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Size-based survival of cultured *Argopecten purpuratus* (L, 1819) under severe hypoxia

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Abstract

During recent years, mass mortalities of cultured scallops became more frequent in Peruvian bays. One of the main drivers related to these mortalities was hypoxic events. This study was designed to understand the hypoxia phenomenon in these bays and to assess how the Peruvian scallop, *Argopecten purpuratus*, can cope with reduced oxygen levels in seawater based on individual size. First, we analyzed the relationships between dissolved oxygen saturation and other environmental parameters (the Coastal El Niño Index, temperature, salinity and pH) in bottom seawater, the frequency and intensity of hypoxic events in two main culture areas (Sechura and Paracas Bays), and their relationship with scallop mass mortalities. Then, we performed experiments with two size groups of *A. purpuratus* (31 and 80 mm shell height; seed and commercial size, respectively) to assess their respective survival time under severe hypoxia (1% oxygen saturation) at 16°C and a salinity of 35. Finally, the results of the field records and the experimental data are used to suggest ways to improve scallop cultivation along the Peruvian coast.

KEYWORDS
Argopecten purpuratus, Lt_{50}, mass mortality, severe hypoxia, size effect

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1 | INTRODUCTION

The Peruvian scallop, *Argopecten purpuratus* (Lamarck, 1819), is a significant resource in Peru and Chile and one of the few marine species cultured in Peru. Its production increased rapidly in the early 2000s due to fast growth (from 7 to 18 months to reach commercial size, depending on site and culture system) (Mendo, Wolff, Carbajal, Gonzales, & Badjeck, 2008; Mendo, Wolff, Mendo, & Ysla, 2016) and lower production costs compared to Chile (Kluger, Taylor, Wolff, Stotz, & Mendo, 2019). In Peru, scallop culture activities support scallop farmer cooperatives and generate incomes to ~20,000 additional workers whose activities rely on scallop processing chains and associated businesses (Kluger et al., 2019). Nevertheless, mass mortality events since 2012 have led to colossal scallop production drops (e.g., from 52,213 tonnes in 2011 to 24,782 tonnes in 2012, and from 67,694 tonnes in 2013 down to 11,927 tonnes in 2017; source: http://www.fao.org/fishery/) and have severely affected the artisanal farmer cooperatives from Sechura and Paracas Bays (two of the main scallop culture areas in Peru). In Sechura Bay (the most impacted area), the economic losses due to mass mortalities in 2017 reached close to $1 million US dollars (source: http://direpro.regionpiura.gob.pe/).

Since 2012, eight mass mortality events were recorded in Sechura Bay (2012, 2015, 2017, and 2019) and Paracas Bay (2012, 2013, 2015, and 2017). Although information about environmental conditions preceding these events is scarce, mortalities were commonly linked to increases in temperature and bottom oxygen-depleted processes (eutrophication, red tides, milky-turquoise waters) (Peruvian Marine Institute – IMARPE, 2012, 2015, 2019; Aguirre-Velarde, Jean, Thouzeau, & Flye-Sainte-Marie, 2016; Aguirre-Velarde et al., 2019; Kluger, Kochalski, Aguirre-Velarde, Vivar, & Wolff, 2018). Temperature rising during these events was related to the summer heat, to the warm phases of the El Niño Southern Oscillation (ENSO; IMARPE, 2015), and to the Coastal El Niño Index (ICEN; ENFEN Comisión, 2012; Takahashi et al., 2017). Low dissolved oxygen levels (hypoxia) in seawater may be human-induced but it is also a natural process in some marine ecosystems. The Peruvian Humboldt upwelling system is associated with a strong oxygen minimum zone (OMZ; permanent hypoxic areas in the deep ocean; Gracco et al., 2017; Altieri & Diaz, 2019). Depending on years, sporadically advected OMZ water or high productivity associated with the coastal upwelling can lead to hypoxia in shallow coastal waters (Chavez, Bertrand, Guevara-Carrasco, Soler, & Csirke, 2008; Levin et al., 2009). Both abrupt temperature increases and deoxygenation in seawater are magnified by climate change, resulting in increasing stress for marine organisms (Bopp et al., 2013; Gunderson, Armstrong, & Stillman, 2016).

Monitoring environmental dynamics is crucial because going over thresholds may induce acute or chronic stress in living organisms. The response to stressful conditions depends on the intensity and relative timing of single and combined environmental stressors. The consequences of multi-stressor exposure are commonly more negative than expected based on responses to single stressor (Gunderson et al., 2016). The upper lethal temperature generating 50% of mortality in *A. purpuratus* is 29 ± 3°C (95% CI, Urban, 1994), a value never recorded in Peruvian bottom waters even during very intense El Niño events (max. temperature lower than 28°C; Tarazona, Salzwedel, & Arntz, 1988; Arntz, Tarazona, Gallardo, Flores, & Salzwedel, 1991; Mendo & Wolff, 2003; Kluger et al., 2018). This species seems well-adapted to high temperatures since it exhibited enhanced growth and reproduction during the warm ENSO events of 1983 and 1998 (Arntz et al., 1991; Wolff, 1987; Yamashiro, Rubio, Taipe, & Aguilar, 2002). Lethal oxygen levels are unknown for *A. purpuratus*, but Aguirre-Velarde et al. (2016) classified this species as a good oxy-regulator under broad oxygen levels at both 16°C and 25°C: the respiration rate of the species starts to decrease below dissolved oxygen saturation (DO_{sat}) of 24.4% (2.02 ppm at 25°C), until ca. 22% of its normoxic value at 5% DO_{sat} (0.44 ppm at 25°C). Another study showed that *A. purpuratus* kept feeding and growing after 21 days under cyclic hypoxia at 5% DO_{sat} (Aguirre-Velarde, Jean, Thouzeau, & Flye-Sainte-Marie, 2018). Nevertheless, more than 50% of bottom-cultured scallops died after chronic and severe hypoxia in Paracas Bay, showing slight size-related mortality (higher survival of scallops in the size range 40–50 mm compared with 60–90 mm; Aguirre-Velarde, Thouzeau, et al., 2019).

Some bivalves show size-dependent survival under hypoxia (Hicks & McMahon, 2005; Seto, Kaneko, & Nii, 2004; Shumway, Scott, & Shick, 1983; Wang & Widdows, 1991), which can vary according to oxygen

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concentration (Hicks & McMahon, 2005) and temperature (Shumway et al., 1983). Robb and Abrahams (2003) hypothesized that increasing body size reduces the ability to cope with hypoxia. Increasing size is related to decreasing surface-to-volume ratio and increasing oxygen diffusion distance, while higher body weight in larger individuals means higher energetic demand (Robb & Abrahams, 2003; Wang & Widdows, 1991). Hence, oxygen limitation and anaerobic metabolism would start earlier in larger individuals than in smaller ones. Under prolonged hypoxia or anoxia however, bivalves consume their body energy reserves (Grieshaber et al., 1988) and the larger individuals have an advantage compared to the smaller ones due to higher reserves (Nilsson & Ostlund-Nilsson, 2008). However, anaerobic pathways produce harmful metabolites (de Zwaan & Wijsman, 1976; Hochachka, 1997; Grieshaber et al., 1988), which may affect the organisms if the hypoxic stress is prolonged.

The degree of individual tolerance to environmental stressors (focusing on severe hypoxia) and the relationship between size and survival are required for better understanding of scallop mortality events and better management of scallop culture in Peru. The present work aimed to analyze the consequences and potential risks of hypoxic conditions for scallop cultivation in two Peruvian bays by coupling environmental surveys with a laboratory experiment on scallop survival. Field surveys were carried out in the cultivation areas of Sechura Bay (Northern coast) and Paracas Bay (Central-southern coast) between the years 2013 and 2019. The laboratory experiment focused on survival time under severe hypoxia according to individual size. The two size groups studied, large (80 ± 3.1 mm SD shell height) and small (31 ± 3.6 mm SD), were representative of commercial size (for consumption) and bottom-collected seed size, respectively. Finally, we used the relevant information on the scallop mortality events, the degree of individual tolerance to environmental stressors, and the relationship between size and survival to formulate some suggestions for better management of scallop aquaculture in these bays, which may contribute to the sustainability of this activity.

2 | MATERIALS AND METHODS

2.1 | Field analysis of environmental conditions and mortality in the two main scallop production areas

2.1.1 | Study sites

Two main scallop growing areas in Peru were investigated: Sechura (5°40′ S, 80°54′ W; Piura region) and Paracas (13°50′ S, 76°16′ W; Ica region; Figure 1) Bays. *A. purpuratus* is the unique species being cultured in both bays. The average relative production in the Piura and Ica regions was 47.2 and 2.1% of the total Peruvian scallop production between the years 2008 and 2018, respectively (http://ogeiee.produce.gob.pe/index.php/).

Sechura Bay, located in the north of Peru, is in a transitional zone between the Humboldt current (cold waters) and the Equatorial current (warm waters), meanwhile Paracas Bay, located in the central-southern coast, is mainly influenced by the Humboldt current. The total surface area of Sechura Bay and Paracas Bay is 1,120 and 36 km^2, respectively. Mean water depth is about 15 m in Sechura (max. depth: 50 m) versus 5 m in Paracas (max. depth: 14 m). The same sediment type can be found in both bays, that is a mixture of gravels, sand, and mud.

Sechura Bay receives little freshwater discharge from the Piura River through the Virrilá estuary overall, but this discharge can strongly increase during intense ENSO events (11.47 million m^3 in 1983; Salas, Solari, & Mejia, 2014), due to high precipitation (total rainy season rainfall in Piura up to 2.14 m in 1982–1983; Takahashi, 2004). In contrast, Paracas Bay does not receive freshwater discharges, the nearest inlet (Pisco seasonal river) is located 14 km further north. Rarely the Pisco river plume may enter the bay when strong winds switch to the southward direction (Merma, personal communication). Extreme events such as algal blooms and sulfur plumes are often observed in both bays (Aguirre-Velarde, Thouzeau, et al., 2019; Chauca Vela, 2018; Gonzales, Jacinto, Segura, & Macalupu, 2012; IMARPE, 2012, 2015, 2019; Morales, 2017; Sanchez, Delgado, Bances, Quintana, & Huamani, 2015).
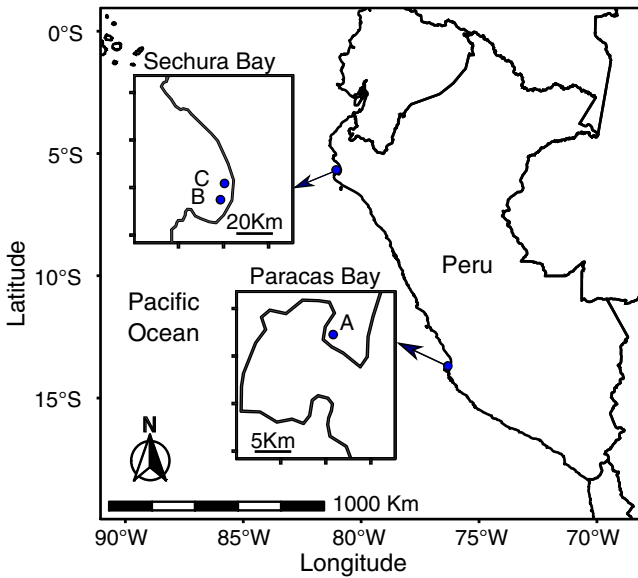
FIGURE 1 Location of the two *Argopecten purpuratus* culture areas studied along the Peruvian coast. Site names: C: Constante, B: Barrancos, and A: Atenas. See Table 1 for site geographical coordinates

2.1.2 | Descriptors of environmental conditions

Prior to the analysis of the environmental stressors in the studied bays, we performed an environment characterization using the ICEN and four local descriptors (temperature, DO_{sat}, salinity, and pH). The ICEN is defined as the three-month running mean of sea surface temperature (SST) anomalies in the "Niño 1 + 2" region (ENFEN Comisión, 2012; Takahashi, Mosquera Vazquez, & Reupo Velez, 2014). The ICEN characterizes the coastal conditions better than the more widely used Oceanic Niño Index (ONI: http://www.cpc.ncep.noaa.gov/); it is also sensitive to regional events such as the coastal event that occurred in 2017–2018 (Garreaud, 2018). ICEN categorizes as coastal El Niño events (CEN) events during, which SST anomalies of +0.4°C occur for three consecutive months, and as coastal La Niña events (CLN) events during which SST anomalies of −1.0°C occur for three consecutive months.

Seawater environmental conditions were defined compiling data from various sources: (1) data records from The National Fisheries Health Agency of Peru (SANIPES: http://179.43.86.24/web-oceano/), (2) data records from two companies (PRISCO scallop farming and ERM environmental consultant), and (3) data loggers from this study. Bi-weekly records of temperature, dissolved oxygen saturation, salinity, and pH were obtained from SANIPES in both sites between 2013 and 2019. From this data set, we get records from near bottom (1 m above the bottom), and at 6 m and 14 m above the bottom, depending on the station. Daily records of temperature, DO, and salinity were obtained from PRISCO in Sechura Bay, while daily records of temperature, DO, and pH in Paracas Bay were obtained from ERM. Finally, between 2012 and 2019, autonomous data-loggers of temperature (HOBO U22-001; Onset Corp., Bourne, MA), DO (DO-1060; RBR Ltd., Ottawa, Canada), and the combined temperature/DO loggers TDO-2050 (RBR Ltd., Ottawa, Canada) and MiniDOT (PME Inc., Vista, CA) were tied on a metal frame placed 0.2 m above the bottom by SCUBA divers in both bays (details in Table 1).

2.1.3 | Review of scallop mortality events in Paracas and Sechura Bays

Mortality events of *A. purpuratus* were documented from 2012 to 2019 in Paracas and Sechura Bays by using the statistics of the Peruvian Ministry of Production (PRODUCE, see www.produce.gob.pe), reports from the IMARPE and sea farmers, and peer-reviewed literature (Aguirre-Velarde, Thouzeau, et al., 2019). Details of the records are given in Table 2.

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TABLE 1 Environmental parameters recorded near bottom in Paracas and Sechura Bays between 2012 and 2019

Period of data recording	Parameter	Station	Depth (m)	Data source	Recording frequency
Sechura Bay					
January 3, 2012–November 9, 2016	Temp, DO$_{sat}$	C	12	This study (a)	Hourly
June 11, 2014–March 16, 2015	Temp, DO$_{sat}$	B[a]	12	This study (a)	Hourly
March 23, 2017–May 24, 2017	Temp, DO$_{sat}$	C	12	This study (a)	Hourly
January 23, 2018–March 1, 2019	Temp, DO$_{sat}$	C	12	This study (b)	Hourly
January 23, 2012–March 6, 2017	Temp, DO, Sal	C	12	PRISCO data (d)	Daily
January 2, 2013–September 2, 2017	Temp, DO$_{sat}$, Sal, pH	C	12	Sanipes data (d)	Bi-weekly
Paracas Bay					
August 28, 2012–March 10, 2013	Temp, DO$_{sat}$	A	5	This study (c)	Hourly
February 20, 2015–March 21, 2015	Temp, DO$_{sat}$	A	3	This study (b)	Hourly
March 19, 2016–October 14, 2017	Temp, DO$_{sat}$	A	5	This study (b)	Hourly
January 2, 2013–September 2, 2017	Temp, DO$_{sat}$, Sal, pH	A	5	Sanipes data (d)	Bi-weekly
January 1, 2012–October 10, 2015	Temp, DO, pH	A	5	ERM data (d)	Daily

Note: (a) Dataloggers HOBO U22-001 and RBR DO-1060. (b) Datalogger MiniDOT. (c) Datalogger RBR TDO. (d) Low-frequency data from Prisco, Sanipes and ERM were used to complete the high-frequency records and characterize the monthly relationships between the four environmental parameters analyzed in this study.

Abbreviations: A, Atenas (13°50′35.8" S, 76°15′59.5" W) in Paracas Bay; DO, dissolved oxygen concentration (mg/L); DO$_{sat}$, dissolved oxygen saturation (%); Sal: salinity, and pH; Temp: temperature (°C); Station refers to the location of the probes: C: Constante (5°40′33.3" S, 80°54′1.6" W) and B: Barrancos (5°47′33.6" S, 80°55′44.8" W) in Sechura Bay.

[a]The Barrancos data were used to replace missing records in Constante during or surrounding a mass mortality event. Barrancos and Constante stations are close and exhibit similar temperature and oxygen conditions.

2.1.4 | Data analyses

To explore the spatio-temporal relationship between the bottom-water (bw) conditions in Sechura and Paracas Bays, the monthly averages of temperature, DO$_{sat}$, salinity, and pH were compared by using principal component analysis (PCA). All variables were scaled to be zero-centered before the PCA. Significant grouping in abiotic conditions according to the ENSO phases and seasons was tested by using the Wilks test (significance level of α = .05). The ENSO phases (according to the ICEN index, ENFEN Comisión, 2012; Takahashi et al., 2014) used were neutral phase (N), weak El Niño (WEN), moderate El Niño (MEN), strong El Niño (SEN), weak La Niña (WLN), moderate La Niña (MLN), and strong La Niña (SLN). All statistical analyses were performed using the R software (version 3.4.4; R Core Team, 2018); PCA was performed using the "FactoMiner" R package (Lê, Josse, & Husson, 2008).

The high frequency (hourly) data (temperature, DO$_{sat}$) available during the 21 days preceding the mass mortality peaks in the field were compared to assess the local environmental conditions during mortality events in both bays (see Table 2). For this analysis, we used temperature and oxygen saturation physiological thresholds for *A. purpuratus* from Peru reported by Aguirre-Velarde et al. (2016) and Urban (1994). To evaluate a possible stress produced by sudden temperature increases in bottom seawater, the hourly records of bw temperature during the mortality events were compared with the LT$_{50}$ value after 24 h (temperature at which 50% of the experimental population was dead after 24 h) estimated by Urban (1994) for scallops originating from the Bay of Independencia in Peru (29°C; 95% CI: 26–32°C).

TABLE 2 Mass mortality events recorded in scallop (*Argopecten purpuratus*) bottom cultures between the years 2012 and 2019 in Sechura and Paracas Bays

Periods of data recording	Mortality (%)	Mortality causes[a]	ICEN	Data sources
Sechura Bay				
January 6, 2012–February 6, 2012	90	A, RT, TI, MTW	−0.4 (N)	ENFEN Comisión (2012); Gonzales et al. (2012)
March 2, 2015–March 14, 2015	Ca. 100	RT, A	0.18 (N)	PRISCO, personal communication
January 17, 2017–February 8, 2017	90	A, RW, MTW4	0.6–0.93 (WEN-MEN)	Sanchez et al. (2015); Kluger et al. (2018)
March 4, 2019–March 12, 2019	Ca. 100	RT, A, RW, RT	0.25 (N)	IMARPE (2019)
Paracas Bay				
April 2, 2012–April 4, 2012	Ca. 100	A, RW, RT	0.66 (WEN)	Morales (2017)
February 28, 2013–March 10, 2013	Ca. 100	A, MTW	−0.79 (N)	Aguirre-Velarde, Thouzeau, et al. (2019)
March 3, 2015–March 19, 2015	Ca. 100	TI, A, MTW, RW	0.18 (N)	Morales (2017)
March 9, 2017–March 17, 2017	70–90	RT, A, MTW	0.93 (MEN)	Cok (2017)

[a]Mortality causes suggested by the authors.

Abbreviations: A, anoxia; ICEN, Corresponding ENSO phases; MEN, Moderate El Niño; MTW, milky-turquoise waters and/ or sulfur plumes records; N, Neutral phase; RT, red tides; RW, freshwater inputs from the river; TI, temperature increases; WEN, weak El Niño.

The hypoxic stress was studied from two thresholds of oxygen saturation, the critical DO_{sat} of 24% and the 5% DO_{sat}, in order to assess the starting of oxy-conformity and metabolic depression for the Peruvian scallop (Aguirre-Velarde et al., 2016; more details in the introduction). By using the temperature and oxygen thresholds mentioned above, moderate heat and hypoxia were defined by temperature below 23°C and 5–24% DO_{sat}, respectively. Severe hypoxia corresponded to DO_{sat} below 5%. Any common stress conditions previous to mass mortality events were assessed by analyzing the relative proportions of moderate and severe hypoxia against normoxia in the 21 days before mass mortality events (Pearson's chi-squared test). For all statistical analyses, a significance level of α = .05 was used. Additionally, to have detailed descriptors of hypoxia along the year, we calculated the percentage of hours per month with hypoxic conditions (P, %) and the duration of hypoxic events (D, consecutive hours under hypoxia), using the thresholds mentioned previously, for all the period analyzed (January 2012 to December 2019).

2.2 | "Survival time under severe hypoxia" experiment

2.2.1 | Biological material and acclimation procedure

A total of 80 small (mean 30.9 ± 3.1 mm SD, shell height) and 80 large (mean 79.7 ± 3.6 mm SD, shell height) scallops were collected in October 2017 in Paracas Bay by Scuba diving. Individuals were transported in a cool box to the Aquatic Ecophysiology Laboratory at the IMARPE (Callao, Peru). Once in the laboratory, scallops were distributed into 80-L tanks for acclimation (20 large-sized and 40 small-sized scallops per tank, respectively). Tanks were supplied with 1-μm filtered seawater at a constant flow of 6 L/hr. The seawater temperature and salinity were maintained at 16.1 ± 0.2°C and 34.9 ± 0.1, respectively. During acclimation, scallops were fed a mix of cultured

microalgae composed by *Isochrysis galbana* IMP-BG-010 and *Chaetoceros calcitrans* (in a 1:1 cell proportion) three times a day to maintain an average concentration of 9.2×10^6 cells/L in the tanks. This cell concentration was shown to allow *A. purpuratus* growth after 21 days in laboratory conditions (Aguirre-Velarde et al., 2018). Due to technical issues, individuals were acclimated for 6 to 9 weeks before starting the experiments. This long acclimation time did not seem to affect the condition index of both size groups prior to the experiments. Food supply was stopped 1 day before starting the experiments.

2.2.2 | Experimental conditions

Four experiments (one control and three replicate hypoxic conditions) were performed between December 2017 and January 2018. For each replicate, 40 scallops (20 small-sized and 20 large-sized individuals) were placed into a 40-L aquarium without food and exposed to severe hypoxia (1% DO saturation) until 100% mortality was reached. Experimental aquaria were continuously supplied with 1-μm filtered and thermoregulated (16°C) seawater (1.8 L/hr). DO_{sat} in the aquarium of the severe hypoxia treatment was maintained to 1% (close to 0.4 mg/L at 16°C) using a computer-controlled gaseous nitrogen injection system (described in Artigaud, Lacroix, Pichereau, & Flye-Sainte-Marie, 2014) interfaced with an FDO 925-3 dissolved oxygen sensor (WTW, USA) allowing to continuously monitor temperature and DO_{sat}. Gas exchanges with the ambient air were limited by placing a floating polystyrene sheet on the water surface. The normoxic condition (c.a. 90% DO_{sat}) in the control was reached by bubbling air into the tank. The control experiment was performed using the same size groups and numbers of individuals as the hypoxic treatments.

2.2.3 | Measurements

Mortality was assessed twice a day by the failure of tissue constriction after the valves of gaping animals were pressed. Shell height (*H*, mm) of each dead scallop was measured to the nearest 0.1 mm using a Vernier caliper; then, soft tissues (muscle, gonad, gills, and mantle tissues) were dissected, dried (96 hr at 60°C), and weighed to the nearest 0.1 μg (DW, g). The Johnstone (1912) condition index (CI, g/cm^3) was calculated as CI = 1,000 (soft tissue DW)/(shell height)^3.

2.2.4 | Data analyses

The survival span for each size group (small-sized and large-sized) was calculated as the number of days from the beginning of the exposition to death. These data were used in the construction of the Kaplan–Meier survival curves, allowing to estimate the Lt_{50} and Lt_{90} (time at which 50 and 90% of the population die, respectively) and the confidence limits for each size group (Kaplan & Meier, 1958). The log-rank test was used to test the possible differences in survival between the size groups (Mantel, 1966). The possible effect of the condition index or experimental time on survival time was tested using Cox proportional hazard models ($p < .05$ from the Wald test statistics; Therneau & Grambsch, 2013). All statistical analyses (significance level of $\alpha = .05$) were performed using the "survival" and "survminer" packages (Therneau & Grambsch, 2013) of the R software (version 3.4.4; R Core Team, 2018).

3 | RESULTS

3.1 | Abiotic conditions in Sechura and Paracas Bays

The ICEN index, monthly averages of temperature, DO saturation, salinity, and pH were highly variable between the years 2012 and 2019 in Sechura and Paracas Bays (Figure 2). Sechura Bay showed the highest variability in the
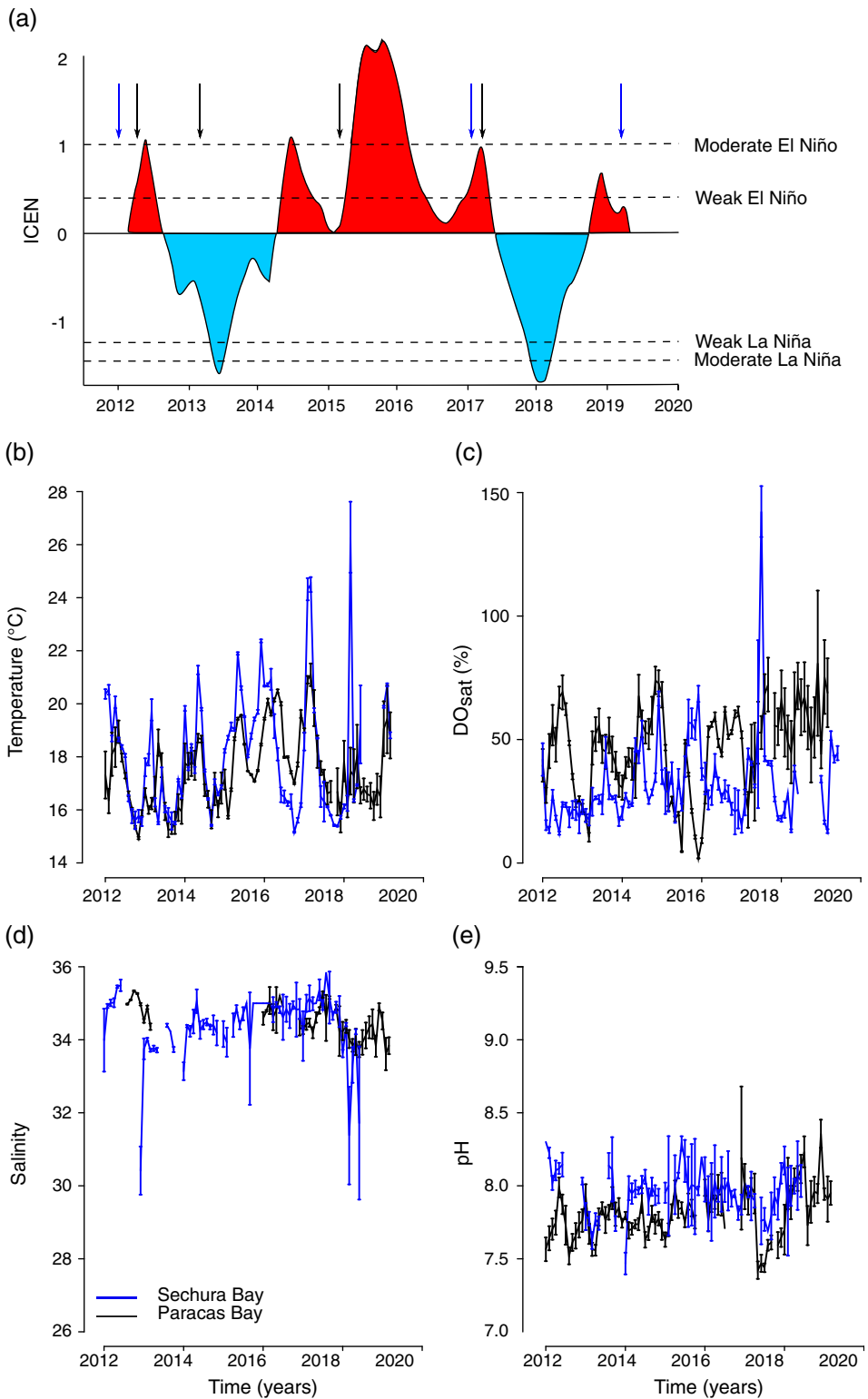
(a)

(b)

(c)

(d)

(e)

Sechura Bay
Paracas Bay
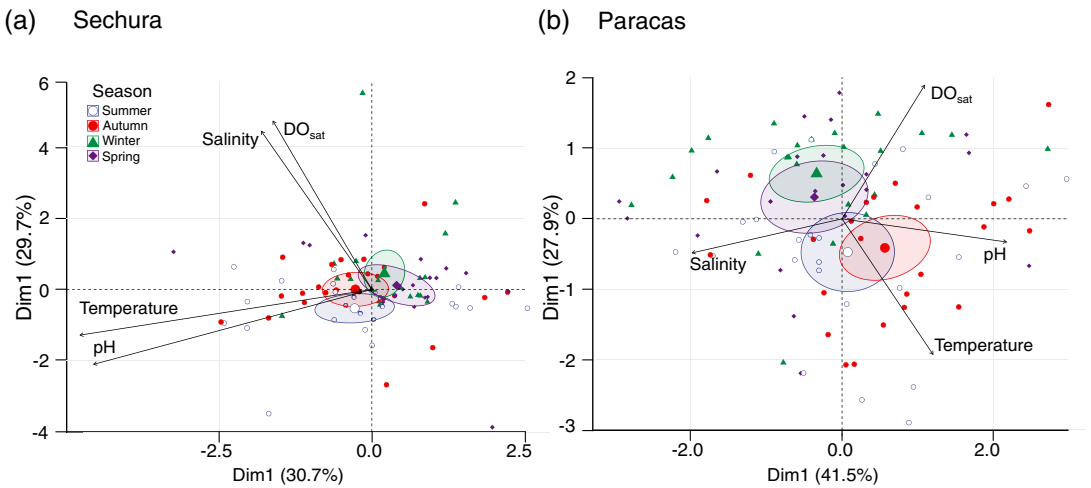
FIGURE 2 Legend on next page.

FIGURE 3 Principal component analysis of the monthly average conditions in bottom seawater at Sechura and Paracas. Biplots represent the two first principal components with 60.39 and 69.38% of the total variability explained in Sechura and Paracas, respectively. DO_{sat}: dissolved oxygen saturation; Sal: salinity; Temp: temperature. There were significant differences ($p < .0001$) between the ENSO phases and seasons at both sites. Ellipses indicate 95% confidence limits of the seasonal average bottom-water-condition groupings

average of monthly temperatures (18.0 ± 2.1°C SD; maximum and minimum values of 31.6 and 14.5, respectively). Paracas showed a bit lower variability than Sechura (18.2 ± 1.9°C SD; maximum and minimum values of 25.7 and 13.8°C, respectively). The rise in temperature was mainly related to the summer austral season. Monthly tempera-ture averages in both bays exhibited similar seasonal patterns (Pearson correlation test, $p < .01$; $R = .595$) along the years with slight differences in the extreme values (Figure 2b). The monthly percentage of DO_{sat} was 36.3 (± 1.4 SD) and 38.1% (± 1.9 SD) in Sechura and Paracas Bays, respectively. Though data sets available for pH and salinity were scarce, Sechura Bay also showed more variability in the averages of monthly salinity and pH. Average monthly salin-ity was 34.5 (± 0.6 SD) in Sechura versus 34.7 (± 0.2 SD) in Paracas. Mean pH was 7.9 (± 0.2 SD) and 7.8 (± 0.1 SD) in Sechura and Paracas, respectively.

PCA analysis between the ENSO phases and monthly averages of environmental parameters in both bays showed that the first and second principal components contributed 60.4 and 69.4% to the global variability at Sechura and Paracas, respectively. The relationships between the abiotic variables (temperature, oxygen, salinity and pH) differed between both bays. In Sechura, clear positive correlations were found between salinity and DO_{sat} on one hand, and between temperature and pH on another hand. In Paracas, there was a strong negative correlation between temperature and DO_{sat} on one hand, and between salinity and pH on another hand (Figure 3). Besides, the abiotic conditions were significantly different depending on the ENSO phases (Wilks' $\lambda = .50$, $p < .0001$ and Wilks' $\lambda = .44$, $p < .00001$, for Sechura and Paracas, respectively) and seasons (Wilks' $\lambda = .57$, $p < .00001$ and Wilks' $\lambda = .56$, $p < .00001$, respectively).

FIGURE 2 Environmental bottom seawater conditions available in Sechura and Paracas Bays between the years 2012 and 2019. (a) Coastal El Niño index (ICEN), (b) Monthly averages of bottom-water temperature, (c) dissolved oxygen saturation, (d) salinity, and (e) pH. Error bars represent 95% confidence intervals. Blue and black arrows indicate the occurrence of scallop mass mortalities in Sechura and Paracas Bays, respectively (details in Table 2). Monthly temperature and salinity averages in both bays exhibited similar seasonal patterns (Pearson correlation test, $p < .01$; $R = .595$ and .429, respectively)
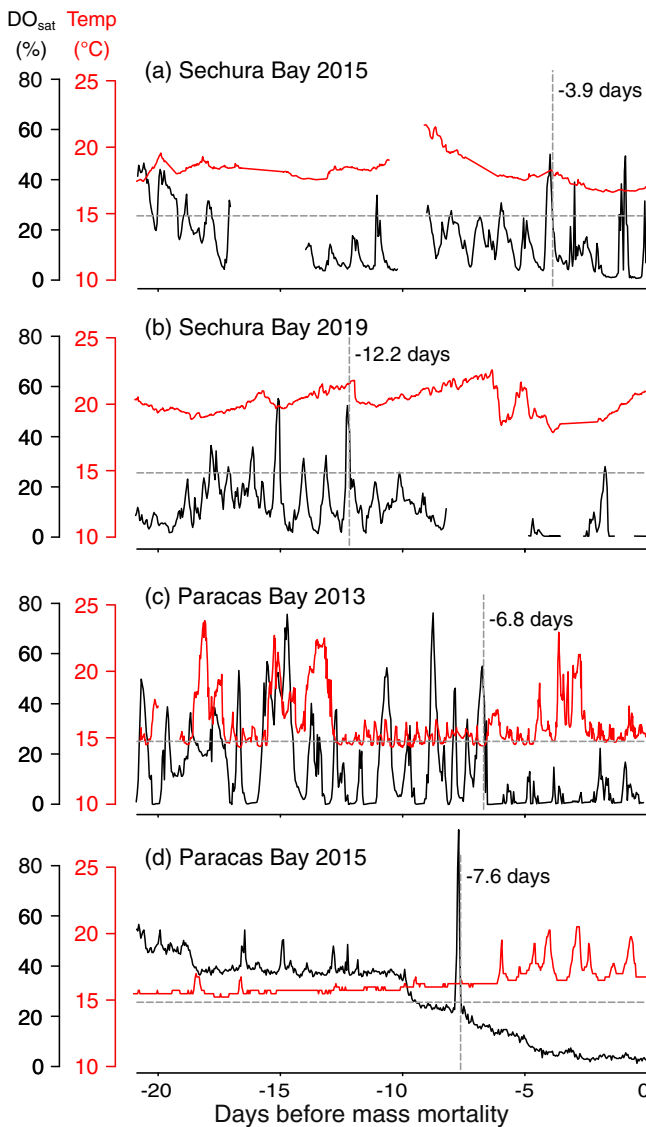
FIGURE 4 Hourly temperature (red lines) and dissolved oxygen saturation (black lines) in the 21 days before scallop mass mortalities recorded in Sechura and Paracas Bays: (a) March 14, 2015, (b) March 12, 2019, (c) March 10, 2013, (d) March 19, 2015. Vertical dashed lines: time from which DO saturation is below 24% for more than 90% percent of the time. Horizontal dashed lines: 24% DO_{sat}

3.2 | Temperature and hypoxic events versus scallop mass mortalities

Temperature did not seem to be a triggering factor for scallop mass mortality events which occurred in the two bays during the study period. There was no common heatwave in the 21 days before the mass mortalities recorded in Sechura and Paracas. Bw temperature was stable and close to 20°C in Sechura Bay during the 3 weeks preceding the mortality events of 2015 and 2019 (Figure 4). In Paracas, bw temperature was lower (ca. 16°C) than in Sechura before the mortality events of 2013 and 2015; the higher value was observed in 2017 (T° > 20°C 3 weeks before the mass mortality), but the lack of data afterward precludes to draw any conclusion.

By contrast, hypoxic conditions were present in all the periods preceding the mortalities. The former could last for more than 2 days, without more than three consecutive hours above the moderate hypoxia threshold (24% DO_{sat}). Hypoxia was present in both bays at both levels of intensity (moderate – 24% DO_{sat} and severe – 5% DO_{sat}),

TABLE 3 Monthly characterization of hypoxic events in bottom waters in Sechura and Paracas Bays between January 2012 and December 2019

DO$_{sat}$		n	P (%)	Sechura Duration (hr)	Max (hr)	n	P (%)	Paracas Duration (hr)	Max (hr)
5%	February, 2012	7	0.7	1.0 ± 0.0	1				
	March, 2012	3	0.3	1.0 ± 0.0	1				
	November, 2012					27	2.8	2.3 ± 1.1	6
	December, 2012					22	2.5	2.6 ± 2.3	7
	January, 2013					45	8.2	4.1 ± 3.7	14
	February, 2013					60	9.9	3.8 ± 3.5	17
	March, 2013					52	9.2	2.8 ± 2.2	10
	March, 2015					29	8.6	4.7 ± 3.6	12
	April, 2015					79	18.4	3.6 ± 3.3	15
	May, 2015					89	18.8	3.4 ± 3.2	17
	June, 2015					73	13.1	2.7 ± 3.0	16
	July, 2015					172	31.7	2.9 ± 2.9	20
	August, 2015					4	0.4	1.5 ± 1.0	3
	September, 2015					11	0.9	1.9 ± 1.2	4
	October, 2015					46	11.5	5.7 ± 5.4	23
	November, 2015					114	20.3	4.0 ± 4.5	30
	December, 2015					28	30.6	25.1 ± 22.1	95
	January, 2016					60	19.1	7.2 ± 12.6	69
	February, 2016					48	12.7	6.1 ± 6.1	32
	March, 2016					30	8.5	4.4 ± 4.1	18
	May, 2016					9	1.3	2.2 ± 2.6	9
	June, 2016					2	0.3	2.5 ± 0.7	3
	November, 2016	9	1.1	1.0 ± 0.0	1				
	December, 2016	13	1.9	1.2 ± 0.6	3	2	0.1	1.5 ± 0.7	2
	January, 2017	1	0.1	1.0 ± NA	1				
	February, 2017	7	0.8	1.1 ± 0.4	2	8	1.1	3.3 ± 1.9	7
	March, 2017					4	0.8	3.0 ± 2.3	5
	November, 2017	12	4.7	3.1 ± 3.3	10				
	December, 2017	14	7.8	4.6 ± 3.1	11				
	January, 2018	29	11.1	5.3 ± 7.9	39				
	February, 2018	11	4.8	4.2 ± 3.9	15				
	April, 2018	17	6.4	7.5 ± 13.8	58				
	January, 2019	2	0.2	1.5 ± 0.7	2				
	February, 2019	15	5.6	3.5 ± 2.9	10				
	March, 2019	53	20.4	3.6 ± 3.4	13				
24%	January, 2012	16	1.7	1.0 ± 0.0	1	7	0.3	1.0 ± 0.0	1
	February, 2012					11	0.5	1.0 ± 0.0	1
	March, 2012	13	1.4	1.0 ± 0.0	1	1	0.1	1.0 ± NA	1
	April, 2012	3	0.2	1.0 ± 0.0	1	1	0.1	1.0 ± NA	1

(Continues)

TABLE 3 (Continued)

DO$_{sat}$		n	P (%)	Sechura Duration (hr)	Max (hr)	n	P (%)	Paracas Duration (hr)	Max (hr)
	May, 2012	13	0.8	1.0 ± 0.0	1	1	0.1	1.0 ± NA	1
	June, 2012	13	5.1	1.0 ± 0.0	1				
	July, 2012	11	18.0	1.0 ± 0.0	1				
	August, 2012	10	1.6	1.0 ± 0.0	1				
	September, 2012	6	0.8	1.0 ± 0.0	1	11	1.3	2.6 ± 2.7	8
	October, 2012	4	0.5	1.0 ± 0.0	1	59	7.9	3.1 ± 2.9	13
	November, 2012	4	0.5	1.0 ± 0.0	1	100	18.6	4.2 ± 4.3	19
	December, 2012	4	0.5	1.0 ± 0.0	1	74	18.2	5.7 ± 6.8	30
	January, 2013	3	0.2	1.0 ± 0.0	1	56	20.2	8.2 ± 10.7	66
	February, 2013	6	0.6	1.0 ± 0.0	1	56	20.0	8.3 ± 8.6	39
	March, 2013	8	0.8	1.0 ± 0.0	1	59	13.5	3.6 ± 3.3	16
	April, 2013	12	0.6	1.0 ± 0.0	1	1	0.1	1.0 ± NA	1
	May, 2013	4	0.2	1.0 ± 0.0	1	3	0.2	1.0 ± 0.0	1
	June, 2013	5	2.0	1.0 ± 0.0	1	1	0.1	1.0 ± NA	1
	July, 2013	6	9.8	1.0 ± 0.0	1	1	0.1	1.0 ± NA	1
	August, 2013	2	0.3	1.0 ± 0.0	1	4	0.2	1.0 ± 0.0	1
	September, 2013	2	0.3	1.0 ± 0.0	1	1	0.0	1.0 ± NA	1
	October, 2013	4	0.5	1.0 ± 0.0	1	2	0.1	1.0 ± 0.0	1
	November, 2013	4	0.5	1.0 ± 0.0	1	5	0.2	1.0 ± 0.0	1
	December, 2013	12	1.4	1.0 ± 0.0	1	13	0.6	1.0 ± 0.0	1
	January, 2014	6	0.4	1.0 ± 0.0	1	11	0.5	1.0 ± 0.0	1
	March, 2014	5	0.5	1.0 ± 0.0	1				
	April, 2014	5	0.3	1.0 ± 0.0	1	9	0.6	1.0 ± 0.0	1
	September, 2014	4	0.5	1.0 ± 0.0	1	12	0.8	1.0 ± 0.0	1
	October, 2014	2	0.3	1.0 ± 0.0	1				
	February, 2015	8	0.8	1.0 ± 0.0	1	1	0.0	1.0 ± NA	1
	March, 2015	9	0.9	1.0 ± 0.0	1	43	19.0	6.9 ± 8.2	47
	April, 2015	2	0.1	1.0 ± 0.0	1	87	30.0	5.3 ± 5.3	22
	May, 2015	5	0.3	1.0 ± 0.0	1	112	35.2	5.0 ± 4.8	32
	June, 2015	2	0.8	1.0 ± 0.0	1	114	30.8	4.1 ± 6.5	52
	July, 2015	5	8.2	1.0 ± 0.0	1	157	47.1	4.7 ± 5.3	32
	August, 2015	1	0.2	1.0 ± NA	1	32	7.6	4.0 ± 3.6	13
	September, 2015					56	11.4	4.5 ± 4.4	19
	October, 2015					50	21.9	10.0 ± 11.2	77
	November, 2015					134	28.1	4.7 ± 6.1	35
	December, 2015					13	32.3	57.2 ± 84.0	312
	January, 2016					69	26.6	8.8 ± 14.9	80
	February, 2016	2	0.2	1.0 ± 0.0	1	67	19	6.6 ± 6.7	32
	March, 2016	6	0.6	1.0 ± 0.0	1	39	14.9	6.0 ± 5.5	22

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TABLE 3 (Continued)

DO$_{sat}$		n	P (%)	Sechura Duration (hr)	Max (hr)	n	P (%)	Paracas Duration (hr)	Max (hr)
	April, 2016	8	0.4	1.0 ± 0.0	1	6	1.3	3.3 ± 2.2	7
	May, 2016	1	0.1	1.0 ± NA	1	28	5.9	3.4 ± 4.2	20
	June, 2016	1	0.4	1.0 ± NA	1	41	12.9	4.8 ± 4.6	17
	July, 2016	3	4.9	1.0 ± 0.0	1	23	5.5	3.7 ± 2.6	10
	August, 2016	5	0.8	1.0 ± 0.0	1	3	0.3	1.7 ± 1.2	3
	September, 2016	1	0.1	1.0 ± NA	1	5	0.6	2.6 ± 1.8	5
	October, 2016	6	0.8	1.0 ± 0.0	1	3	0.3	2.3 ± 2.3	5
	November, 2016	25	3.7	1.2 ± 0.6	4	8	1.6	4.5 ± 3.2	10
	December, 2016	31	4.7	1.3 ± 0.6	3	23	6.9	6.9 ± 3.7	13
	January, 2017	21	2.1	1.4 ± 0.7	3	22	5.4	5.6 ± 3.6	11
	February, 2017	27	3.6	1.3 ± 0.5	3	73	14.6	4.6 ± 5.5	35
	March, 2017	10	3.4	3.2 ± 2.7	9	5	1.0	3.2 ± 3.2	8
	April, 2017	7	2.3	6.4 ± 4.1	13	2	0.1	1.0 ± 0.0	1
	May, 2017	11	6.7	10.0 ± 9.5	33				
	August, 2017	6	3.7	3.8 ± 2.3	7				
	September, 2017	11	4.3	3.0 ± 2.2	8				
	October, 2017	30	15.3	4.1 ± 3.0	12				
	November, 2017	45	39.5	7.0 ± 7.5	32				
	December, 2017	42	67.1	13.3 ± 16.9	68				
	January, 2018	59	40.9	9.7 ± 27.6	176				
	February, 2018	17	11.0	6.1 ± 4.5	15				
	April, 2018	63	29.2	9.2 ± 20.5	159				
	May, 2018	8	1.6	3.3 ± 2.2	7	1	0.1	1.0 ± NA	1
	January, 2019	17	13.3	10.9 ± 22.6	96				
	February, 2019	103	56	5.2 ± 10.7	85				
	March, 2019	109	59.1	5.1 ± 5.1	25				
	April, 2019	6	2.2	7.3 ± 7.0	16	1	0.1	1.0 ± NA	1
	May, 2019	23	5.8	4.1 ± 5.2	25				
	June, 2019	1	1.6	4.0 ± NA	4				

Note: n is the number of interrupted events of severe (DO$_{sat}$ below 5%) and moderate hypoxia (DO$_{sat}$ below 24%). P (%) is the percentage of hours per day with DO$_{sat}$ under severe or moderate hypoxia; duration (hours) represents the average consecutive hours (mean ± SD) per month under severe or moderate hypoxia. Max is the maximum number of consecutive hours under the hypoxic stress conditions aforementioned. NA: SD-values not available (only one record of hypoxia in the month).

but the relative proportions of each hypoxic condition were significantly different between years (chi-square = 155.5, *df* = 8, *p* < .0001).

Hypoxia occurs not only during mass mortality events, but it is frequent in austral summer (December to March) and early autumn (April and May, Table 3). The extent of bw hypoxic conditions along the year was higher in Paracas Bay (only the months of July and August were free from hypoxia), compared with Sechura Bay (6 months, from May
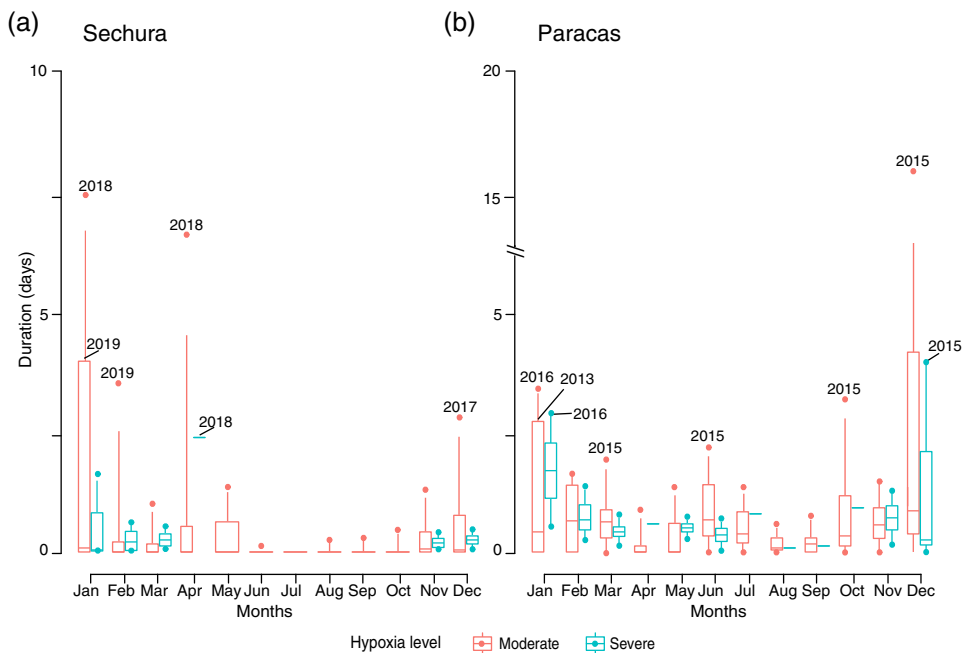
FIGURE 5 Box-and-whisker plots of the longest duration of hypoxic events (in days, calculated from continuous hours of hypoxia) recorded by month/year in Sechura and Paracas Bays between 2012 and 2019. Horizontal lines within boxes are medians, the lower and the upper limits of the boxes are the 25th and 75th percentiles, respectively, and the whiskers extend to the 5th and 95th percentiles, respectively. Outliers of the longest monthly durations are indicated by points and years of occurrence. The duration of the hypoxic events are detailed in Table 3

to October, free of hypoxia; Table 3). In Sechura, the longest episode of severe hypoxia occurred in April during the study period (58 hr, that is, 2.4 days), while the longest moderate hypoxia event happened in January (176 hr, that is, 7.3 days). In Paracas, the longest severe (95 hr, that is, 4.0 days) and moderate (312 hr, that is, 13 days) hypoxia episodes occurred in December (Figure 5). Whatever the bay and year, however, mass scallop mortalities were generally recorded in March (Table 2), which questions the multi-stressor combination generating such collapses. Last, the highest number of hours below or up to 1% DO_{sat} was 13 hr in both bays.

3.3 | Lethal times in *A. purpuratus*

The normoxic control treatment (without feeding) exhibited a high survival rate (92.5 ± 2.5%, 95% CI), and mortality started from the seventh day. The shortest median lethal time under severe hypoxia (1% DO_{sat}) was 40.5 hr (1.7 days) in the large-sized group, whereas it was 48 hr (2 days) in the small-sized group. Both groups exhibited different survival times (Figure 6a): the Lt_{50} was 3.9 ± 0.25 days (95% CI) for the small-sized group versus 2.7 ± 0.35 days (95% CI) in the large-sized group. Similarly, Lt_{90} was 5.0 and 3.9 days in the small- and large-sized groups, respectively. A positive and significant correlation (linear regression, p < .0001; R^2 = .41 and .32 in the small and large-sized groups, respectively) was found between the scallop survival time and condition index (Figure 6b). Although we carried out replicates at different times (e.g., 2 weeks between the first and the third replicate), there was no effect of the experiment time (i.e., no effect of the maturation stage and acclimation time) on survival (Wald test, p > .05).
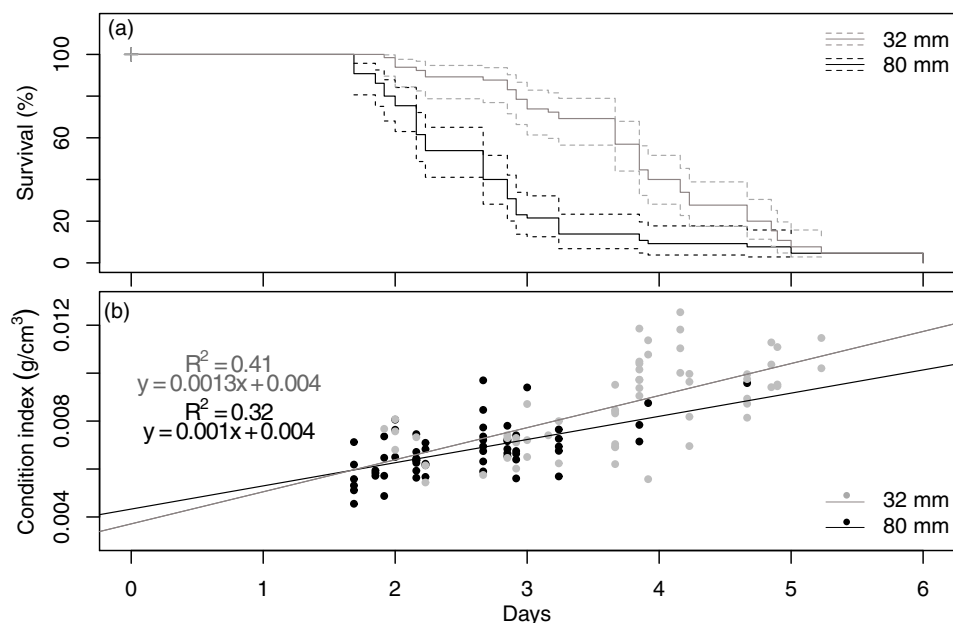
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FIGURE 6 Survival of small- and large-sized groups of *Argopecten purpuratus* at 1% DO_{sat}: (a) survival curves and (b) the relationship between individual survival time and condition index. Dashed and dotted lines represent 95% confidence intervals and the median lethal time, respectively. Linear regression models represent the significant positive relationships ($p < .0001$) between the survival time and condition index in both size groups

4 | DISCUSSION

4.1 | Environmental characterization of Sechura and Paracas Bays

Sechura and Paracas Bays exhibited similar patterns in bw temperature variations (Figure 2). These similarities can be explained by seasonality and the fact that both bays are under the influence of large-scale events such as ENSO. The latter was a significant factor in explaining the monthly environmental variability in both bays (Figure 3). This synchronicity in temporal trends extends further south within the geographic range of *A. purpuratus*: in Tongoy Bay (Chile), Ramajo et al. (2019) observed patterns in DO, pH and temperature apparently synchronous with ours during the years 2016–2017. Nevertheless, Peruvian bays exhibited lower DO concentrations and pH, and fluctuations in temperature, oxygen, and pH were more abrupt than those observed in Tongoy Bay. Sechura Bay, being located in a transition zone between tropical water masses and the colder Humboldt Current, exhibited a higher variability in environmental parameters (i.e., high peaks of temperature, but low salinity due to rainfalls). Conversely, Paracas Bay, located near one of the most intense upwelling cells of Peru (Zuta & Urquizo, 1972), exhibited higher DO variability and more frequent low-DO_{sat} periods. Such variability is probably due to the advection of hypoxic water masses from the upwelling system combined to local sediment oxygen uptake (Aguirre-Velarde, Thouzeau, et al., 2019; Chauca Vela, 2018; Ohde, 2018). Both bays exhibited long periods of occurrence of moderate hypoxia (below 24% DO_{sat}), but different relationships with other environmental variables. In Sechura, lower DO_{sat} in bw was positively correlated to lower salinity, which suggests that hypoxia in this bay is probably linked to stratification. In Paracas, low DO_{sat} was positively related to higher bw temperatures. This result seems to contradict the observations of Aguirre-Velarde, Thouzeau, et al. (2019) for Paracas, but may be explained by the frequency in data acquisition and analysis between the two studies. The present study analyzed low-frequency data and the correlation between high temperature and low DO can be explained by seasonality: low DO events occurred mainly during summer when the

temperature was on average higher, but also more variable (Aguirre-Velarde, Thouzeau, et al., 2019). The analysis of high-frequency data in Aguirre-Velarde, Thouzeau, et al. (2019) showed that hypoxia events occurred concomitantly with sudden drops in temperature in summer, suggesting the advection of upwelled cold and oxygen-depleted water. Indeed, the same trend can be observed in our high-frequency data (when available) in both bays (Figure 4b–e). Hypoxia thus appears as a chronic stressor in Sechura and Paracas Bays, which exhibited more than 38% of the summer time under moderate hypoxia (below 24% DO_{sat}; Table 3). Both bays exhibited much longer periods in hypoxia than Seatuck Cove, USA (5.3% of the time under 29.7% DO_{sat}, Gurr et al., 2018), where hypoxia has been reported as a problem for the Atlantic Bay scallop, *A. irradians*. Moderate hypoxia was also more prolonged in Sechura Bay than in Tongoy Bay (Ramajo et al., 2019) during the last 3 months of 2017.

4.2 | Hypoxia-related mortality and size-related tolerance to hypoxia

All scallop mass mortalities in Sechura and Paracas (years 2012, 2013, 2015, 2017, and 2019) occurred during the warmer months (austral Summer and early Autumn) and were always preceded by the occurrence of severe (below 5% DO_{sat}) to moderate (below 24% DO_{sat}) hypoxia within the previous 2 weeks (Figure 4). Additionally, continuous moderate hypoxia was present for more than 2 days in bw before mass mortality events (Figure 4), which emphasizes the need of evaluating the ability of *A. purpuratus* to cope with hypoxia. Many studies stated that the adverse effects of hypoxia on aquatic organisms depend on the intensity and duration of hypoxic events (e.g., Brokordt, Pérez, & Campos, 2013; Diaz & Rosenberg, 1995; Llansó, 1991, 1992). Our experimental results highlight the higher ability of *A. purpuratus* to cope with severe hypoxia compared with other pectinids: the first specimen died after 40.5 hr at continuous exposure to 1% DO_{sat} (Figure 6a), which is 1.4- to 3.4-fold higher than the 28, 16, and 12 hr reported in *A. irradians* (Gurr et al., 2018), *Patinopecten yessoensis* (Sakurai, Seto, Makiguchi, & Ogata, 2000), and *Chlamys delicatula* (Mackay & Shumway, 1980), respectively. This ability would be an adaptive response of the species to this recurrent selective pressure linked to the upwelling system.

Facing severe hypoxia ($\cong$ 1% DO_{sat}), *A. purpuratus* survival was size-dependent (negative relationship; Figure 6a), which agree with observations for other bivalves such as *P. yessoensis* (Lt_{50} of 4 and 2.6 days for 8.8- and 59.4-mm size groups, respectively; Seto et al., 2004), *Mulinia lateralis* (Lt_{50} of 7 and 4 days for 5- and 10-mm size groups, respectively; Shumway et al., 1983), and *Perna perna* (Lt_{50} of 19 and 12 days for 29- and 58-mm size groups, respectively; Hicks & McMahon, 2005). Lower tolerance (survival time) of large-sized specimens to severe hypoxia is consistent with the hypothesis that a lower surface-to-volume ratio in larger individuals confers lower ability to extract oxygen from the water (related to the surface area) in light of their oxygen requirements (at least partly related to the volume). Another non-exclusive hypothesis is that reproductive investment in larger scallops may reduce their capacity to cope with hypoxia. Indeed, Brokordt, Pérez, Herrera, and Gallardo (2015) observed that mature and post-spawning *A. purpuratus* are more vulnerable to hypoxia than juveniles. Such a pattern could be due to the additional energy mobilization towards spawning after maturation (Kraffe et al., 2008), which would increase oxygen demand, and/or to reduced reserves for aerobic and anaerobic metabolisms under hypoxia (Brokordt et al., 2015). The higher proportion of juveniles after mass mortalities in the years 1995 to 2014 in the natural bed of Lobos de Tierra Island (south of Sechura, Flores-Valiente et al., 2019) would agree with a higher tolerance of small-sized scallops to environmental stressors. In fine, smaller body size would be an outcome to global warming and deoxygenation of seawater (Baudron, Needle, Rijnsdorp, & Tara Marshall, 2014; Daufresne, Lengfellner, & Sommer, 2009; Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011).

In contrast, Nilsson and Ostlund-Nilsson (2008) hypothesized that large-sized individuals have an advantage over the smaller ones during prolonged severe hypoxia and anoxia, when individuals rely on anaerobic ATP production for survival. The small-sized individuals would run out of energy reserves or would reach lethal levels of toxic anaerobic end-products faster than the large-sized specimens, due to their higher mass-specific metabolic rate. Indeed, the Lt_{50} of *P. perna* increased with increasing shell length (SL) under anoxia (~7 and 21 days at 20°C for 29

and 58 mm SL, respectively; Hicks & McMahon, 2005). This feature was not so clear; however, for *P. yessoensis* (Lt_{50} of 0.8 and 1.3 days at 15°C for 8.8 and 59 mm SL, respectively; Seto et al., 2004). *P. perna* (Hicks & McMahon, 2005), *Mytilus edulis* (Babarro & de Zwaan, 2002, 2008), and *Mytilus galloprovincialis* (de Zwaan, Cortesi, Van den Thillart, Roos, & Storey, 1991) are very tolerant to anoxia. These mytilid species, frequently exposed to anoxia when their valves are hermetically closed, may have efficient anaerobic metabolism. These periods of "self-imposed" anoxia lead to hypometabolic conditions, activation of the anaerobic pathways for energy production, and an effective antioxidant system (Hermes-Lima, Storey, & Storey, 1998). *M. edulis* and *Mytilus trossulus*, when closing their shells, maintain the pallial fluid in a hyperosmotic state for a while (Qiu, Tremblay, & Bourget, 2002) and may reduce sulfide diffusion. Anoxia does occur with some co-stressors, such as hydrogen sulfide and bacterial proliferation, which may reduce bivalve survival (Vaquer-Sunyer & Duarte, 2010; Yamada, Miyamoto, Nakano, & Okamura, 2016). The present experimental study could not be compared to the studies aforementioned since scallops were not exposed to anoxia and co-stressors were not measured in our experiments.

Interestingly, individual survival time under severe hypoxia was positively related to the condition index (CI, Figure 6b). Such a pattern might be explained by higher availability of energetic reserves for anaerobic metabolism in individuals presenting higher CI (Nilsson & Ostlund-Nilsson, 2008). Several bivalves use the glycogen stored in all the body tissues to maintain the organism's total energy demand (Barber & Blake, 2016). Specifically, Pectinidae switch their metabolism toward anaerobic metabolism during hypoxia, forming octopine within their adductor muscle (Grieshaber, Hardewig, Kreutzer, & Portner, 1994). The positive relationship between scallop survival and individual CI during the laboratory experiments highlights that a high CI would allow the individuals, whatever their size, to maintain their metabolism for a longer time.

4.3 | Sustainable management of scallop aquaculture

During recent decades, the frequency, duration, and severity of hypoxic crises have increased worldwide (Diaz and Rosenberg, 2008), including Sechura and Paracas Bays. The latter has more risk of facing severe hypoxia than Sechura because milky-turquoise waters and anoxic events are frequent in summer, leading to reproduction disruptions, somatic weight losses, and increased scallop mortality (Aguirre-Velarde, Thouzeau, et al., 2019). Exposure to severe hypoxia and related environmental conditions affect scallop bioenergetics and subsequently growth and reproduction (Aguirre-Velarde et al., 2019). Hypoxic crises mainly extend in summer and early fall, from January to April in Sechura Bay and from December to April in Paracas Bay (Table 3). Hypoxia during summer is associated with more stratified seawater along the Peruvian coast compared to the winter time when the water column is totally mixed and colder (Gutiérrez et al., 2011). In the last decades, scallop farming in Peru showed competitive advantages compared to Chile because of lower production costs and high availability of seeds on natural beds (Bossier, 2015; Kluger et al., 2019). This may not be true anymore because environmental stressors are more frequent in Peruvian bays. The present study focused on hypoxia, but other stressors (red tides, hydrogen sulfide episodes, ocean acidification, etc.) might also affect scallop farming and lead to production losses. Unfortunately, the long-time scallop cultivation process increases the risk of mortality due to a higher probability of mismatch between environmental conditions and scallop ecophysiological requirements. The long-term cultivation of this species may also include loss of genetic diversity due to generational breeding and cause a gradual decline of natural stocks.

The failure of current scallop production strategies in Peru requires new farming modalities in order to limit summer mass mortalities in culture and economic losses for producers and the food chain industry. This is particularly true in the context of climate change and other anthropogenic pressures, which will probably lead to increased frequency of hypoxic events in the bottom water of Peruvian shallow coastal bays in the next decades. The future management plan in Sechura and Paracas Bays could include a combination of high-frequency environmental monitoring, changes in culture techniques and annual planning, ecosystem management and experimental management (with direct intervention to enhance productivity and survival rate: see Avendaño, Cantillánez, & Thouzeau, 2017):

(a) Real-time and high-frequency environmental surveys would allow farmers to get an early warning on environmental changes in the culture areas. Bottom-water characteristics (temperature, DO, salinity, hydrogen sulfide, red tides) are essential to monitor as long as bottom scallop culture remains the rule, especially in summer. Temperature records more offshore could also allow farmers to anticipate changes in the upwelling intensity and ENSO phases, in order to predict the onset of hypoxic crises. (b) The cultivation technique should be changed from bottom to suspended culture whenever possible (e.g., by using lantern nets) to avoid severe hypoxia (and likely hydrogen sulfide) peaks in bw and at the water–sediment interface. Seed collection in suspended artificial devices could be also tried out, in order to provide substrates for post-larval settlement off bottom. In addition, better growth in suspended culture (Aguirre-Velarde, Thouzeau, et al., 2019; Cisneros & Argüelles, 1996; Mendo, Cosavalente, Tam, & Bandin, 2002) would allow reducing the culture cycle duration and further decrease the scallop mortality risk. Experimental management could deal with optimal depth for seed settlement and growth, density-dependent seed survival and growth in lantern nets, and the ecological side effects of scallop production off bottom. Usually, the cost of suspended culture in lantern nets, baskets, or cages is lower than that relative to bottom culture that may require SCUBA diving (depending on depth conditions). However, one may consider the relatively small total surface area being cultivated with suspended devices (defined by the number of lantern nets) compared with bottom culture (Alcazar and Mendo, 2008). Suspended culture has been well-implemented in another scallop culture area called Los Chimus Bay, with no significant mortality reports and constant production during the last years. (c) Harvesting schedules should be planned to avoid having large-sized individuals in culture during the austral summer and fall months (these months exhibit frequent severe hypoxia). The critical month of December could be the last month of harvesting, at least on bottom. (d) In parallel with seed collection on artificial substrates, monitoring recruitment in natural beds would ensure to catch seed for the next cultivation period and likely to increase the survival rate of these juveniles when cultivated off bottom. (e) When relevant, the culture sites should be located far from freshwater inputs, especially during the rainy ENSO warm phases. Coping with climate change and in order to reduce the risk of production losses, artisanal producers should try to optimize their practices. Ecosystem management options may include habitat manipulation (e.g., by providing artificial substrates, such as Japanese devices, to replace natural ones which are located on bottoms with unsuitable environmental conditions), restocking of depleted areas (by seeding of juveniles on predator-cleaned bottom), and estimating the carrying capacity of Paracas and Sechura Bays taking into account the seasonal variability in oxic conditions. Finally and as suggested by Aguirre-Velarde, Thouzeau, et al. (2019), whether cultured scallops could be transferred in other coastal areas during hypoxic/anoxic events and co-occurring episodes of milky-turquoise waters ("aguas blancas") would also need to be evaluated in terms of technical feasibility and economic profitability, as the ultimate chance to avoid or reduce mortalities.

5 | CONCLUSIONS

Environmental surveys conducted in this study showed that hypoxia is persistent throughout most months in Peruvian shallow coastal waters such as Sechura and Paracas Bays, with higher intensity and duration during summer and early fall. Prolonged exposure to hypoxia and other co-occurring environmental stressors may affect scallop survival. We demonstrated the importance of using the individual size in the subsequent environmental stress experiments. The present study showed that the smaller individuals (31 mm shell height) were more tolerant to severe hypoxia than the bigger ones (80 mm shell height). The positive relationship between scallop survivorship and individual condition index during the laboratory experiments highlights that a high condition index would allow the individuals to maintain their basal metabolism for a longer time. Further studies should consider survival when scallops face other single thresholds (e.g., salinity, pH, hydrogen sulfide, red tides) and most importantly the combination of multiple stressors since they may affect the tolerance and the ability of recovery of the scallops in a greater portion than single stressors. Finally, as a consequence of global change, rising temperatures, oxygen depletion, and acidification in seawater are expected to be more frequent, so scallop managers must account for the potential risks of these

environmental stressors in planning their production activities. Clearly, there is a need for site-specific management strategies in Peru due to the distinctive environmental features of the various coastal bays hosting scallop culture.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

R.C.V., G.T., J.F.S.M., A.A.V., F.J., and P.G.K. designed research, performed research, analyzed data, and wrote the article.

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