

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

Rosa Cueto-vega, Jonathan Flye-Sainte-Marie, Arturo Aguirre-velarde, Fred Jean, Patricia Gil-kodaka, Gérard Thouzeau

# ► To cite this version:

Rosa Cueto-vega, Jonathan Flye-Sainte-Marie, Arturo Aguirre-velarde, Fred Jean, Patricia Gilkodaka, et al.. Size-based survival of cultured Argopecten purpuratus (L, 1819) under severe hypoxia. Journal of the World Aquaculture Society, 2022, 53 (1), pp.151-173. 10.1111/jwas.12777. insu-03457249

# HAL Id: insu-03457249 https://insu.hal.science/insu-03457249

Submitted on 30 Nov 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Check for updates

WILEY

World Aquaculture Society

QUACULTURE

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

Rosa Cueto-Vega<sup>1,2</sup> | Jonathan Flye-Sainte-Marie<sup>1</sup> Gérard Thouzeau<sup>1</sup>

Arturo Aguirre-Velarde<sup>3</sup> | Fred Jean<sup>1</sup> | Patricia Gil-Kodaka<sup>2</sup> 

<sup>1</sup>Facultad de Pesquería, UMR 6539 - LEMAR (CNRS/UBO/IRD/IFREMER), IUEM, Technopôle Brest-Iroise, Plouzané, France

<sup>2</sup>Facultad de Pesquería, Universidad Nacional Agraria la Molina, Lima, Peru

<sup>3</sup>Laboratorio de Ecofisiología Acuática, Instituto del Mar del Perú, Chucuito, Peru

#### Correspondence

Rosa Cueto-Vega, Facultad de Pesquería, Universidad Nacional Agraria la Molina, Av. La Molina S/N, La Molina 15023, Peru. Email: rosacueto@lamolina.edu.pe

#### **Funding information**

Franco-Peruvian Doctoral School in Life Sciences, Grant/Award Number: EPG/ Co180053; French National Research Institute for Sustainable Development (IRD, France)

# 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<sub>50</sub>, mass mortality, severe hypoxia, size effect

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes. © 2021 The Authors. Journal of the World Aquaculture Society published by Wiley Periodicals LLC on behalf of World Aquaculture Society.

# 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 (eutro-phication, 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% Cl, 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 (DOsat) of 24.4% (2.02 ppm at 25°C), until ca. 22% of its normoxic value at 5% DO<sub>sat</sub> (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<sub>sat</sub> (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

2

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 ( $80 \pm 3.1 \text{ mm SD}$  shell height) and small ( $31 \pm 3.6 \text{ mm SD}$ ), 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<sup>2</sup>, 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<sup>3</sup> 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  $+0.4^{\circ}$ C occur for three consecutive months, and as coastal La Niña events (CLN) events during which SST anomalies of  $-1.0^{\circ}$ 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.

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

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

*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<sub>sat</sub>, 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. <sup>a</sup>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  $\alpha = .05$ ). 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).

| Periods of data recording         | Mortality (%) | Mortality causes <sup>a</sup> | ICEN                  | Data sources  |
|-----------------------------------|---------------|-------------------------------|-----------------------|---|
| Sechura Bay                       |               |                               |                       |   |
| January 6, 2012-February 6, 2012  | 90            | A, RT, TI, MTW                | -0.4 (N)              | ENFEN Comisión<br>(2012); Gonzales<br>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<br>(WEN-MEN) | Sanchez et al. (2015);<br>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,<br>Thouzeau,<br>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)  |

**TABLE 2**Mass mortality events recorded in scallop (Argopecten purpuratus) bottom cultures between the years2012 and 2019 in Sechura and Paracas Bays

<sup>a</sup>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<sub>sat</sub> of 24% and the 5% DO<sub>sat</sub>, 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<sub>sat</sub>, respectively. Severe hypoxia corresponded to DO<sub>sat</sub> 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  $\alpha$  = .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  $30.9 \pm 3.1$  mm SD, shell height) and 80 large (mean  $79.7 \pm 3.6$  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  $16.1 \pm 0.2^{\circ}$ C and  $34.9 \pm 0.1$ , 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  $9.2 \times 10^6$  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- $\mu$ m filtered and thermoregulated (16°C) seawater (1.8 L/hr). DO<sub>sat</sub> 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<sub>sat</sub>. 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<sub>sat</sub>) 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  $\mu$ g (DW, g). The Johnstone (1912) condition index (CI, g/cm<sup>3</sup>) was calculated as CI = 1,000 (soft tissue DW)/(shell height)<sup>3</sup>.

## 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 "surviminer" 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

8



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 ±  $1.9^{\circ}$ 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 temperature 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<sub>sat</sub> 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 salinity 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<sub>sat</sub> on one hand, and between temperature and pH on another hand. In Paracas, there was a strong negative correlation between temperature and DO<sub>sat</sub> 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)

0 1 10

-20

-15



**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<sub>sat</sub>

#### 3.2 | Temperature and hypoxic events versus scallop mass mortalities

-10

Days before mass mortality

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  $20^{\circ}$ 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.  $16^{\circ}$ C) than in Sechura before the mortality events of 2013 and 2015; the higher value was observed in 2017 (T<sup>o</sup> >  $20^{\circ}$ C 3 weeks before the mass mortality), but the lack of data afterward precludes to draw any conclusion.

-5

0

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%  $DO_{sat}$ ),

11

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

|                   |                 |    |       | Sechura       |          |     |       | Paracas       |          |
|-------------------|-----------------|----|-------|---------------|----------|-----|-------|---------------|----------|
| DO <sub>sat</sub> |                 | n  | P (%) | Duration (hr) | Max (hr) | n   | P (%) | Duration (hr) | Max (hr) |
| 5%                | February, 2012  | 7  | 0.7   | 1.0 ± 0.0     | 1        |     |       |               |          |
|                   | March, 2012     | 3  | 0.3   | $1.0 \pm 0.0$ | 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   | $1.0 \pm 0.0$ | 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   | $1.0 \pm 0.0$ | 1        | 7   | 0.3   | $1.0 \pm 0.0$ | 1        |
|                   | February, 2012  |    |       |               |          | 11  | 0.5   | 1.0 ± 0.0     | 1        |
|                   | March, 2012     | 13 | 1.4   | $1.0 \pm 0.0$ | 1        | 1   | 0.1   | 1.0 ± NA      | 1        |
|                   | April, 2012     | 3  | 0.2   | $1.0 \pm 0.0$ | 1        | 1   | 0.1   | 1.0 ± NA      | 1        |

(Continues)

# TABLE 3 (Continued)

|            |                 |    |       | Sechura       |          |     |       | Paracas       |          |
|------------|-----------------|----|-------|---------------|----------|-----|-------|---------------|----------|
| $DO_{sat}$ |                 | n  | P (%) | Duration (hr) | Max (hr) | n   | P (%) | Duration (hr) | Max (hr) |
|            | May, 2012       | 13 | 0.8   | $1.0 \pm 0.0$ | 1        | 1   | 0.1   | 1.0 ± NA      | 1        |
|            | June, 2012      | 13 | 5.1   | $1.0 \pm 0.0$ | 1        |     |       |               |          |
|            | July, 2012      | 11 | 18.0  | $1.0 \pm 0.0$ | 1        |     |       |               |          |
|            | August, 2012    | 10 | 1.6   | $1.0 \pm 0.0$ | 1        |     |       |               |          |
|            | September, 2012 | 6  | 0.8   | $1.0 \pm 0.0$ | 1        | 11  | 1.3   | 2.6 ± 2.7     | 8        |
|            | October, 2012   | 4  | 0.5   | $1.0 \pm 0.0$ | 1        | 59  | 7.9   | 3.1 ± 2.9     | 13       |
|            | November, 2012  | 4  | 0.5   | $1.0 \pm 0.0$ | 1        | 100 | 18.6  | 4.2 ± 4.3     | 19       |
|            | December, 2012  | 4  | 0.5   | $1.0 \pm 0.0$ | 1        | 74  | 18.2  | 5.7 ± 6.8     | 30       |
|            | January, 2013   | 3  | 0.2   | $1.0 \pm 0.0$ | 1        | 56  | 20.2  | 8.2 ± 10.7    | 66       |
|            | February, 2013  | 6  | 0.6   | $1.0 \pm 0.0$ | 1        | 56  | 20.0  | 8.3 ± 8.6     | 39       |
|            | March, 2013     | 8  | 0.8   | $1.0 \pm 0.0$ | 1        | 59  | 13.5  | 3.6 ± 3.3     | 16       |
|            | April, 2013     | 12 | 0.6   | $1.0 \pm 0.0$ | 1        | 1   | 0.1   | 1.0 ± NA      | 1        |
|            | May, 2013       | 4  | 0.2   | $1.0 \pm 0.0$ | 1        | 3   | 0.2   | $1.0 \pm 0.0$ | 1        |
|            | June, 2013      | 5  | 2.0   | $1.0 \pm 0.0$ | 1        | 1   | 0.1   | 1.0 ± NA      | 1        |
|            | July, 2013      | 6  | 9.8   | $1.0 \pm 0.0$ | 1        | 1   | 0.1   | 1.0 ± NA      | 1        |
|            | August, 2013    | 2  | 0.3   | $1.0 \pm 0.0$ | 1        | 4   | 0.2   | $1.0 \pm 0.0$ | 1        |
|            | September, 2013 | 2  | 0.3   | $1.0 \pm 0.0$ | 1        | 1   | 0.0   | 1.0 ± NA      | 1        |
|            | October, 2013   | 4  | 0.5   | $1.0 \pm 0.0$ | 1        | 2   | 0.1   | $1.0 \pm 0.0$ | 1        |
|            | November, 2013  | 4  | 0.5   | $1.0 \pm 0.0$ | 1        | 5   | 0.2   | $1.0 \pm 0.0$ | 1        |
|            | December, 2013  | 12 | 1.4   | $1.0 \pm 0.0$ | 1        | 13  | 0.6   | 1.0 ± 0.0     | 1        |
|            | January, 2014   | 6  | 0.4   | $1.0 \pm 0.0$ | 1        | 11  | 0.5   | $1.0 \pm 0.0$ | 1        |
|            | March, 2014     | 5  | 0.5   | $1.0 \pm 0.0$ | 1        |     |       |               |          |
|            | April, 2014     | 5  | 0.3   | $1.0 \pm 0.0$ | 1        | 9   | 0.6   | $1.0 \pm 0.0$ | 1        |
|            | September, 2014 | 4  | 0.5   | $1.0 \pm 0.0$ | 1        | 12  | 0.8   | $1.0 \pm 0.0$ | 1        |
|            | October, 2014   | 2  | 0.3   | $1.0 \pm 0.0$ | 1        |     |       |               |          |
|            | February, 2015  | 8  | 0.8   | $1.0 \pm 0.0$ | 1        | 1   | 0.0   | 1.0 ± NA      | 1        |
|            | March, 2015     | 9  | 0.9   | $1.0 \pm 0.0$ | 1        | 43  | 19.0  | 6.9 ± 8.2     | 47       |
|            | April, 2015     | 2  | 0.1   | $1.0 \pm 0.0$ | 1        | 87  | 30.0  | 5.3 ± 5.3     | 22       |
|            | May, 2015       | 5  | 0.3   | $1.0 \pm 0.0$ | 1        | 112 | 35.2  | 5.0 ± 4.8     | 32       |
|            | June, 2015      | 2  | 0.8   | $1.0 \pm 0.0$ | 1        | 114 | 30.8  | 4.1 ± 6.5     | 52       |
|            | July, 2015      | 5  | 8.2   | $1.0 \pm 0.0$ | 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   | $1.0 \pm 0.0$ | 1        | 67  | 19    | 6.6 ± 6.7     | 32       |
|            | March, 2016     | 6  | 0.6   | $1.0 \pm 0.0$ | 1        | 39  | 14.9  | 6.0 ± 5.5     | 22       |
|            |                 |    |       |               |          |     |       |               |          |

### TABLE 3 (Continued)

|            |                 |     |       | Sechura       |          |    |       | Paracas       |          |
|------------|-----------------|-----|-------|---------------|----------|----|-------|---------------|----------|
| $DO_{sat}$ |                 | n   | P (%) | Duration (hr) | Max (hr) | n  | P (%) | Duration (hr) | Max (hr) |
|            | April, 2016     | 8   | 0.4   | $1.0 \pm 0.0$ | 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   | $1.0 \pm 0.0$ | 1        | 23 | 5.5   | 3.7 ± 2.6     | 10       |
|            | August, 2016    | 5   | 0.8   | $1.0 \pm 0.0$ | 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   | $1.0 \pm 0.0$ | 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   | $1.0 \pm 0.0$ | 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<sub>sat</sub> 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% Cl), and mortality started from the seventh day. The shortest median lethal time under severe hypoxia (1% DO<sub>sat</sub>) 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<sub>50</sub> was 3.9 ± 0.25 days (95% Cl) for the small-sized group versus 2.7 ± 0.35 days (95% Cl) in the large-sized group. Similarly, Lt<sub>90</sub> 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).



**FIGURE 6** Survival of small- and large-sized groups of *Argopecten purpuratus* at  $1\% \text{ DO}_{sat}$ : (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 & Urguizo, 1972), exhibited higher DO variability and more frequent low-DO<sub>sat</sub> 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<sub>sat</sub>), but different relationships with other environmental variables. In Sechura, lower DO<sub>sat</sub> in bw was positively correlated to lower salinity, which suggests that hypoxia in this bay is probably linked to stratification. In Paracas, low DOsat 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 (≅ 1% DO<sub>sat</sub>), A. purpuratus survival was size-dependent (negative relationship; Figure 6a), which agree with observations for other bivalves such as P. yessoensis (Lt<sub>50</sub> of 4 and 2.6 days for 8.8- and 59.4mm size groups, respectively; Seto et al., 2004), Mulinia lateralis (Lt<sub>50</sub> of 7 and 4 days for 5- and 10-mm size groups, respectively; Shumway et al., 1983), and Perna perna (Lt<sub>50</sub> 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 postspawning 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<sub>50</sub> 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<sub>50</sub> 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-turguoise 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.

#### ACKNOWLEDGMENTS

We thank the IMARPE and especially the staff from the Aquatic Ecophysiology Laboratory, the Phytoplankton laboratory, and the Chemical Oceanography Laboratory. We thank Lucero Achaya for its active help during the experiments and APROPRISCO for allowing us to dive into the Company's aquaculture concession to collect the scallops used in the laboratory experiments. This work is part of a Ph.D. thesis supported by the French National Research Institute for Sustainable Development (IRD-France) within the frameworks of the LMI DISCOH, the PICS BISCOT, and the JEAI DYSRUP. The lead author was supported by a grant from the Franco-Peruvian Doctoral School in Life Sciences.

#### 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.

#### ORCID

Rosa Cueto-Vega D https://orcid.org/0000-0002-4434-7757

#### REFERENCES

- Aguirre-Velarde, A., Jean, F., Thouzeau, G., & Flye-Sainte-Marie, J. (2016). Effects of progressive hypoxia on oxygen uptake in juveniles of the Peruvian scallop, Argopecten purpuratus (Lamarck, 1819). Aquaculture, 451, 385–389. https://doi.org/ 10.1016/j.aquaculture.2015.07.030
- Aguirre-Velarde, A., Jean, F., Thouzeau, G., & Flye-Sainte-Marie, J. (2018). Feeding behavior and growth of the Peruvian scallop (Argopecten purpuratus) under daily cyclic hypoxia conditions. *Journal of Sea Research*, 131, 85–94. https://doi. org/10.1016/j.seares.2017.11.001
- Aguirre-Velarde, A., Pecquerie, L., Jean, F., Thouzeau, G., & Flye-Sainte-Marie, J. (2019). Predicting the energy budget of the scallop Argopecten purpuratus in an oxygen-limiting environment. Journal of Sea Research, 143, 254–261. https://doi. org/10.1016/j.seares.2018.09.011
- Aguirre-Velarde, A., Thouzeau, G., Jean, F., Mendo, J., Cueto-Vega, R., Kawazo-Delgado, M., ... Flye-Sainte-Marie, J. (2019). Chronic and severe hypoxic conditions in Paracas Bay, Pisco, Peru: Consequences on scallop growth, reproduction, and survival. Aquaculture, 512, 734259. https://doi.org/10.1016/j.aquaculture.2019.734259
- Alcazar, J., & Mendo, J. (2008). Crecimiento y supervivencia de juveniles de Argopecten purpuratus en sistemas de fondo y suspendido en la zona de Casma. Perú. *Ecología aplicada*, 7(1-2), 71–80. http://www.scielo.org.pe/scielo.php?pid= S1726-22162008000100010&script=sci\_arttext&tlng=en.
- Altieri, A. H., & Diaz, R. J. (2019). Dead zones: Oxygen depletion in coastal ecosystems. In C. Sheppard (Ed.), World seas: An environmental evaluation. Vol. III: Ecological issues and environmental impacts (pp. 453–473). London: Elsevier Inc., Academic Press.
- Arntz, W. E., Tarazona, J., Gallardo, V. A., Flores, L. A., & Salzwedel, H. (1991). Benthos communities in oxygen deficient shelf and upper slope areas of the Peruvian and Chilean Pacific coast, and changes caused by El Niño. *Geological Society*, 58, 131–154.
- Artigaud, S., Lacroix, C., Pichereau, V., & Flye-Sainte-Marie, J. (2014). Respiratory response to combined heat and hypoxia in the marine bivalves Pecten maximus and Mytilus spp. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology, 175, 135–140. https://doi.org/10.1016/j.cbpa.2014.06.005
- Avendaño, M., Cantillánez, M., & Thouzeau, G. (2017). Evidence of clandestine harvest and failure of conservation policies for Argopecten purpuratus in the Rinconada marine reserve (Chile). Aquatic Conservation: Marine and Freshwater Ecosystems, 27(3), 588–603. https://doi.org/10.1002/aqc.2721
- Babarro, J., & de Zwaan, A. (2002). Influence of abiotic factors on bacterial proliferation and anoxic survival of the sea mussel Mytilus edulis L. Journal of Experimental Marine Biology and Ecology, 273, 33–49. https://doi.org/10.1016/S0022-0981(02)00139-9

20

- Babarro, J. M., & de Zwaan, A. (2008). Anaerobic survival potential of four bivalves from different habitats: A comparative survey. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 151, 108–113. https://doi. org/10.1016/j.cbpa.2008.06.006
- Barber, B. J., & Blake, N. J. (2016). Reproductive physiology. Developments in Aquaculture and Fisheries Science, 40, 253–299. http://doi.org/10.1016/B978-0-444-62710-0.00006-7
- Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20, 1023–1031. http://doi.org/10.1111/ gcb.12514
- Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., ... Vichi, M. (2013). Multiple stressors of ocean ecosystems in the 21st century: Projections with CMIP5 models. *Biogeosciences*, 10, 6225–6245. https://doi.org/10.5194/ bg-10-6225-2013
- Bossier, S. (2015). Performance differences between scallop culture in Peru and Chile: A bio-economical modeling approach. Master thesis, University of Ghent, Belgium, 37 pp. https://mosetip.files.wordpress.com/2015/07/bossier\_thesis.pdf.
- Brokordt, K., Pérez, H., & Campos, F. (2013). Environmental hypoxia reduces the escape response capacity of juvenile and adult scallops Argopecten purpuratus. Journal of Shellfish Research, 32, 369–376. https://doi.org/10.2983/035.032.0216
- Brokordt, K., Pérez, H., Herrera, C., & Gallardo, A. (2015). Reproduction reduces hsp70 expression capacity in Argopecten purpuratus scallops subject to hypoxia and heat stress. Aquatic Biology, 23, 265–274. https://doi.org/10.3354/ab00626
- Chauca Vela, Z. (2018). Caracterización de los eventos de aguas blancas frente a Pisco y Chincha (entre los 13°-15° S). Master Thesis, Universidad Peruana Cayetano Heredia, Lima, 204 pp. http://repositorio.upch.edu.pe/handle/upch/3751.
- Chavez, F. P., Bertrand, A., Guevara-Carrasco, R., Soler, P., & Csirke, J. (2008). The Northern Humboldt Current System: Brief history, present status and a view towards the future. *Progress in Oceanography*, 79, 95–105. https://doi.org/10.1016/j. pocean.2008.10.012
- Cisneros, R., & Argüelles, J. (1996). Cultivo experimental de la concha de abanico a diferentes densidades y profundidades en sistema suspendido. Instituto del Mar del Perú, Callao, Perú, Informe Progresivo N° 22, 16 pp. http://biblioimarpe. imarpe.gob.pe/handle/123456789/903.
- Cok, J. (2017). Revelan gran mortandad de conchas en Paracas. Diario Correo, March 9. Retrieved from https://diariocorreo. pe/edicion/ica/revelan-gran-mortandad-de-conchas-en-paracas-736091.
- Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences, 106(31), 12788–12793. https://doi.org/10.1073/pnas.0902080106
- de Zwaan, A., Cortesi, P., Van den Thillart, G., Roos, J., & Storey, K. B. (1991). Differential sensitivities to hypoxia by two anoxia-tolerant marine molluscs: A biochemical analysis. *Marine Biology*, 111(3), 343–351. https://doi.org/10.1007/ BF01319405
- de Zwaan, A., & Wijsman, T. C. M. (1976). Anaerobic metabolism in bivalvia (Mollusca). Characteristics of anaerobic metabolism. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry, 54(3), 313–323. https://doi.org/10. 1016/0305-0491(76)90247-9
- Diaz, R. J., & Rosenberg, R. (1995). Marine benthic hypoxia: A review of its ecological effect and the behavioural responses of benthic macrofauna. Oceanography and Marine Biology: An Annual Review, 33, 245–303.
- Diaz R. J., & Rosenberg R. (2008). Spreading dead zones and consequences for marine ecosystems. Science, 321(5891), 926–929. http://doi.org/10.1126/science.1156401
- ENFEN Comisión (2012). Comisión Multisectorial del Estudio Nacional del Fenómeno El Niño (http://enfen.gob.pe/), Esquina Gamarra y Gral. Valle S/N Chucuito-Callao. Definición operacional de los eventos el Niño y la Niña y sus magnitudes en la costa del Perú.
- Flores-Valiente, J., Tam, J., Brochier, T., Colas, F., Pecquerie, L., Aguirre-Velarde, A., ... Lett, C. (2019). Larval supply of Peruvian scallop to the marine reserve of Lobos de Tierra Island: A modeling approach. *Journal of Sea Research*, 144, 142–155. https://doi.org/10.1016/j.seares.2018.12.003
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? Trends in Ecology & Evolution, 26, 285–291. https://doi.org/10.1016/j.tree.2011.03.005
- Garreaud, R. D. (2018). A plausible atmospheric trigger for the 2017 coastal el Niño. International Journal of Climatology, 38, e1296–e1302. https://doi.org/10.1002/joc.5426
- Gonzales, I., Jacinto, P., Segura, M., & Macalupu, J. (2012). Mortandad de concha de abanico frente a Vichayo, Barrancos y Parachique (Sechura), 16 febrero. 2012. IMARPE Piura, Technical report.
- Graco, M. I., Purca, S., Dewitte, B., Castro, C. G., Moron, O., Ledesma, J., ... Gutierrez, D. (2017). The OMZ and nutrient features as a signature of interannual and low-frequency variability in the Peruvian upwelling system. *Biogeosciences*, 14, 4601–4617. https://doi.org/10.5194/bg-14-4601-2017
- Grieshaber, M. K., Hardewig, I., Kreutzer, U., & Portner, H. O. (1994). Physiological and metabolic responses to hypoxia in invertebrates. *Reviews of Physiology*, *Biochemistry and Pharmacology*, 125, 43–147. https://doi.org/10.1007/ BFb0030909

- Grieshaber, M. K., Kreutzer, U., & Pörtner, H. O. (1988). Critical PO2 of euryoxic animals. Oxygen sensing in tissues (pp. 37– 48). Berlin, Heidelberg: Springer. https://link.springer.com/book/10.1007%2F978-3-642-83444-8#page=44.
- Gunderson, A. R., Armstrong, E. J., & Stillman, J. H. (2016). Multiple stressors in a changing world: The need for an improved perspective on physiological responses to the dynamic marine environment. *Annual Review of Marine Science*, 8, 357– 378. https://doi.org/10.1146/annurev-marine-122414-033953
- Gurr, S. J., Goleski, J., Lima, F. P., Seabra, R., Gobler, C. J., & Volkenborn, N. (2018). Cardiac responses of the bay scallop Argopecten irradians to diel-cycling hypoxia. Journal of Experimental Marine Biology and Ecology, 500, 18–29. https://doi. org/10.1016/j.jembe.2017.12.011
- Gutiérrez, D., Bouloubassis, I., Sifeddine, A., Purca, S., Goubanova, K., Graco, M., ... Ortlieb, L. (2011). Coastal cooling and increased productivity in the main upwelling zone off Peru since the mid-twentieth century. *Geophysical Research Let*ters, 38, L07603. https://doi.org/10.1029/2010GL046324
- Hermes-Lima, M., Storey, J. M., & Storey, K. B. (1998). Antioxidant defenses and metabolic depression. The hypothesis of preparation for oxidative stress in land snails. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 120(3), 437–448. https://doi.org/10.1016/s0305-0491(98)10053-6
- Hicks, D. W., & McMahon, R. F. (2005). Effects of temperature on chronic hypoxia tolerance in the non-indigenous brown mussel, *Perna perna* (Bivalvia: Mytilidae) from the Texas Gulf of Mexico. *Journal of Molluscan Studies*, 71(4), 401–408. https://doi.org/10.1093/mollus/eyi042
- Hochachka, P. (1997). Oxygen, a key regulatory metabolite in metabolic defense against hypoxia. American Zoologist, 37, 595–603.
- IMARPE (2012). Condiciones oceanográficas anómalas y su relación con la mortandad de concha de abanico Argopecten purpuratus en la Bahía de Paracas durante abril y mayo del 2012. Instituto del Mar del Perú. Callao, Perú. Technical report.
- IMARPE. (2015). Anuario Científico Tecnológico IMARPE (Vol. 15). Callao: Instituto del Mar del Perú.
- IMARPE. (2019). Mortandad de concha de abanico Argopecten purpuratus y varazón de peces en Bahía de Sechura. Press release. Callao: Instituto del Mar del Perú. http://www.imarpe.gob.pe/imarpe/archivos/noticia/imarpe\_notic\_nota\_ varazon\_sechura.pdf
- Johnstone, J. (1912). Report on measurements of the plaice made during the year 1910. Transactions of the Liverpool Biological Society, 26, 85–102.
- Kaplan, E. L., & Meier, P. (1958). Nonparametric estimation from incomplete observations. Journal of the American Statistical Association, 53, 457–481.
- Kluger, L. C., Kochalski, S., Aguirre-Velarde, A., Vivar, I., & Wolff, M. (2018). Coping with abrupt environmental change: The impact of the coastal el Niño 2017 on artisanal fisheries and mariculture in North Peru. ICES Journal of Marine Science, 76, 1122–1130. https://doi.org/10.1093/icesjms/fsy171
- Kluger, L. C., Taylor, M. H., Wolff, M., Stotz, W., & Mendo, J. (2019). From an open-access fishery to a regulated aquaculture business: The case of the most important Latin American bay scallop (*Argopecten purpuratus*). *Reviews in Aquaculture*, 11, 187–203. https://doi.org/10.1111/raq.12234
- Kraffe, E., Tremblay, R., Belvin, S., LeCoz, J., Marty, Y., & Guderley, H. (2008). Effect of reproduction on escape responses, metabolic rates and muscle mitochondrial properties in the scallop *Placopecten magellanicus*. *Marine Biology*, 156, 25–38. https://doi.org/10.1007/s00227-008-1062-4
- Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multivariate analysis. Journal of Statistical Software, 25 (1), 1–18. https://doi.org/10.18637/jss.v025.i01
- Levin, L., Ekau, W., Gooday, A., Jorissen, F., Middelburg, J., Naqvi, S., ... Zhang, J. (2009). Effects of natural and humaninduced hypoxia on coastal benthos. *Biogeosciences*, 6, 2063–2098. https://doi.org/10.5194/bg-6-2063-2009
- Llansó, R. J. (1991). Tolerance of low dissolved oxygen and hydrogen sulfide by the polychaete Streblospio benedicti (Webster). Journal of Experimental Marine Biology and Ecology, 153, 165–178. https://doi.org/10.1016/0022-0981(91) 90223-J
- Llansó, R. J. (1992). Effects of hypoxia on estuarine benthos: The lower Rappahannock River (Chesapeake Bay), a case study. Estuarine Coastal Shelf Science, 35, 491–515. https://doi.org/10.1016/S0272-7714(05)80027-7
- Mackay, J., & Shumway, S. E. (1980). Factors affecting oxygen consumption in the scallop Chlamys delicatula (hutton). Ophelia, 19, 19–26. https://doi.org/10.1080/00785326.1980.10425503
- Mantel, N. (1966). Evaluation of survival data and two new rank order statistics arising in its consideration. Cancer Chemotherapy Reports, 50(3), 163–170.
- Mendo, J., Cosavalente, C., Tam, J., & Bandin, R. (2002). Growth and survival of the Peruvian scallop Argopecten purpuratus in suspended cultures in Independencia Bay (Pisco, Perú). In J. Mendo & M. Wolff (Eds.), Memorias de la I Jornada Científica de la Reserva Nacional de Paracas, Pisco, 28–31 Marzo del 2001. Lima: Universidad Nacional Agraria La Molina.
- Mendo, J., & Wolff, M. (2003). El impacto de El Niño sobre la producción de concha de abanico (Argopecten purpuratus) en Bahía Independencia, Pisco, Perú. Ecologia Aplicada, 2, 51–57.

- Mendo, J., Wolff, M., Carbajal, W., Gonzales, I., & Badjeck, M. (2008). Manejo y explotación de los principales bancos naturales de concha de abanico (Argopecten purpuratus) en la costa peruana. In A. Lovatelli, A. Farías, & I. Uriarte (Eds.), Estado actual del cultivo y manejo de moluscos bivalvos y su proyección futura: factores que afectan su sustentabilidad en América Latina. Taller Técnico Regional de la FAO. 20–24 de agosto de 2007, Puerto Montt, Chile. FAO Actas de Pesca y Acuicultura, No. 12 (pp. 101–114). Roma: FAO.
- Mendo, J., Wolff, M., Mendo, T., & Ysla, L. (2016). Scallop fishery and culture in Peru. In S. Shumway & G. J. Parsons (Eds.), Scallops: biology, ecology, aquaculture, and fisheries (Vol. 40, 3rd ed., pp. 1089–1109). London: Elsevier. Developments in Aquaculture and Fisheries Science. https://doi.org/10.1016/B978-0-444-62710-0.00028-6
- Morales, F. (2017). Vigilantes de la bahía: el caso APROPISCO. Master thesis. Universidad de Piura, Programa de Alta Dirección, Lima, Perú.
- Nilsson, G. E., & Ostlund-Nilsson, S. (2008). Does size matter for hypoxia tolerance in fish? *Biological Reviews*, 83, 173–189. https://doi.org/10.1111/j.1469-185X.2008.00038.x
- Ohde, T. (2018). Coastal sulfur plumes off Peru during El Niño, La Niña, and neutral phases. Geophysical Research Letters, 45, 7075–7083. https://doi.org/10.1029/2018GL077618
- Qiu, J. W., Tremblay, R., & Bourget, E. (2002). Ontogenetic changes in hyposaline tolerance in the mussels Mytilus edulis and M. trossulus: Implications for distribution. Marine Ecology Progress Series, 228, 143–152.
- R Core Team. (2018). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Ramajo, L., Fernandez, C., Nuñez, Y., Caballero, P., Lardies, M. A., & Poupin, M. J. (2019). Physiological responses of juvenile Chilean scallops (Argopecten purpuratus) to isolated and combined environmental drivers of coastal upwelling. ICES Journal of Marine Science, 76(6), 1836–1849. https://doi.org/10.1093/icesjms/fsz080
- Robb, T., & Abrahams, M. (2003). Variation in tolerance to hypoxia in a predator and prey species: An ecological advantage of being small? *Journal of Fish Biology*, 62, 1067–1081. https://doi.org/10.1046/j.1095-8649.2003.00097.x
- Sakurai, I., Seto, M., Makiguchi, N., & Ogata, T. (2000). Tolerance of the Japanese scallop, Patinopecten yessoensis, to low concentrations of dissolved oxygen and salinity. Aquaculture Science, 48, 137–138.
- Salas, F., Solari, G., & Mejia, D. (2014). Flooding in Piura River basin. Retrieved from http://www.ttdatavis.onthinktanks.org/ 2014-15-competition-entries/flooding-in-piura-river-basin-1.
- Sanchez, S., Delgado, E., Bances, S., Quintana, P., & Huamani, A. (2015). Floraciones algales en aguas costeras del mar peruano Paita-Ilo (Enero-Marzo 2015). Callao, Perú: Informe Instituto del Mar del Perú.
- Seto, M., Kaneko, K., & Nii, H. (2004). Influence of anoxic water on japanese scallop survival rate of lake Notoro. In Proceedings of Civil Engineering in the Ocean, Japan Society of Civil Engineers. pp. 1049–1054.
- Shumway, S. E., Scott, T. M., & Shick, J. M. (1983). The effects of anoxia and hydrogen sulphide on survival, activity and metabolic rate in the coot clam, Mulinia lateralis (say). Journal of Experimental Marine Biology and Ecology, 71, 135–146.
- Takahashi, K. (2004). The atmospheric circulation associated with extreme rainfall events in Piura, Peru, during the 1997-1998 and 2002 El Niño events. Annales Geophysicae, 22, 3917–3926. https://doi.org/10.5194/angeo-22-3917-2004
- Takahashi, K., Mosquera Vazquez, K. A., & Reupo Velez, J. A. (2014). El índice costero el Niño (ICEN): historia y actualización. Instituto Geofísico del Perú (Ed.), Lima. Boletín Técnico: Generación de Modelos Climáticos Para el Pronóstico de la Ocurrencia del Fenómeno El Niño, 1, 8–9.
- Takahashi, K., Peña, M., Sulca, J., Mosquera, K., Reupo, J., & Segura, B. (2017). Generación de información y monitoreo del fenómeno el Niño. Instituto Geofísico del Perú (Ed.), Lima. Boletín Técnico, 4(6), 1–15.
- Tarazona, J., Salzwedel, H., & Arntz, W. (1988). Positive effects of "El Niño" on macrozoobenthos inhabiting hypoxic areas of the Peruvian upwelling system. Oecologia, 76, 184–190.
- Therneau, T. M., & Grambsch, P. M. (2013). Modeling survival data: Extending the cox model. In *Statistics for biology and health series*. New York: Springer-Verlag.
- Urban, H. J. (1994). Upper temperature tolerance of ten bivalve species off Peru and Chile related to El Niño. Marine Ecology Progress Series, 107, 139–145.
- Vaquer-Sunyer, R., & Duarte, C. M. (2010). Sulfide exposure accelerates hypoxia-driven mortality. *Limnology Oceanography*, 55(3), 1075–1082. https://doi.org/10.4319/lo.2010.55.3.1075
- Wang, W. X., & Widdows, J. (1991). Physiological responses of mussel larvae Mytilus edulis to environmental hypoxia and anoxia. Marine Ecology Progress Series, 70, 223–236. https://doi.org/10.3354/meps070223
- Wolff, M. (1987). Population dynamics of the Peruvian scallop Argopecten purpuratus during the el Niño phenomenon of 1983. Canadian Journal of Fisheries and Aquatic Sciences, 44(10), 1684–1691. https://doi.org/10.1139/f87-207
- Yamada, K., Miyamoto, Y., Nakano, T., & Okamura, K. (2016). Inter-and intraspecific variation in anoxic survival among three bivalve species in intertidal and subtidal areas along the coast of Japan. *Plankton and Benthos Research*, 11(2), 49–56. https://doi.org/10.3800/pbr.11.49
- Yamashiro, C., Rubio, J., Taipe, A., & Aguilar, S. (2002). Fluctuaciones de la población de concha de abanico Argopecten purpuratus (lamarck, 1819) en la Bahía Independencia (Pisco, Perú) durante el periodo 1984-2000. In J. Mendo & M.

Wolff (Eds.), Memorias de la I Jornada Científica de la Reserva Nacional de Paracas, Pisco, 28–31 Marzo del 2001 (pp. 77– 87). Lima: Universidad Nacional Agraria La Molina.

Zuta, S., & Urquizo, W. (1972). Temperatura promedio de la superficie del mar frente a la costa peruana, periodo 1928-1969. Boletín IMARPE, 2(8), 459–520.

How to cite this article: Cueto-Vega R, Flye-Sainte-Marie J, Aguirre-Velarde A, Jean F, Gil-Kodaka P, Thouzeau G. Size-based survival of cultured *Argopecten purpuratus* (L, 1819) under severe hypoxia. *J World Aquac Soc.* 2021;1–23. https://doi.org/10.1111/jwas.12777