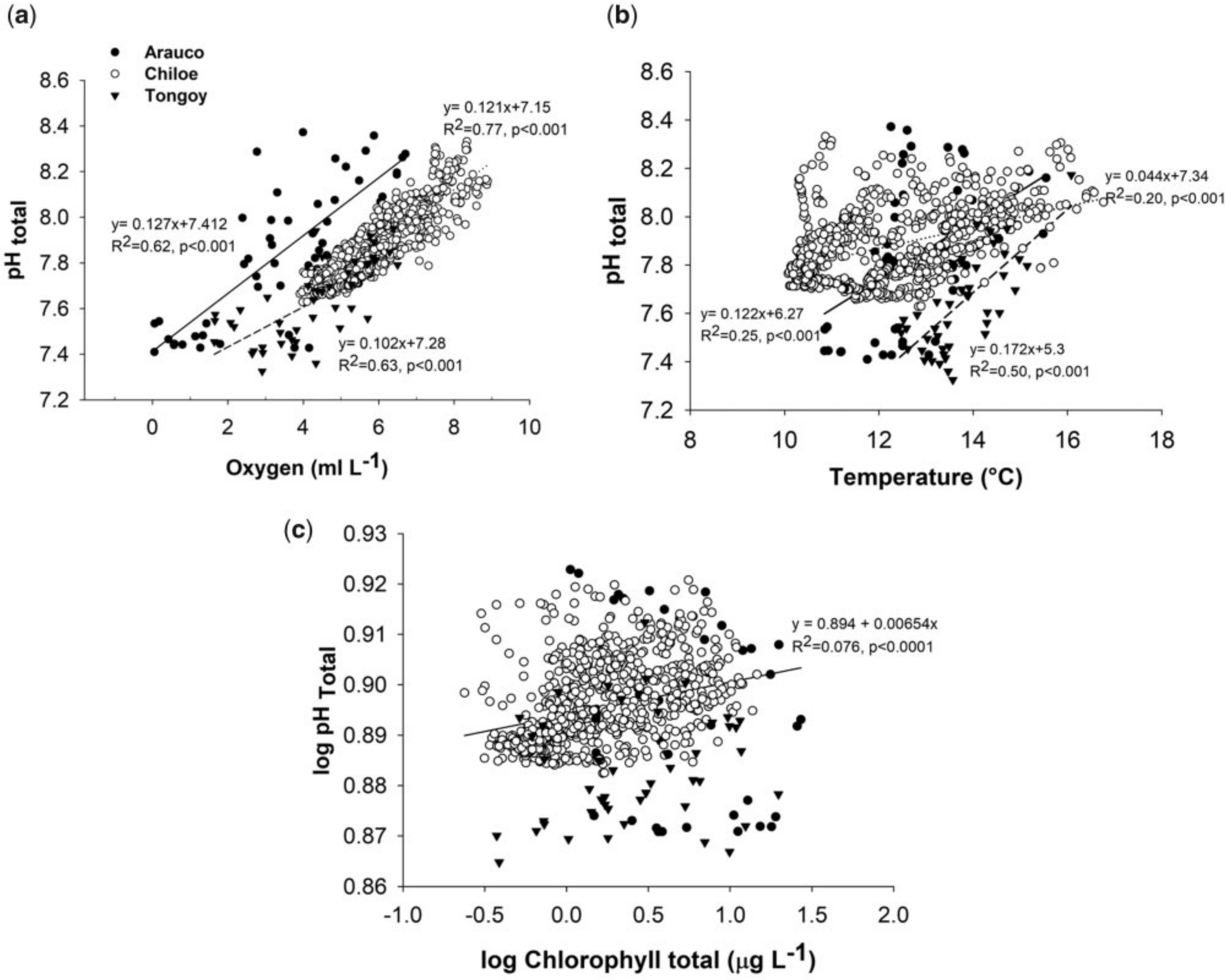


Figure 5. Relation between oceanographic parameters and pH_T in three nearshore zones along the Chilean coast, (a) DO and pH_T; (b) subsurface temperature and pH_T; and (c) total chlorophyll and pH_T in a logarithmic scale to normalize their distributions.

site differences. Due to their impact on shellfish aquaculture, they should be the focus of future research in these areas.

Biological implications for shellfish farming species

During the last 15 years, different studies have been conducted for different coastal regions worldwide of biological responses of shellfish farming species to changing temperature, oxygen, total chlorophyll, and/or pH/pCO$_2$. The study of reaction norms, the phenotypic expression of a single genotype across a range of environmental conditions (Platt and Sanislow, 1988), has been a useful experimental tool to address questions related to the effect of environmental drivers on different populations of marine organisms (Vargas *et al.*, 2017). Useful patterns have emerged from biological response experiments. For instance, some studies demonstrated the relevance of temperature on the growth and physiology of adult *M. chilensis* (Guenuman, 2014; Navarro *et al.*, 2016) and on their larval development and growth (Lagos *et al.*, 2012). For *A. purpuratus*, temperature is relevant for metabolic rate (González *et al.*, 2002), gonad maturation, and larval survival (Martínez et al., 2000a, b). Lagos *et al.* (2016) found an interactive effect between temperature and pH on juvenile scallop growth rate, demonstrating that, under upwelling conditions (low temperature and low pH/high pCO$_2$), this species decreased its growth, favouring reproduction (Cantillanez *et al.*, 2005). The seedstock used by the aquaculture industry for all the studied species comes mainly from wild larvae settled on artificial larval collectors (Lara *et al.*, 2016; Von Brand *et al.*, 2016). Seeds are then transferred to locations that can be hundreds of km away from the source populations, which disrupts connectivity patterns and hinders the replenishment of benthic populations. Although *M. chilensis* populations seem to be mixing over scales of tens to hundreds of km, there is evidence of local adaptation processes (Araneda *et al.*, 2016; Astorga *et al.*, 2020). Population genetic studies have shown that transplanting seedstock between locations can interact with dispersal processes, driving an artificial genetic population structure (Moehler *et al.*, 2011), and interfering with processes of local adaptation that are important for population persistence in variable environments (Silliman, 2019). As the larval development times of *A. purpuratus* and both *Mytilus* species are similar (16–25 days, Ruiz *et al.*, 2008; Von Brand *et al.*, 2016), it is likely that similar processes may operate for scallops. Despite the relevance of these studies for understanding the

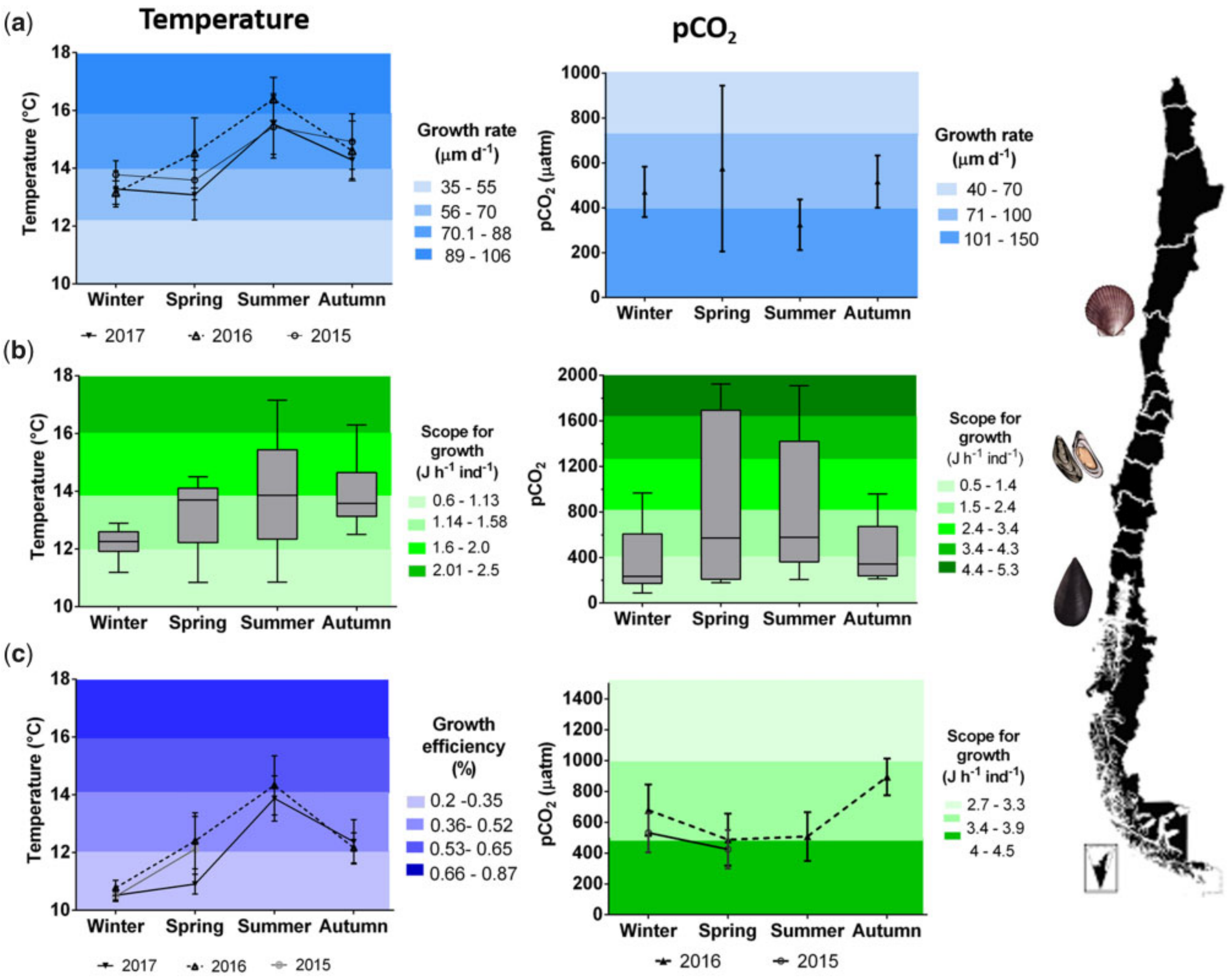
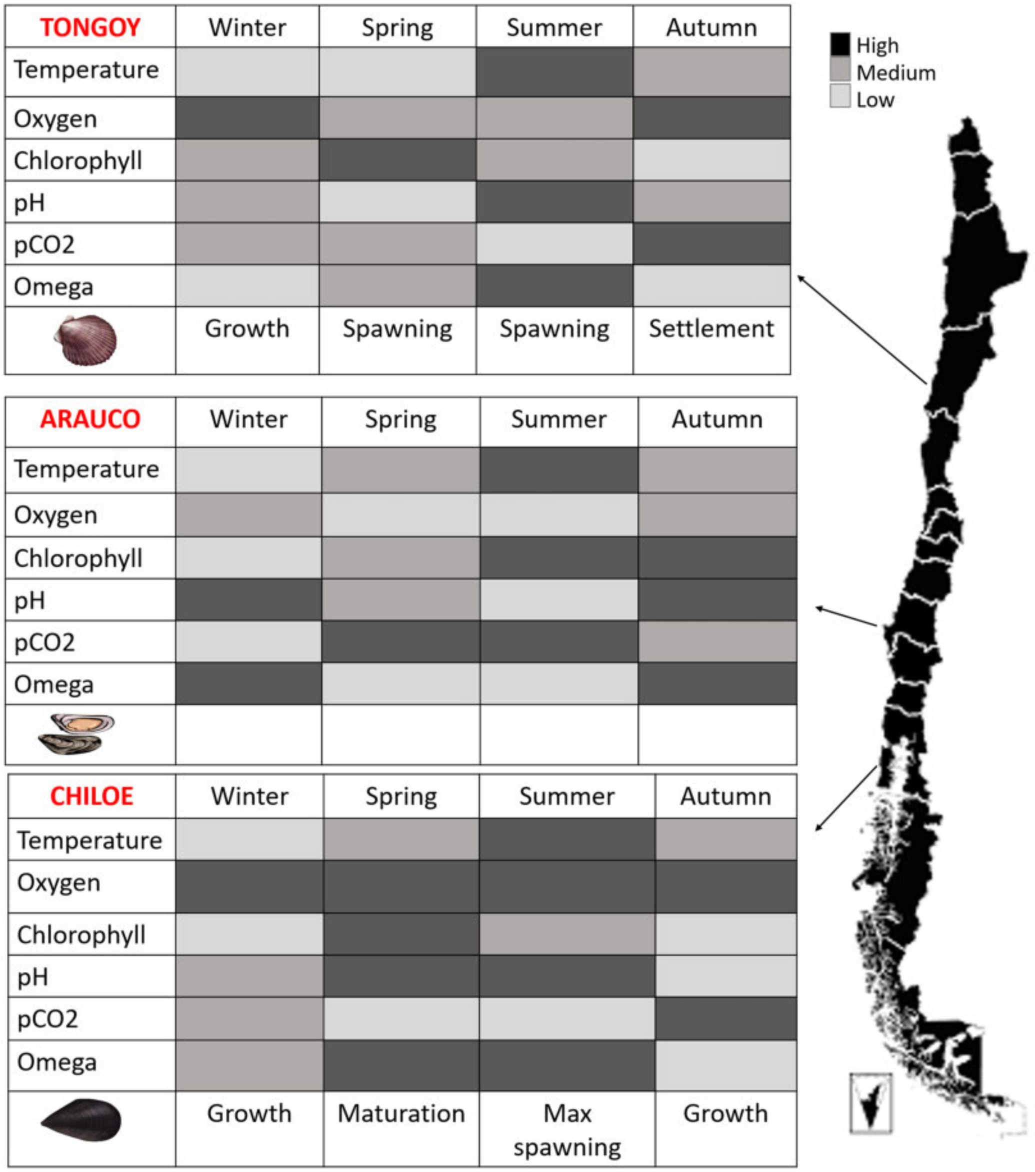


Figure 6. Relation between seawater temperature and pCO_2 levels for growth rate, growth efficiency, and scope for growth of aquaculture-relevant bivalves along a latitudinal gradient. (a) *Argopecten purpuratus* in the northern zone, (b) *Mytilus galloprovincialis* in the central zone, and (c) *M. chilensis* in the southern zone. Growth responses to pCO_2 and temperature were obtained from different laboratory and *in situ* experiments with this species (Fernández-Reiriz *et al.*, 2012, Fly and Hilbish, 2013, Guenuman, 2014, Lagos *et al.*, 2016, Navarro *et al.*, 2016).

influence of environmental variability on the biology of the organisms, it is still difficult to interpret this information in the context of natural environmental variability.

We represented the relevance of the environmental and chemical variability in the biology of relevant aquaculture bivalves through a schematic representation of mean seasonal temperature and pCO_2 variability observed in the studied aquaculture areas, and a gradient of growth responses associated with these parameters (Figure 6). These growth responses are based on a literature review of different experimental studies conducted with the same scallop and mussel species (Fernández-Reiriz *et al.*, 2012; Fly and Hilbish, 2013; Navarro *et al.*, 2013, Guenuman, 2014; Lagos *et al.*, 2016; Navarro *et al.*, 2016). Here, we aimed to discuss the relation between natural environmental variability and potential biological responses (Supplementary material). Based on this approach, we suggest that scallop growth could be enhanced due to higher temperatures (>16°C) and lower pCO_2 levels (<400) during summer (Figure 6a). It is clear that this species can grow properly year-round, with lower growth only during spring, following the periodic upwelling events that bring more acidic, hypoxic, and cold waters near the coast (Figure 6a). Interestingly, this interpretation was recently confirmed by Ramajo *et al.* (2019), where the lowest growth rates were found in cold–hypoxic–acidic waters.

In the Arauco Gulf area, where *M. galloprovincialis* is the main aquaculture species, our analysis suggests that environmental conditions could be favourable for growth especially during spring and summer, following higher temperatures and high pCO_2 levels (>1400 µatm) (Figure 6b). The scope for growth in this species is enhanced by higher pCO_2 levels (Fernández-Reiriz *et al.*, 2012), explaining the potential for aquaculture in this geographic location during upwelling-favourable conditions (spring and summer). The shellfish farming area is subject to hypoxic waters (<2 ml l^{-1}) during and after upwelling events, reaching values <0.5 ml l^{-1} during some days in spring and summer, especially in deeper waters. This means that organisms exposed to a combination of hypoxic and acidic waters have high food concentrations (Chl *a*), which, in turn, may allow mussels to counteract the effects of these stressful conditions (Ramajo *et al.*, 2016). In Chiloé, *M. chilensis* growth also appeared to be



TONGOY	Winter	Spring	Summer	Autumn
Temperature	□	□	■	▨
Oxygen	■	▨	▨	■
Chlorophyll	▨	■	▨	□
pH	▨	□	■	▨
pCO2	▨	▨	□	■
Omega	□	▨	■	□
	Growth	Spawning	Spawning	Settlement

ARAUCO	Winter	Spring	Summer	Autumn
Temperature	□	▨	■	▨
Oxygen	▨	□	□	▨
Chlorophyll	□	▨	■	■
pH	■	▨	□	■
pCO2	□	■	■	▨
Omega	■	□	□	■

CHILOE	Winter	Spring	Summer	Autumn
Temperature	□	▨	■	▨
Oxygen	■	■	■	■
Chlorophyll	□	■	▨	□
pH	▨	■	■	□
pCO2	▨	□	□	■
Omega	▨	■	■	□
	Growth	Maturation	Max spawning	Growth

Figure 7. Conceptual model of favourable environmental conditions and life-cycle events of the main cultured species in three nearshore zones of Chile. High, medium, and low levels were chosen in relation to the local range of environmental variability. More specific data are shown in Table 2.

enhanced during summer due to elevated temperatures (>14°C) and lower $p\text{CO}_2$ levels (<500 µatm) (Figure 6c).

A key parameter for shellfish aquaculture is the aragonite saturation state, especially for protoconch formation in bivalve larvae (Waldbusser *et al.*, 2015a, b). This is a highly predictive parameter linking carbonate chemistry changes to biological impacts on molluscs and therefore for shellfish aquaculture (Barton *et al.*, 2015). Waldbusser *et al.* (2015b) proposed a threshold of tolerance for bivalve shell formation in larvae of <1.5 Ω_{arag} in the seawater used for oyster larval hatcheries to break even. The saturation state of Tongoy Bay was above 1 throughout the year, with only a few days of undersaturation (Figure 4). In this zone, *A. purpuratus* lives throughout the year in oversaturated waters, especially during spring and summer, suggesting favourable conditions for shell formation and larval development (Barton *et al.*, 2012, 2015). However, these carbonate system data were obtained from few samples due to the lack of a longer pH_T and A_T time series, which would allow a detailed description of Ω_{arag} variability in this coastal zone. The available pH data from Tongoy Bay indicated potential undersaturation of calcium carbonate during spring, which agrees with the intense CO_2 outgassing of this upwelling system (Torres and Ampuero, 2009). Considering the lower temperature, higher $p\text{CO}_2$, lower pH, and Ω_{arag} <1, decreased scallop growth should be observed during spring, which would then increase during summer due to higher temperatures, overcoming the negative impact of acidic upwelling waters (Lagos *et al.*, 2016).

Undersaturated waters were present in the Arauco Gulf area during all seasons, particularly during austral spring and summer. Therefore, the optimal season for *M. galloprovincialis* development and growth is winter and autumn, following the lower incidence of days with low Ω_{arag} conditions (Barton *et al.*, 2012, 2015; Waldbusser *et al.*, 2015b). In Chiloé, mussels were exposed during colder seasons (winter and autumn) to almost undersaturated waters ($\Omega_{arag} \sim 1$), and thus, the optimal seasons for development and shell growth may be during spring and summer, which agrees well with higher concentrations of *M. chilensis* larvae found during both seasons in the Inner Sea of Chiloé (Guzmán *et al.*, 2014; Lara *et al.*, 2016).

Interestingly, our results also indicate that studies that have attempted to evaluate the effects of ocean warming or acidification using future scenarios have tested parameter values that are within the range of local variability for populations of some species (Vargas *et al.*, 2017). For instance, Ramajo *et al.* (2016) and Lagos *et al.* (2016) considered present conditions and OA projection as pH levels of 8.0 and 7.6, respectively, which are within the range of natural variability for Tongoy Bay in northern Chile. This is a highly relevant issue, since although those results are highly useful for understanding the biological response of scallops on changing $p\text{CO}_2$ or temperature natural conditions, null or positive biological responses cannot assume that those species are tolerant or adapted to future OA or warming conditions; scientific input for climate change adaptation strategies with local and small-scale fishing communities is required.

Considering all parameters, we developed a conceptual model relating the life cycle of the main cultured species and the environmentally favourable conditions (Figure 7). The optimal conditions for scallops occur during summer, matching the main spawning season, while for the Chilean mussel, in spring and summer favourable environmental conditions coincide with maturation and spawning events. For *M. galloprovincialis*, the lack of local life-cycle studies complicates making clear associations with environmental conditions, yet autumn appears as the favourable season for growth and development.

Our conceptual model clearly demonstrates the need for more and better time series of environmental conditions in the coastal zone, especially in aquaculture areas. This information will allow for an improved connection between environmental conditions and the biological responses of farmed species. This type of information is crucial to understand the scale and magnitude of fluctuations in aquaculture potential under future climate (Boehm *et al.*, 2015; Yáñez *et al.*, 2017; Froehlich et al., 2018), thus informing decision-makers and stakeholders about pathways to sustainable aquaculture (Broitman *et al.*, 2017). A surprising issue detected by our study is the lack of detailed studies examining life-cycle variability for the different bivalves cultured under the environmental fluctuations they encounter in their native habitats, together with whole-organism responses to these fluctuations (Calosi *et al.*, 2013; Ramajo *et al.*, 2016; Thomsen *et al.*, 2017). Following the potential introduction of new species or the use of seedstock sourced from other latitudes (Astorga *et al.*, 2020), cultured populations will be exposed to new environmental conditions that may affect proper development and growth. We highlight that a better understanding of the plastic response of cultured species to environmental variability and a detailed characterization of the reaction norms of relevant traits are key for sustainable shellfish aquaculture in the face of climate change.

Data availability statement

Oceanographic and carbonate chemistry data was generated in the course of the study, while wind results was generated through analysis of third-party data. Most part of the data is available on Global Ocean Acidification Observing Network (GOA-ON portal (Tongoy Balsa CMET: http://portal.goa-on.org/Explorer?action=oiw:mobile_platform:ARGO_702) and (Chiloé: http://portal.goa-on.org/Explorer?action=oiw:mobile_platform:ARGO_702)). Any other data will be shared on reasonable request to the corresponding author.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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