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CO_2-driven compromises to marine life along the Chilean coast

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Abstract

CO_2-driven compromises to marine life were examined along the Chilean sector of the Humboldt Current System, a particularly vulnerable hypoxic and upwelling area, applying the Respiration index ($RI = \log_{10} \frac{pO_2}{pCO_2}$) and the pH-dependent aragonite saturation (Ω) to delineate the water masses where aerobic and calcifying organisms are stressed. There was a remarkable negative relationship between oxygen concentration and pH or pCO_2 in the studied area, with the subsurface hypoxic Equatorial Subsurface Waters extending from 100 m to about 300 m depth and supporting elevated pCO_2 values. The RI reached a minimum at about 200 m depth and decreased towards the Equator. Increased pCO_2 in the hypoxic water layer reduced the RI values by as much as 0.59 RI units, with the upper water layer that presents conditions suitable for aerobic life (RI>0.7) declining by half between 42° S and 28° S. The intermediate waters hardly reached those stations closer to the equator so that the increased pCO_2 lowered pH and the saturation of aragonite. A significant fraction of the water column along the Chilean sector of the Humboldt Current System suffers from CO_2–driven compromises to biota, including waters corrosive to calcifying organisms, stress to aerobic organisms or both. The habitat free of CO_2-driven stresses was restricted to the upper mixed layer and to small water parcels at about 1000 m depth. pCO_2 acts as a hinge connecting respiratory and calcification challenges expected to increase in the future, resulting in a spread of the challenges to aerobic organisms.

1 Introduction

The evolution of the concentrations of atmospheric CO_2 and O_2 over the history of the Earth has played a crucial role in the evolution of life (Dudley, 1998; Berner, 2002). After 800 000 years of relative stability in atmospheric concentration, anthropogenic emissions have driven atmospheric CO_2 to reach 385 ppmv, well above the range of atmospheric CO_2 of 172–300 ppmv observed over the 800 000 years preceding industrial

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development (Lüthi et al., 2008), with a dramatic impact in the Earth's climate (Meehl et al., 2007).

Oceans have absorbed almost 50% of the 7 Gt C yr^{-1} released by anthropogenic activities (Sabine et al., 2004), and its surface waters now hold approximately 45 µmol kg^{-1} of CO_2 in excess compared to preindustrial concentrations (Broecker et al., 1985). Increased CO_2 in ocean waters has already lead to a decline of 0.1 units in ocean pH, and will decrease by an additional 0.3 pH units by the end of the century, with a large impact on marine calcifying organisms (Orr et al., 2005; Doney et al., 2009). The thresholds of ocean acidification to marine calcifying organisms are given by the aragonite and calcite saturation values, Ω (Feely et al., 2004; Orr et al., 2005), with aragonite saturation being more sensitive to ocean acidification than that for calcite. Indeed, calcification processes are already affected at aragonite Ω values <2 (Hauri et al., 2009; Hendriks et al., 2010), although these thresholds are species-specific. Ocean acidification has received considerable attention as the main direct impact of increased ocean CO_2, but other potential impacts of increased CO_2have been overlooked. Indeed increased CO_2 and lowered pH also affect respiratory processes by driving reduced binding affinity for oxygen in blood (Pörtner et al., 2004) and a direct ventilatory sensitivity to CO_2 (Burleson and Smatresk, 2000; McKendry et al., 2001). Hence, increased CO_2 also poses challenges to aerobic respiration, threatening marine life, an impact that has only recently been addressed (Brewer and Peltzer, 2009).

Indeed, the efficiency of aerobic respiratory processes depends on the partial pressures of both CO_2 and O_2, which are tightly coupled through the metabolic activity of marine organisms. Brewer and Peltzer (2009) indicated that the efficiency of aerobic respiratory processes is dependent on the ratio of the partial pressures of O_2 and CO_2, which defines the range of conditions compatible with aerobic marine life. Hence, present concerns on the threat posed by on-going declines of marine oxygen in the ocean (Díaz and Rosenberg, 2008; Vaquer-Sunyer and Duarte, 2008; Gilbert et al., 2010) are further aggravated by the parallel increase in CO_2 (Brewer and Peltzer, 2009). Yet, the impacts of hypoxia on marine biota have been traditionally studied in

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isolation from the effects of increased CO_2. Brewer and Peltzer (2009) highlight the importance of studying the coupled effects of changes in both CO_2 and O_2 on aerobic marine life, and used the basic oxic respiration equation in relation to free-energy to derive a Respiration Index (RI), given by the expression:

$$RI = \log_{10} \frac{pO_2}{pCO_2} \qquad (1)$$

where RI≤0 corresponds to the thermodynamic aerobic limit, a formal dead zone; at RI = 0 to 0.4 aerobic respiration does not occur; the range RI = 0.4 to 0.7 represents the practical limit for aerobic respiration, and the range RI = 0.7 to 1.0 delimits the aerobic stress zone. Thus, increased CO_2 aggravates the impacts of hypoxia (Brewer and Peltzer, 2009).

Hence, elevated CO_2 acts as a hinge, connecting two otherwise independent threats to marine life, acidification and hypoxia. This connection had not been elaborated to date. The areas of the world ocean most sensitive to both these threats are upwelling regions, as they are typically low in oxygen (Grantham et al., 2004) and corrosive to carbonate structures due to high CO_2 levels (Feely et al., 2008).

A particularly vulnerable area is the Humboldt Current System along the Chilean coast, the largest naturally hypoxic area and an important upwelling center (Thiel et al., 2007; Ulloa and Pantoja, 2009). Here we examine the CO_2-driven compromises to marine life along part of the Chilean sector of the Humboldt Current System, an area sensitive to hypoxia and acidification associated to latitudinal variation of CO_2, O_2 and pH across the water column. We demonstrate how RI and Ω can be used to delineate the water masses where aerobic and calcifying organisms are stressed.

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2 Materials and methods

2.1 Study site

The study was conducted along the Humboldt 2009 cruise on board the R/V Hespérides from 5 to 16 March 2009. The cruise track followed the Chilean coast, starting in the Patagonia channels (54.9° S) proceeding North along the Humboldt Current System until Antofagasta (Chile, 23.6° S, Fig. 1). The Humboldt Current System is one of the largest naturally hypoxic areas of the world's oceans (Levin, 2002; Thiel et al., 2007; Ulloa and Pantoja, 2009), characterized by upwelling of cold, oxygen-poor waters supersaturated in CO_2 (Torres et al., 2002). The top 200 m are oxygen-saturated, with surface Tropical waters encountering and mixing with near-surface Subantarctic waters. Below these we find oxygen depleted Equatorial waters propagating poleward overlying the oxygen-rich Antarctic waters flowing toward the equator (Silva et al., 2009).

2.2 Sampling

A series of 15 stations spaced along the meridional cruise track were sampled. Hydrographic properties were profiled down to 1400 m depth using a Seabird 9 CTD probe. Water samples were collected at different depths (5, 15, 30, 50, 100, 200, 300, 600, 1000, 1400 m) using 12 L Niskin bottles fitted on a Rosette sampler system. Water samples were analyzed for pCO_2, O_2, and pH immediately after sampling.

2.3 CO_2 measurement

The partial pressure of CO_2in the water (pCO_2) was measured using a non dispersive infrared gas analyzer (EGM-4, PP systems) that measures pCO_2 with a precision of ± 1 ppm. For pCO_2, near surface water (about 1 m depth) was collected and passed through a gas exchange column (Mini-Module Membrane Contactor) and pCO_2

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measured, details of this methodology have been described elsewhere (Calleja et al., 2005; Silva et al., 2008).

2.4 O_2 measurement

Oxygen concentration was analysed using high-precision Winkler titration using a potentiometric electrode and automated endpoint detection (Mettler Toledo, DL28 titrator) (Carpenter, 1965).

2.5 pH and aragonite saturation (Ω) measurement

Seawater samples for pH, collected immediately after the Niskin bottles were sampled for oxygen determinations, were siphoned into 500 mL glass bottles, allowed to overflow and immediately stopped. After temperature stabilization to 25 °C on a water bath, pH samples where transferred carefully to 10 cm pathlength optical glass cells fitted with a jacket to circulate water at 25 °C, to control temperature during measurements using a double-wavelength spectrophotometric procedure (Clayton and Byrne, 1993). Oxygen concentrations were converted into pO_2 and RI were calculated following Brewer and Peltzer (2009). Ω values for aragonite saturation were calculated from pH, pressure, temperature, salinity and alkalinity using CO_2 SYS (Pierrot et al., 2006). Because the pH-pCO_2 paired couple is not a good predictor of alkalinity, total alkalinity was obtained from the CDIAC data base (Lamb et al., 2001).

3 Results

3.1 Description of water masses and its associated pCO_2, O_2 and pH levels

The ship's meridional transect encompassed waters of equatorial and Antarctic origin, displaying substantial changes in pCO_2 and O_2. The surface waters, down to 100–150 m, correspond to Subtropical and a Subantarctic water masses (STW and SAAW, respectively), they were characterized by pCO_2 and O_2 concentrations close to atmospheric equilibrium (Fig. 2). Immediately below there were hypoxic Equatorial Subsurface Waters (ESSW), its thickness increasing towards the Equator, where it extended from 100 m to about 300 m depth (Fig. 2). Below this layer and down to about 1000 m we found Antarctic Intermediate waters (AAIW), characterized by much higher oxygen concentrations (Fig. 2). The hypoxic ESSW were also characterized by elevated pCO_2 values (>1000 µatm pCO_2, Fig. 2), while the AAIW were characterized by comparatively low pCO_2 (Fig. 2). Further below we find the moderately oxygen-depleted Pacific Deep Waters (PDW).

We also present three temperature-salinity diagrams with colour-coded values of the oxygen concentration (Fig. 3a), pCO_2 (Fig. 3b), and pH (Fig. 3c). The oxygen-coded diagram shows interleaving between oxygen-rich AAIW and ESSW, with the latter overlaying the former (Fig. 3a). The STW and SAAW surface waters have relatively large oxygen concentrations, with maximum values corresponding to the high-latitude relatively cold SAAW (Fig. 3a). The oxygen depleted equatorial subsurface waters were also characterized by elevated pCO_2 (>1000 µatm pCO_2; Fig. 3b) and acidic (pH<8.0) waters (Fig. 3c). Indeed, there was a strong negative relationship between oxygen concentration and pH and pCO_2 values in the studied area (Fig. 4).

3.2 Respiration index and threatened aerobic life

The respiration index, which describes the adequacy of the gaseous composition of the water to maintain aerobic life, reached a minimum at about 200 m depth, with the minimum RI values generally decreasing towards the Equator (Fig. 5). The minimum RI values were below the 0.7 threshold value across most of the study area (Fig. 5). Evaluation of the bearing of pCO_2 on RI, holding pCO_2 constant at atmospheric equilibrium (Fig. 6a), and calculating the difference between the observed RI and that calculated (Fig. 6b) shows that increased pCO_2 in the hypoxic water layer increases the thickness of the water column with RI values below the 0.7 threshold and reduces the RI values by as much as 0.59 RI units at the oxygen minimum zone. Indeed, the thickness of the water column with RI values below the 0.7 threshold increases greatly towards the Equator, encompassing 1/3 of the studied water column at 28° S (Fig. 7a). It is important to emphasize that the pattern described also involves a reduction toward the Equator in the thickness of the upper water layer that presents conditions suitable for aerobic life (RI>0.7), declining by half between 42° S and 28° S (Fig. 7b).

3.3 pH and saturation of aragonite levels as a threat to calcification processes

In addition to reducing the RI values, the increased pCO_2 in intermediate waters also lowers pH and, therefore, the saturation limit for aragonite (Fig. 8a). The thickness of the water column whose aragonite saturation levels may compromise calcification processes ($\Omega < 2$) corresponds to 1325 m of the studied water column, declining by 50 m from 42° S to 28° S (Fig. 8b). This pattern is opposite to that observed in RI due to the increase in pCO_2 in the oxygen minimum zone toward the Equator, and the parallel warming of the waters that result in increased saturation levels, by as much as 50% across the 3° C meridional gradient encompassed by surface waters.

4 Discussion

The results demonstrate that the bulk of the water column (0–1400 m) along the Chilean sector of the Humboldt Current System present values of acidity or RI compromising for biota, associated with the subsurface hypoxic Equatorial waters that flow South. These compromises are particularly acute regarding the capacity to support aerobic organisms, as oxygen concentrations declined and approached closer to the water surface (O_2 concentrations <8 µmol kg^{-1} at 100 m depth in 30.51° S) towards the north of the study area. pCO_2 levels were also very high (up to 1460 ppm) in association with the hypoxic layer. The distribution of water masses, in particular the oxygen minimum zone, along the study area followed those previously reported (Fuenzalida et al., 2009; Silva et al., 2009).

The additional stress to biota in the hypoxic water mass of the Humboldt Current System arising from the high pCO_2 levels has not been discussed earlier. Our results show that a significant fraction of the water column along the Chilean sector of the Humboldt Current System suffers from CO_2–driven compromises to biota, including corrosive waters to calcifying organisms, stress to aerobic organisms or both. Only the surface layer shallower than 100 m presents conditions free of stress to aerobic organisms (Fig. 9). The extent of challenges to aerobic organisms, as indicated by the RI values, is highly increased by consideration of the increased pCO_2 levels, which lowered the RI value by up to 0.59 RI units and increased the thickness of the water column with RI values indicative of compromises to aerobic organisms (RI<0.7). Hence, our results concur with those of Brewer and Peltzer (2009) to suggest that increased pCO_2 levels aggravate the challenges to aerobic organisms in oxygen deficient waters, such as those in the Humboldt Current System.

Whereas our study represents a quasi-synoptic assessment of the extent of challenges derived from pCO_2, and associated pH levels, and O_2 in the water column of the Humboldt Current System, these are expected to be highly dynamic. The oxygen minimum of the Humboldt Current System shows seasonal and interannual variability, possibly driven by upwelling events and large-scale perturbations in regional circulation, such as those accompanying El Niño events. The oxygen content in the top 100 m layer is higher in the region during El Niño events (Morales et al., 1999; Ulloa et al., 2001). In addition to seasonal and interannual oscillations, the CO_2-driven challenges to biota reported here are expected to increase in the future. Atmospheric pCO_2 levels are expected to reach 700 to 1000 ppm by the end of the 21st Century (Meehl et al., 2007), with an increase in pCO_2 at depth more than 1000 µatm in the Pacific (Brewer and Peltzer, 2009), resulting in a spread of the respiratory challenges to aerobic organisms. The corresponding pH levels are expected to continue to decline, being reduced by 0.3 units below present values by the end of the 21st Century and by up to 0.7 units by 2300 (Caldeira and Wickett, 2003; Doney et al., 2009). In addition, oxygen concentrations are declining across the ocean (Stramma et al., 2008; Gilbert et al., 2010), further affecting the RI ratio.

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The area where biocalcification processes may be close to being compromised can be delineated from the water column with saturation levels, Ω for aragonite <2 (cf. Orr et al., 2005; Yates and Halley, 2006; Guinotte and Fabry, 2008; Hauri et al., 2009, Hendriks et al., 2010), which encompasses most of the water column, except for the upper layer (above 70 m). The thickness of the water column where biocalcification processes may be impacted is largest at mid-latitudes (between about 30 and 37° S) and decreases slowly towards high latitudes and rapidly towards the Equator. This swift change in the equatorial region is opposite to what happens to the layer where aerobic respiration is compromised. Whereas both parameters, reduced RI and aragonite saturation levels, are driven by $p\mathrm{CO}_2$, each includes a second, independent, driver: oxygen concentration in the case of aerobic respiration and temperature in the case of biocalcification. $p\mathrm{CO}_2$ acts, therefore, as a hinge connecting respiratory and calcification challenges.

In general, ocean acidification affects mostly waters below 200 m, while respiratory compromises are located within the 200 to 400 m layer (Fig. 9). These two challenges show similar trends at mid and high latitudes but have opposite trends within the equatorial water column. In general, the 200 to 400 m depth layer combines these two stresses, with the thickness of the layer affected simultaneously by both stresses increasing from high to mid-latitudes and decreasing towards the Equator (Fig. 9). The habitat free of CO_2-driven stresses was restricted to the upper mixed layer and to small water parcels at about 1000 m depth (Fig. 9). Increased $p\mathrm{CO}_2$ in the future may further compress this stress-free habitat.

In addition, both the aragonite saturation threshold for biocalcification and the threshold RI affecting respiration probably vary across taxa (cf. Hendriks et al., 2010 and Vaquer-Sunyer and Duarte, 2008, respectively), depending on their metabolic capacities. Indeed, whereas most metazoans are excluded from the oxygen minimum zone of the Humboldt Current System, specialized crustacean communities, including copepods and euphasids, have been reported to enter this hypoxic layer (Escribano et al., 2009). Use of the RI value as a predictive tool to evaluate and project the impact of increased pCO_2 on aerobic organisms in this region requires, therefore, experimental evidence of the RI thresholds for aerobic respiration of the main taxa in the ecosystem. This evidence is urgently needed, as our assessment clearly shows that increased pCO_2 progressively compresses the water column available for aerobic organisms and may become a factor limiting fisheries production in the region. This upwelling region supports one of the most important fisheries in the world (Montecino and Lange, 2009) and the increase in these stress zones, as those observed in the past (Ulloa and Pantoja, 2009), may compress the habitat suitable for important commercial species, driving changes in the ecosystem in a high-CO_2 future.

5 Conclusions

In this study we present the risk for aerobic and calcifying marine organisms associated to high pCO_2 and low O_2 levels. The study was centered in an area naturally low in oxygen and with high pCO_2 levels, potentially corrosive to carbonate structures. Therefore, this study can be used as a predictive model of the future situation that oceans are likely to exhibit, when considering the expected trends in the evolution of both O_2 and pCO_2 levels. Relating pCO_2 and O_2 values by means of the respiration index is key in understanding the dimension of the threat that aerobic organisms are faced with. As well as this respiratory threat, it is also necessary to take into account the stress inflicted upon calcifying processes, associated to increased pCO_2 levels resulting in decreased pH levels and low saturation levels Ω for aragonite, where calcification may be compromised. The RI and saturation state of aragonite was used in this work as a predictive tool to evaluate and project the impact of increased pCO_2 on aerobic and calcifying organisms, showing that the habitat free of CO_2-driven stresses was restricted to the upper mixed layer and to small water parcels at about 1000 m depth.

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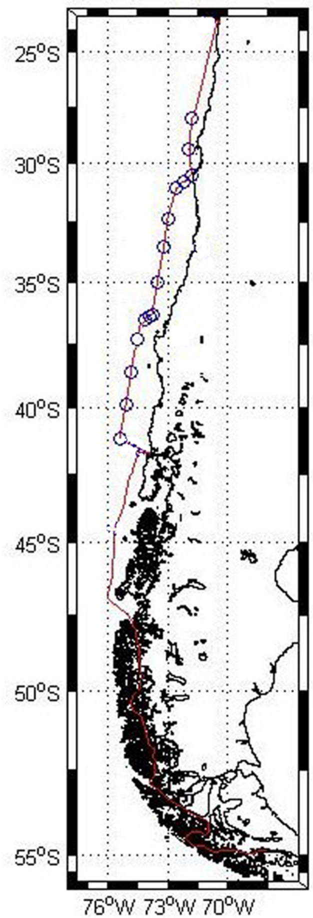

Fig. 1. Cruise track (red line) and sampling stations (blue circles) along the Humboldt Current System (54.9° to 23.6° S).

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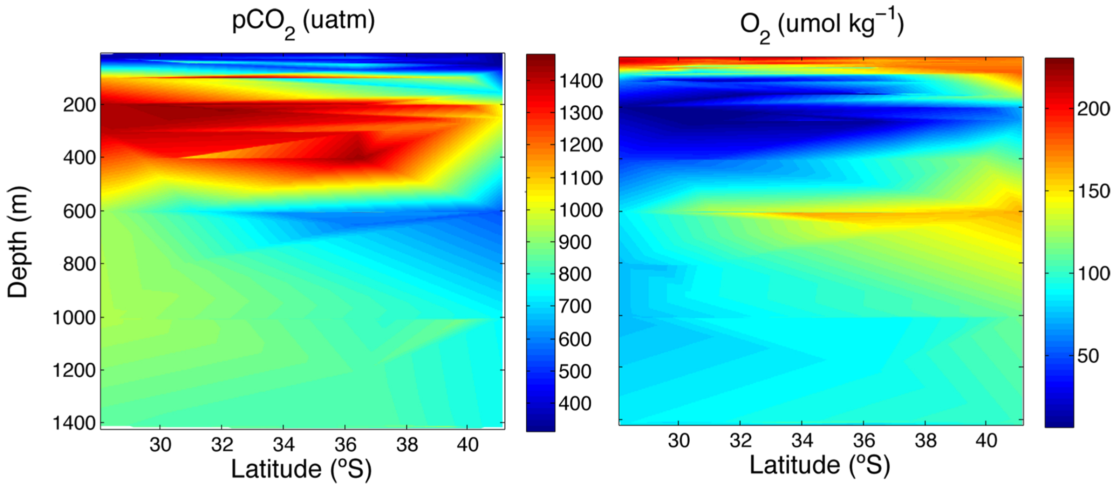

Fig. 2. Contour plots showing the variation in pCO_2 and O_2 levels along the studied transect.

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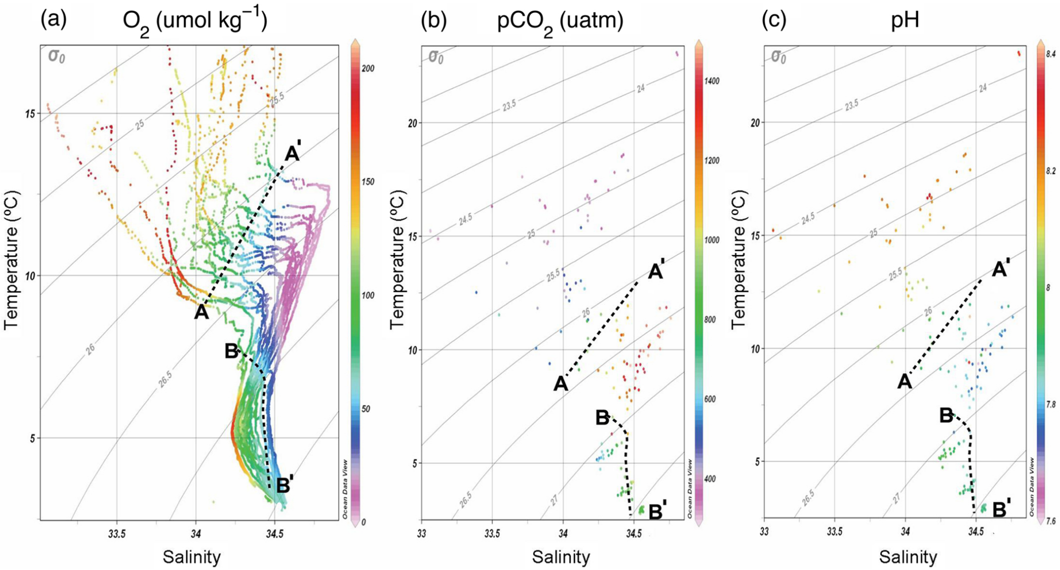

Fig. 3. Temperature-salinity diagram colour-coded for oxygen **(a)**, pCO_2 **(b)**, and pH **(c)** with potential-density isolines superposed. The dashed lines in (a) illustrate the location of intermediate waters (points denser than defined by line A–A') and their partitioning between waters of Equatorial origin (points above line B–B' and lighter than 27.0) and those of Antarctic origin (points to the left of line B–B'). Deep-water points are found to the right of line B–B' and with densities higher than 27.0. Oxygen values in (a) were derived from the CTD-mounted oxygen sensor calibrated with Winkler analyses from bottle casts, while pCO_2 (b) and pH (c) correspond to the values measured from the bottle casts.

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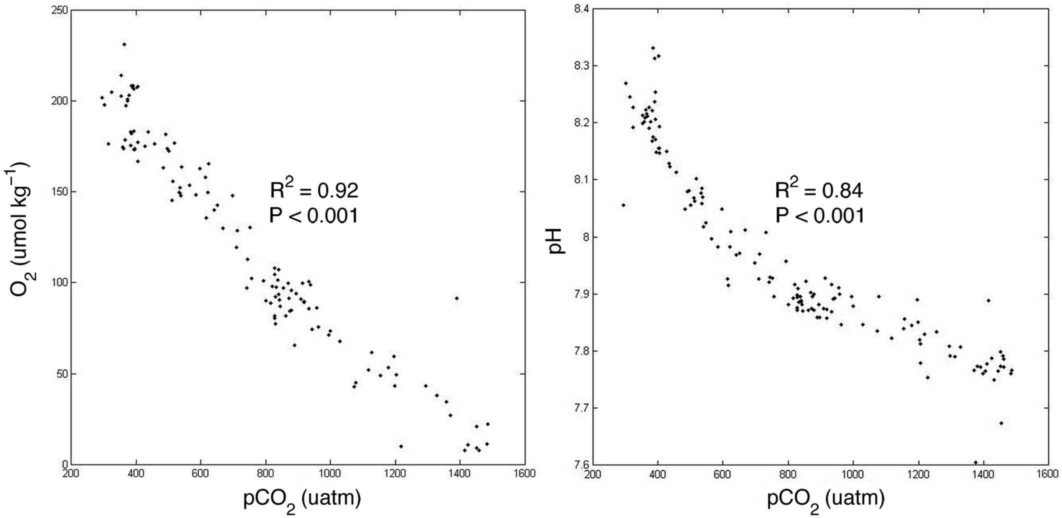

Fig. 4. Relationship between pCO_2 and O_2 or pH, showing the R^2 from fitted least squares regression analyses and the P value.

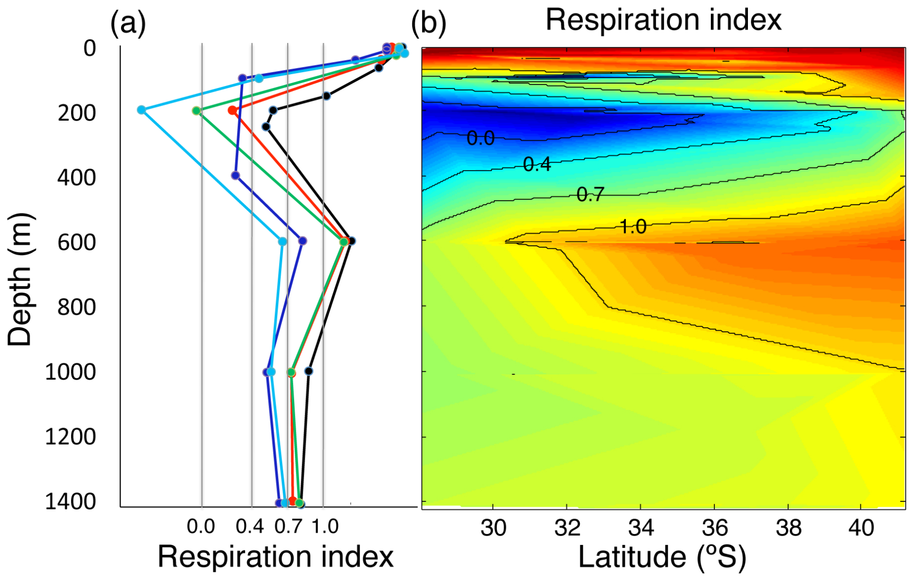

Fig. 5. (a) Vertical profile of RI for five representative stations along the meridional transect (black: station 41.2° S; red: station 37.4° S; green: station 33.6° S; blue: station 30.8° S and light-blue: station 28.03° S). The limits indicated by gray lines correspond to the different thresholds proposed by Brewer and Peltzer (2009): RI≤0 corresponds to the thermodynamic aerobic limit, a formal dead zone; RI = 0 to 0.4 aerobic respiration is not observed; RI = 0.4 to 0.7 practical limit for aerobic respiration and RI = 0.7 to 1.0 aerobic stress zone. **(b)** Contour plot showing the variability in RI along the studied transect.

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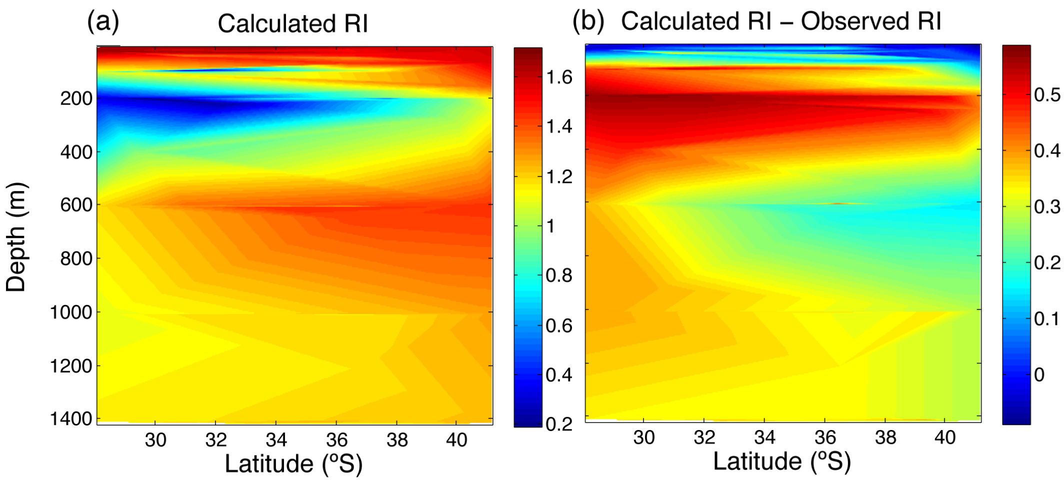

Fig. 6. Contour plot showing the distribution of **(a)** the calculated RI assuming a constant pCO_2 in atmospheric equilibrium (385 µatm) and **(b)** the difference between the calculated RI and that observed along the studied transect.

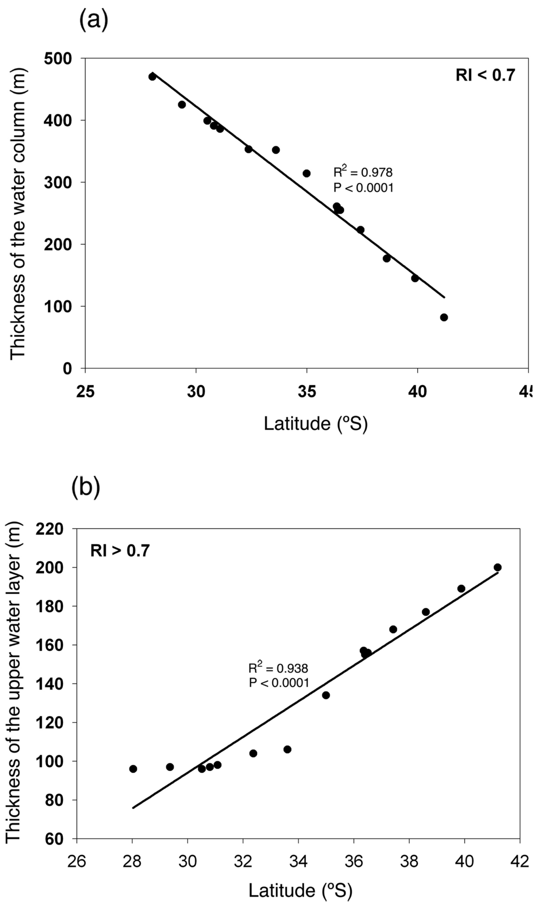

Fig. 7. The relationship between the thickness of the water column and latitude for **(a)** RI< 0.7; $P < 0.0001$ (down to 1.400 depth) and **(b)** RI> 0.7; $P < 0.0001$ (top 200 m of the water column) along the studied transect.

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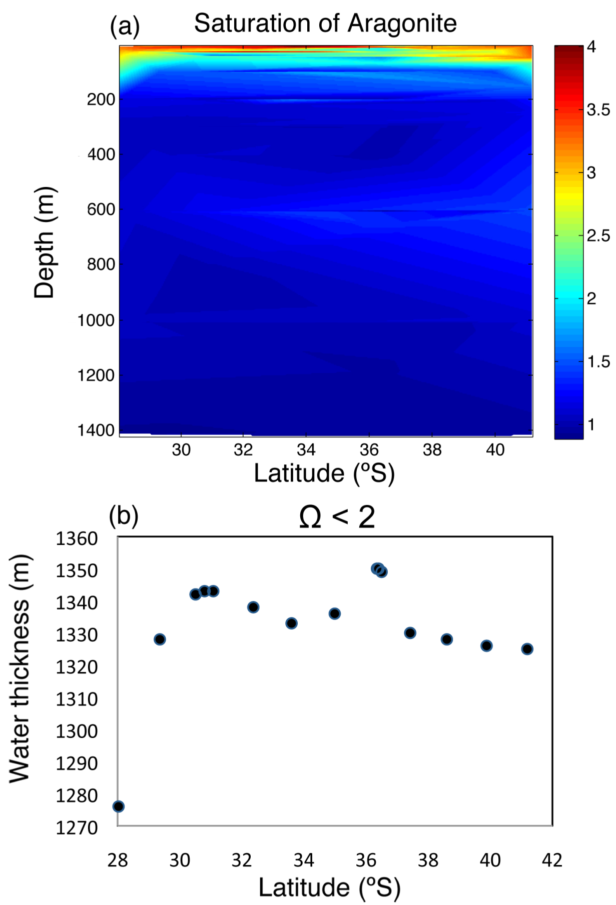

Fig. 8. **(a)** Contour plot showing the distribution of aragonite saturation index (Ω) and **(b)** the thickness of the water column with $\Omega < 2$ along the studied transect.

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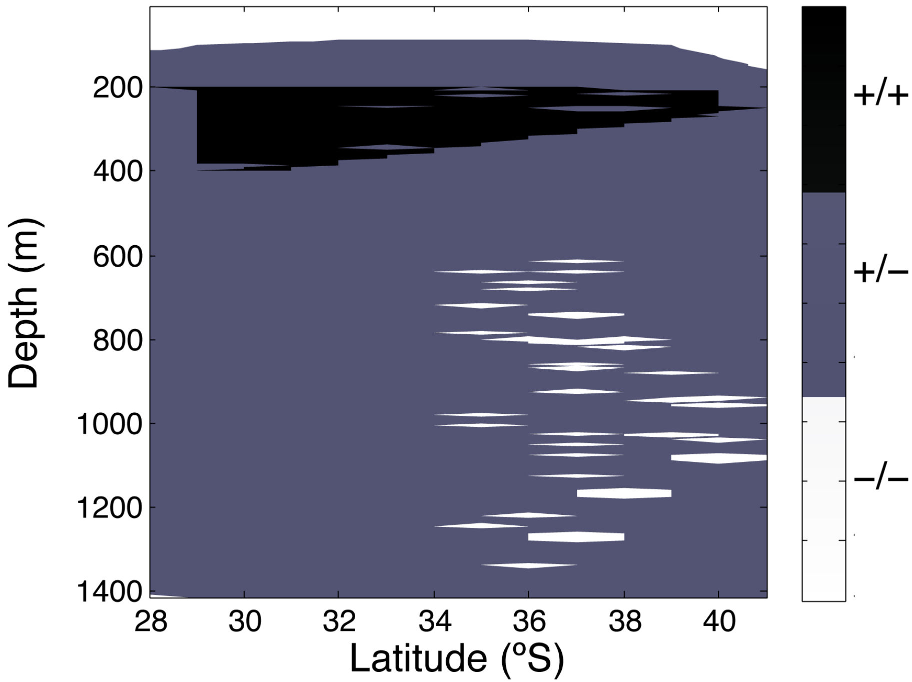

Fig. 9. Distribution of compromises (aerobic respiration compromised, RI<0.7; biocalcification compromised, Ω <2) to marine life along the studied transect. +/+ = both respiration and biocalcification compromised; +/− = only biocalcification compromised; −/− = no compromises. The missing combination (−/+ = only respiration compromised) was not observed.