Inter-Research Science Publisher

Marine Ecology Progress Series
Volume 755:79–93

Published February 27, 2025
https://doi.org/10.3354/meps14797

Maternal investment of kelp crabs from central Chile is associated with the level of environmental fluctuations and predictability

Francisca Fernández[1], Fabián Guzmán-Rivas[2,6], Ángel Urzúa[2], Mauricio F. Landaeta[3,4], Marco Fusi[4,5], Simone Baldanzi[1,4,*]

[1]Laboratorio de Ecofisiología y Ecología Evolutiva (e°CO2lab), Facultad de Ciencias Instituto de Biología, Universidad de Valparaíso, 2340000 Valparaíso, Chile
[2]Departamento de Ecología, Facultad de Ciencias y Centro de Investigación en Biodiversidad y Ambientes Sustentables (CIBAS), Universidad Católica de la Santísima Concepción, 4030000 Concepción, Chile
[3]Laboratorio de Ictiología e Interacciones Biofísicas (LABITI), Instituto de Biología, Facultad de Ciencias, Universidad de Valparaíso, 2340000 Valparaíso, Chile
[4]Centro de Observación y Análisis del Ambiente Costero (COSTA-R), Universidad de Valparaíso, 2340000 Valparaíso, Chile
[5]The Dove Marine Laboratory, School of Natural and Environmental Sciences, Newcastle University, Newcastle NE1 7RU, UK

[6]*Present address*: Programa de Doctorado en Ciencias con mención en Biodiversidad y Biorecursos, Universidad Católica de la Santísima Concepción, 4030000 Concepción, Chile

ABSTRACT: Environmental fluctuation dictates life cycles in many ecosystems on earth, especially within marine coastal areas. The magnitude of those fluctuations at ecologically relevant time scales (i.e. hours and days) induces phenotypical adjustment in aquatic organisms, including maternal investment in offspring. However, the effect of the magnitude and the periodicity of those fluctuations on animal physiology has been poorly investigated. In this study, we investigated the correlation between environmental fluctuation and maternal investment in offspring. We focused on one population of the kelp crab *Taliepus dentatus* from central Chile and considered whether fluctuations in water temperature, dissolved oxygen and salinity are associated with temporal changes in maternal investment in early embryos (volume, lipid content and fatty acid composition) over a period of 1 yr. We used remote data loggers deployed at an ecologically relevant temporal scale to calculate the monthly magnitude, periodicity and predictability of environmental fluctuations. We found substantial variation among females in embryo volume, lipid content and fatty acid composition during the year, mostly associated with seasonality (average environmental conditions). However, embryo lipid content and essential fatty acids (arachidonic acid, docosahexaenoic acid, eicosapentaenoic acid) showed a clear negative relation with the monthly predictability of the environmental fluctuations. This study shows how the integration of environmental fluctuations and their predictability can improve our understanding of the reproductive ecology of marine coastal species.

KEY WORDS: Environmental variability · Predictability · Temperature · Dissolved oxygen · Salinity · Maternal investment · Climate change

1. INTRODUCTION

Coastal areas harbour dynamic ecosystems where environmental fluctuations (e.g. temperature, pH, salinity, dissolved oxygen [DO]) shape the diversity of species, the assembly of the communities and the functioning of entire ecosystems (Boero 1994). Environmental fluctuations can be observed at different time scales which are relevant to individuals and populations as they can influence/change physiological

---

*Corresponding author: simone.baldanzi@uv.cl

tolerance and promote plasticity (Rilov et al. 2019, Bitter et al. 2021, Fusi et al. 2022). For example, short-term (i.e. diurnal) variability in temperature and light availability determines rates of photosynthesis and respiration of aquatic primary producers and consumers that are mainly detected at molecular or individual levels, but with important repercussions in populations and communities (Kroeker et al. 2020). The biological response of individuals to short-term fluctuations is fundamental, as it can affect the biological responses that emerge at greater temporal scales. Thus, adopting precise methods of investigation that consider ecologically relevant fluctuations, and the related variability, can explain the response of marine populations and communities to environmental drivers and can help us to foresee how species will adapt to changes imposed by global warming.

An organism's perception of environmental variability through time defines its capacity to predict near-future conditions (Kroeker et al. 2020). More precisely, predictability emerges when environmental variables are temporally autocorrelated, reflecting the increased likelihood for individuals to anticipate and adjust to the near future (physiologically bearable) conditions (Helmuth et al. 2006, Bernhardt et al. 2020, Bitter et al. 2021). In the context of evolution of maternal effects (MEs, an important eco-evolutionary trait), constant environments will reduce the phenotypic variance (canalization) in future generations, whereas in fluctuating environments, MEs evolve according to the autocorrelation between maternal and offspring environments, with positive or negative MEs triggered by the high or low predictability of the environmental fluctuation, respectively (Kuijper & Hoyle 2015). Importantly, many benthic species have evolved energy-saving mechanisms to cope with predictable environmental variability at different time scales. Many examples come from seasonal variability in the environment (e.g. dormancy or quiescence of many ectotherms in polar and cold temperate ecosystems; see Clarke 1988). On shorter temporal scales, many marine species can also depress their metabolism when exposed to extreme, warm temperatures (i.e. aestivation or temperature-insensitive metabolism; Marshall & McQuaid 2011). This mechanism is very efficient to overcome processes that might make ectotherms more vulnerable to thermal stress (e.g. movement), by reducing their energetic demands.

An important phenomenon associated with MEs is the maternal investment (MI), defined as the expenditure of energy, time and nutrients that females spend for the correct development of their offspring, thereby increasing reproductive success (Trivers 1972). MI is influenced by fluctuations in the physical environment (e.g. water temperature, DO and salinity) and resources (e.g. food sources) since mothers must adjust their investment strategies to respond in the most appropriate way to prevailing environmental conditions (Melbinger & Vergassola 2015) by being able to predict the immediate future conditions for their offspring (Gulyas & Powell 2019). Proxies of MI, such as egg number (i.e. fecundity), size, bioenergetics (e.g. lipid content), brood protection, oxygenation and grooming have been largely used to understand how the average environment affects the population reproductive ecology of coastal marine species (Lardies & Castilla 2001, Hernáez & Palma 2003, Baldanzi et al. 2018, Fernández et al. 2020, Fields et al. 2020). For example, average values of water temperature have a well-documented negative correlation with egg size and lipid content in many marine taxa (Wehrtmann & Graeve 1998, Laptikhovsky 2006, Bascur et al. 2017), while oxygen availability and salinity were associated with embryo oxygenation and female parental care (Fernández et al. 2020) as well as with egg size (due to osmoregulation processes) and lipid metabolism (Giménez & Anger 2001). Nonetheless, there is a lack of understanding of the role of fluctuating environments, such as diel changes in temperature and oxygen and the predictability of such fluctuations, on traits associated with MI (e.g. egg size and biochemical composition) in marine coastal invertebrates. Furthermore, in coastal areas affected by upwelling events and riverine inputs, fluctuations in temperature and DO are associated with changes in nutrient inputs (Tapia et al. 2009, Aparicio-Rizzo & Masotti 2019, Aparicio-Rizzo et al. 2020), potentially affecting the food sources available and adding a certain degree of complexity when investigating the effects of environment on MI traits. Few studies have tested the correlation between environmental predictability and species from subtidal ecosystems (e.g. Kroeker et al. 2020, Gill et al. 2022), and to our knowledge, no studies have investigated environmental predictability in association with population-level reproductive traits in marine coastal species and the potential energy-saving mechanisms to cope with predictable environmental variability.

To investigate the correlation between environmental fluctuations (and their predictability) and MI, we used the Chilean kelp crab *Taliepus dentatus* (H. Milne Edwards, 1834), which thrives from 11.9° S to Chilean Patagonia (51.0° S), experiencing widely different local environmental conditions (e.g. temperature; Baldanzi et al. 2020). Female *T. dentatus* are known for their capacity to modulate their MI in different ecological conditions (Baldanzi et al. 2018, 2020). Here we expected that females' MI in early embryos changes according to different levels of environmental fluctuations and their predictability experienced throughout a year. To explore this correlation, we collected ovigerous females to measure the MI (embryo size, lipid content and fatty acid [FA] composition) on a monthly basis for 11 mo and correlated the MI with a high-resolution time series of DO, salinity and temperature (mean, daily variance and its predictability) extracted from *in situ* environmental logging.

2. MATERIALS AND METHODS

2.1. Study area

The study was performed in the shallow rocky subtidal area at Montemar, situated on the northern side of the Valparaiso Bay in central Chile (32.96° S, 71.55° W; Fig. 1). The sampling area is characterised by dense patches of the brown macroalgae *Lessonia spicata* and *L. trabeculata* that provide habitat to many invertebrate and vertebrate species, including crustaceans, gastropods, echinoderms, fishes, sea otters and sea lions (Vásquez & Buschmann 1997, Fariña et al. 2008). The area is characterised by a low upwelling intensity (i.e. upwelling shadow), intermediate productivity and semi-protected oceanographic conditions (Montecinos & Balbontín 1993, Aparicio-Rizzo et al. 2020).

2.2. *In situ* environmental characterisation of the study area

To characterise the environmental conditions that animals experienced in their habitat during the study period, we installed *in situ* data loggers at ecologically relevant depths (max. 2 m) to measure water temperature (T), DO and salinity (S). An optical sensor (miniDOT, PME Electronics) measured DO concentration and T every 10 min, while a mini CTD sensor (WiSens, NKE Instrumentation) measured water conductivity every 5 min. Conductivity was then converted to salinity values applying the conventional Gibbs formula using the software provided.

2.3. Sampling procedures, female morphometrics and embryo size

Females (n = 10–20) were collected monthly from June 2021 to April 2022 (spanning 4 seasons) by free-diving to a depth of 2–3 m. Given the temporal resolution of this sampling design, we opted for a non-invasive method involving a capturing, marking, and releasing of females in their environment to avoid unnecessary impact on local population density. Specifically, collected females were marked with 1 cm^2 fluorescent polyethylene tape (3M 483) which was attached to the upper part of the carapace and then sealed using ethyl cyanoacrylate instant glue (La Gotita®, Fenedur). After embryo collection (see below), females were released in their habitat. The marking allowed us to avoid repeated sampling of the same individual female during the monthly surveys.

Collected females were transported to the laboratory (maximum distance 50 m) using cooler bags filled with seawater from the site of collection. Following procedures from Baldanzi et al. (2018), each female was sized, measuring both carapace width and length using a precision calliper (Toolmak®, precision to the nearest 0.01 mm). For each female, 3 subsamples of about 0.05 g of embryo wet weight (roughly 100 embryos each) were randomly

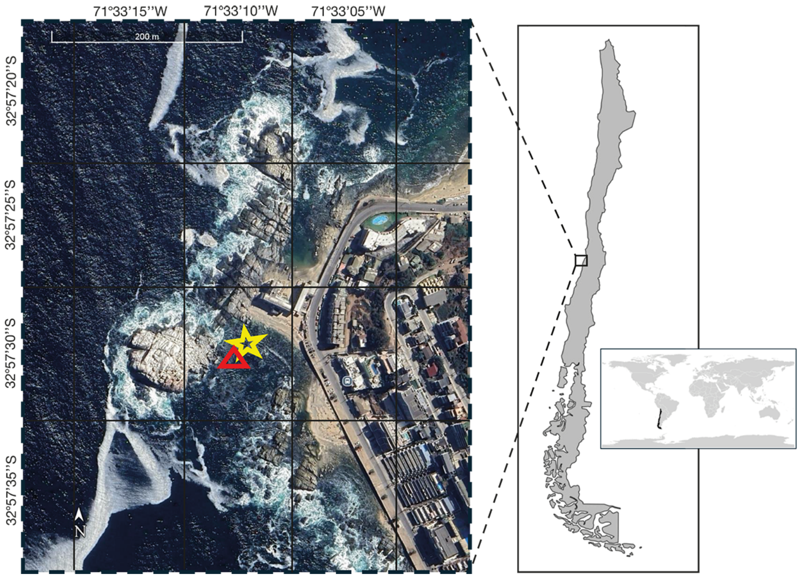

Fig. 1. Study area in Valparaíso, Chile. Left panel shows a high-resolution satellite image of the area, highlighting 2 key locations: (1) the sampling site (yellow star); (2) the location of miniDOT and WiSens sensors (red triangle)

extracted from the embryo mass to measure their size using image analysis (Baldanzi et al. 2018). Only early-staged embryos (with homogeneous yolk, as defined by Vargas 1995) were collected to examine the initial MI (before the losses during development; Parichy & Kaplan 1992, Lorioux et al. 2012) and to avoid multiple stages of embryos. Briefly, embryos were placed in a Petri dish filled with 1 µm- and UV-prefiltered seawater and separated from one another using a fine needle to facilitate handling and photographing. Using a USB portable digital microscope (model TL005, Tecnolab®) we photographed each subsample to obtain the area of each egg. From the area, we derived the volume of each embryo by using the formula of a sphere:

$$V = \frac{3}{4}\pi r^3 \qquad (1)$$

where V is the volume, r is the radius calculated from the area, and π is equal to 3.14. The average embryo volume per female is given in mm^3.

2.4. Embryo dry weight, lipid content and FA composition of embryos

For each female, 200 embryos were randomly extracted from the embryo mass and stored at −80°C for further processing. To calculate embryo dry weight (EDW), samples were freeze-dried in a lyophilizer (Operon FDU-7012) for 48 h and then weighed using an analytical balance (Sartorius LA230s) to the nearest 0.0001 g. EDW was then expressed in µg.

For lipid extraction, the standard method developed by Folch et al. (1957) was slightly adapted to our samples following Cequier-Sánchez et al. (2008) and Baldanzi et al. (2018). Lyophilized samples were placed in a 15 ml tube to which 5 ml of dichloromethane–methanol (2:1) solution was added to extract lipids. Tubes were then placed in an ultrasonic bath for about 60 min at 20–25°C until embryo tissue had completely broken with the addition of potassium chloride (4 ml; 0.88%). Sonicated samples were centrifuged for 5 min at 1500 rpm (250 × *g*) for lipid deposition. The lipid-rich, lower phase was then removed, placed in a pre-weighed flask to evaporate the solution with a sample concentrator (109A YH-1, Glas-Col) and weighed using an analytical balance (Sartorius LA230s) to the nearest 0.0001 g to determine total lipid content (µg). Lipid content per embryo was estimated by dividing the total lipid content by 200. The proportion of lipids to the total EDW was also calculated and given as a percentage.

Lipid extracts were used to determine FA composition following procedures from Cequier-Sánchez et al. (2008) and subsequent modifications of Urzúa & Anger (2013). Extracts were resolved using 5 ml of dichloromethane–methanol solution (2:1), and 2 ml of 1% sulfuric acid were added to 1 ml of the resolved solution to allow for the esterification of FAs. Tubes were then shaken for 3 h at 70°C using a thermo-shaker (model MRC DBS-001), washed 3 times with hexane and vortexed. Two phases formed, and the higher layer was extracted, placed in a 2 ml amber glass vial suitable for gas chromatography and evaporated using a gentle stream of nitrogen. To obtain FAs present in the sample (from 200 embryos), a gas chromatograph (Agilent 7890A) equipped with an autosampler was used. The samples were analysed with a GC DB-225ms column (30 m long, 0.25 mm in diameter, 0.25 µm fill). FAs are expressed as µg egg^{-1} by dividing the total FA mass by the total number of embryos (200).

2.5. Statistical analysis

2.5.1. Daily means, variability and predictability of environmental data

The time series retrieved from data loggers were analysed to provide ecologically relevant proxies of how individuals may perceive, respond to and integrate environmental fluctuations (see Burgess & Marshall 2014, Bernhardt et al. 2020). Time series of T, DO and S were first checked for any gaps in the data. Minor gaps were interpolated or filled with observations from nearby days as required by the statistical methodology using a generalized additive model (for further methodology, see Dierschke et al. 2022).

Mean daily values of T, DO and S were calculated from the data set and plotted against time to visualise daily temporal changes in the environmental conditions. The daily variability was calculated as the variance around the mean daily values for each of the 3 environmental variables.

To create an index of predictability, we first performed wavelet analysis to identify the dominant periodicities in the time series of T, DO and S and determine whether they were taking place as regular, periodic oscillations or were only found in certain moments or periods, for example as isolated or intermittent bursts. To compute the continuous wavelet power spectrum (Maraun & Kurths 2004), each time series was percentile transformed and analysed using the Morlet wavelet. Significance levels were assessed against a null hypothesis of red noise. The analysis was limited to the longest period of each time series. Calculations were performed using the R software (version 4.3.1, R Core Team 2023) and the package 'WaveletComp' (Roesch & Schmidbauer 2018). The method of the wavelet analysis allowed us to determine the relative contribution of variability at each period or frequency to the total variation observed in each T, DO and S time series. In simpler terms, this analysis tests for the cyclical periodicity of the environmental variables (environmental parameters in our case) and the correlation of these periodicities. Since results of the wavelet analysis showed significant fluctuations in T, DO and S at a daily scale (see Results), for each day (144 measures d^{-1}) and variable (T, DO and S), we applied a sine−cosine (sin-cos) model (Shumway & Stoffer 2017) to capture the harmonic daily fluctuation of the environmental variable, and we calculated the coefficient of the sin, cos and the relative R^2. We applied the sin-cos model on DO, T and S data retrieved 15 d earlier than the date of animal collection. Since (1) the embryo developmental time of *T. dentatus* at 14°C lasts about 36 d (Baldanzi et al. 2020) and (2) early stages last about 10 d (S. Baldanzi unpubl. data), 15 d is a reasonable time lag to test for the association between the predictability of the daily fluctuation during reproduction and/or embryo deposition and the near-future MI on early embryos (see details in Section 2.5.3). We used analysis of the residual capture with R^2 to assess the fit of the harmonic model. If the R^2 was high, meaning that observed daily fluctuation followed or tended toward an expected harmonic oscillation, the daily predictability was high. If the R^2 was low, meaning that observed daily fluctuation deviated from an expected harmonic oscillation, a non-daily (unpredictable) variation of the variable was occurring. We then averaged the R^2 for month and year (Table S1 in the Supplement at www.int-res.com/articles/suppl/m755p079_supp.pdf) and this average was used as a predictor for the biological response measured for the crabs.

2.5.2. Temporal variation in embryo volume, lipid content, EDW and FAs

To test for differences among months in the embryo volume, lipid content and EDW, we performed generalized linear models (GLMs) using month as a categorical explicatory variable with a fixed term. For the embryo volume, we applied a gamma family distribution of the error with a negative inverse link function, as data were not normally distributed, while for lipid content and EDW, we applied a Gaussian family distribution of the error with an identical link function, as data were normally distributed. To further explore the temporal trend of embryo volume, lipid content and EDW, we performed general additive models (GAMs) using days from first sampling (elapsed time) as a continuous explanatory variable.

To test for the temporal variation in FAs, we performed a permutational multivariate analysis on the Bray-Curtis dissimilarity matrix of the FA data using 999 permutations of the raw data. To graphically visualise the decomposition of principal coordinates of the Bray-Curtis dissimilarity matrix of the FA data, we performed a principal coordinates analysis (PCoA). Comparisons in the FA contribution among seasons were also made using permutational multivariate analysis of variance (PERMANOVA) and SIMPER analysis. GLMs, PERMANOVA, PCoA and SIMPER were performed using the R packages 'stats' (Wickham & Bryan 2023), 'vegan' (Oksanen et al. 2007), and 'ape' (Paradis & Schliep 2019) from the R environment, respectively.

2.5.3. Relationships between environmental and biological data

Relationships between the mean, variance and predictability of T, DO and S and embryo volume, lipid content and dry weight were concurrently evaluated for additive effects by performing linear regression models in R. We then selected the best model explaining the MI traits based on the higher level of variance explained among the significant ones. To test for the overall effects of the mean, variance and daily predictability of environmental variables (T, DO and S) on FA composition, we performed a multivariate GLM (manyGLM) using the R package 'mvabund' (Wang et al. 2022), followed by single GLMs for each FA to test which produced the most significant change with the change in the mean, variance and predictability of the environmental variable considered (T, DO and S). A p-value with a false discovery rate correction was applied for multiple testing. A heatmap was produced to graphically visualise significant results of the single GLMs using the package 'ggplot2' (Wickham 2016) in the R environment. Prior to running the model presented above, we checked the explanatory variables (mean, variance and predictability of the 3 environmental variables analysed, i.e. DO, T and S) for collinearity using variance inflation factor (VIF) analysis (see Figs. S3 & S4) using the R package 'car' (Fox et al. 2019). No significant collinearity was detected among the explanatory variables considered that could have inflated the tested model.

3. RESULTS

3.1. *In situ* environmental characterisation of the study area

The T time series showed greater variability (i.e. variance) during the austral Autumn 2021 (March to June) and during Summer 2022 (December to February) (Fig. 2A; Table S1) compared to winter months. DO concentrations showed low variability during Spring and Winter 2021 (except for August), while during Spring 2021 and Summer 2021–2022, variability of DO was higher (Fig. 2C; Table S1). The time series of S showed fairly constant values from March to October 2021, with some sporadic events of low S during April 2021 (Fig. 2E; Table S1). Daily mean values of S showed a marked decrease from October to December 2021 (Fig. 2E; Table S1) and a maximum variability (variance = 15.46) during April 2021 (Table S1).

Wavelet analysis showed a significant dominant periodicity at a diurnal scale for T and DO concentrations (Fig. 2B,D) from October 2021 to April 2022, while no signal of daily periodicity was detected during winter months. S did not show any significant dominant periodicity in its time series (Fig. 2F). The daily predictability of T showed high values during the sampling period (R^2 always >0.4) with maximum predictability in February 2022 ($R^2 = 0.91$) (Table S1). The daily predictability of DO concentrations showed a steady increase in R^2 from December 2021 to February 2022 (Table S1). The daily predictability of S

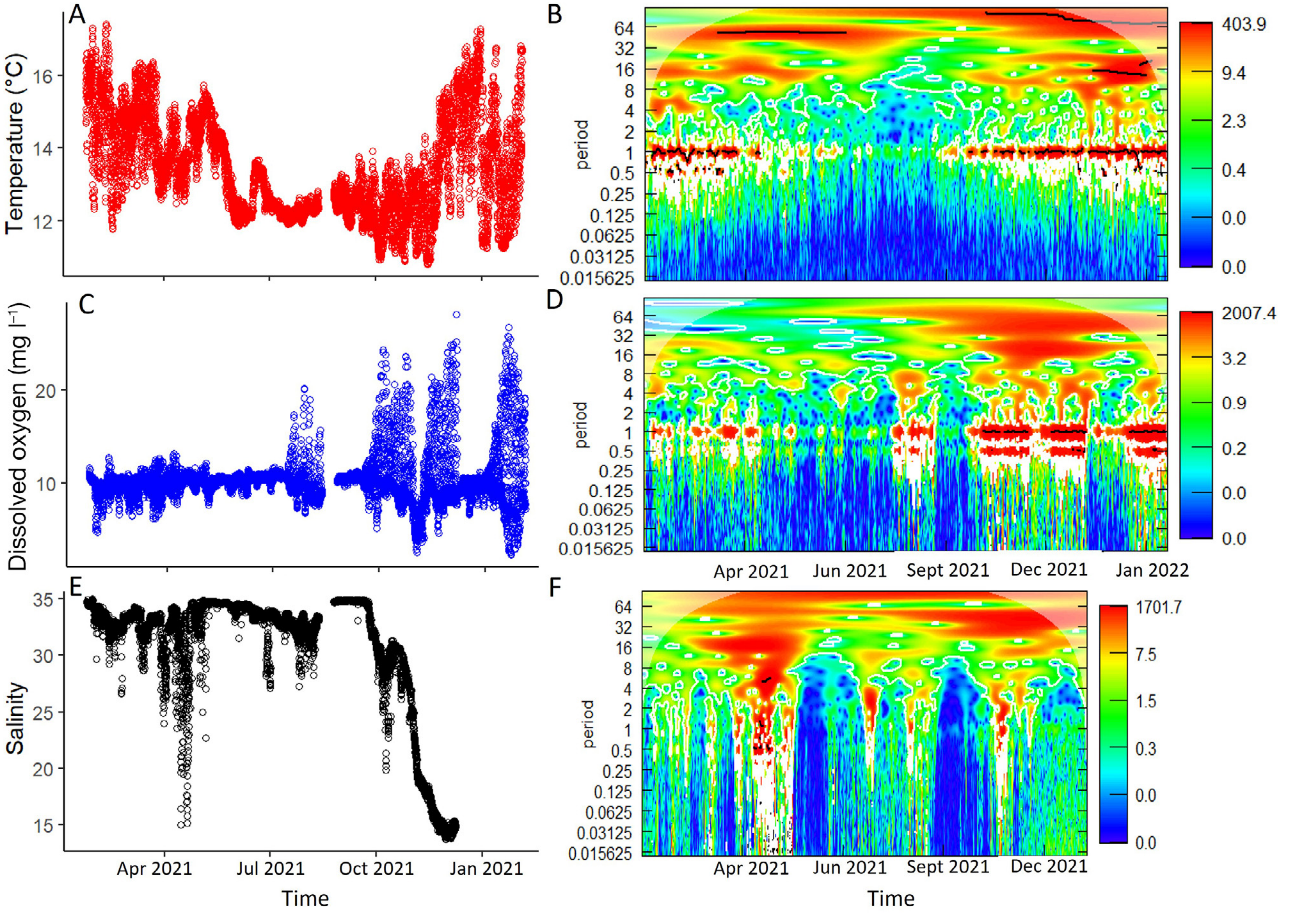

Fig. 2. Time series and wavelet analysis of environmental data of the study area retrieved by *in situ* data logging. Time series of (A) temperature, (C) dissolved oxygen (DO) and (E) salinity, given as hourly data. For each time series, a wavelet transformation of detrended (B) temperature, (D) DO and (F) salinity is given. The *x*-axis represents time (in days), while the *y*-axis represents the periodicity (in half hours). Wavelet power (given as colour legend) quantifies the relative contribution of variation in the environmental variable at each period to the total variance over time. High (low) power is represented by warm (cool) colours. Black contours designate regions of significantly high temporal variation compared to a null model (red noise). Values outside of the cone of influence — the bolder colour arch shape — are less reliable due to edge effects. Thick lines with white contour indicate the 5% significance level against red noise

showed R^2 values always below 0.50, with a maximum value of 0.41 during October 2021 (Table S1).

3.2. Temporal variation in embryo volume, lipid content and dry weight

The average volume of *Taliepus dentatus* early embryos was significantly different over the sampling period (GLM: $\text{Deviance}_{10,83}$ = 1.02; p = 0.034). Embryo volume was significantly higher from October 2021 to January 2022 compared to the other months (Fig. 3A; Table S2). There was a significant increase in embryo volume over time, with a peak between 160 and 200 d after the first sampling (GAM: R^2 = 0.10, F = 3.75, p = 0.012; Fig. S1A) corresponding to the austral spring to summer transition. The lipid content of early embryos showed significant differences among months ($F_{10,83}$ = 9.52; $p < 0.0001$). Particularly, the embryo lipid concentrations from June to September 2021 were significantly higher than those from October 2021 to March 2022, except for November 2021 (Fig. 3B; Table S2). There was a clear trend of decreasing lipid content with elapsed time up until 255 d (corresponding to January 2022) and then increasing until the end of the sampling period (GAM: R^2 = 0.45; F = 19.25; $p < 0.0001$; Fig. S1B). The EDW showed significant differences among months ($F_{10,83}$ = 4.19; p = 0.0001), mostly associated with August 2021 and April 2022 being significantly lower and higher than the rest, respectively (Fig. 3C; Table S2). EDW steadily increased during the sampling period except in October 2021 (GAM: R^2 = 0.22; F = 9.99; $p < 0.001$; Fig. S1C).

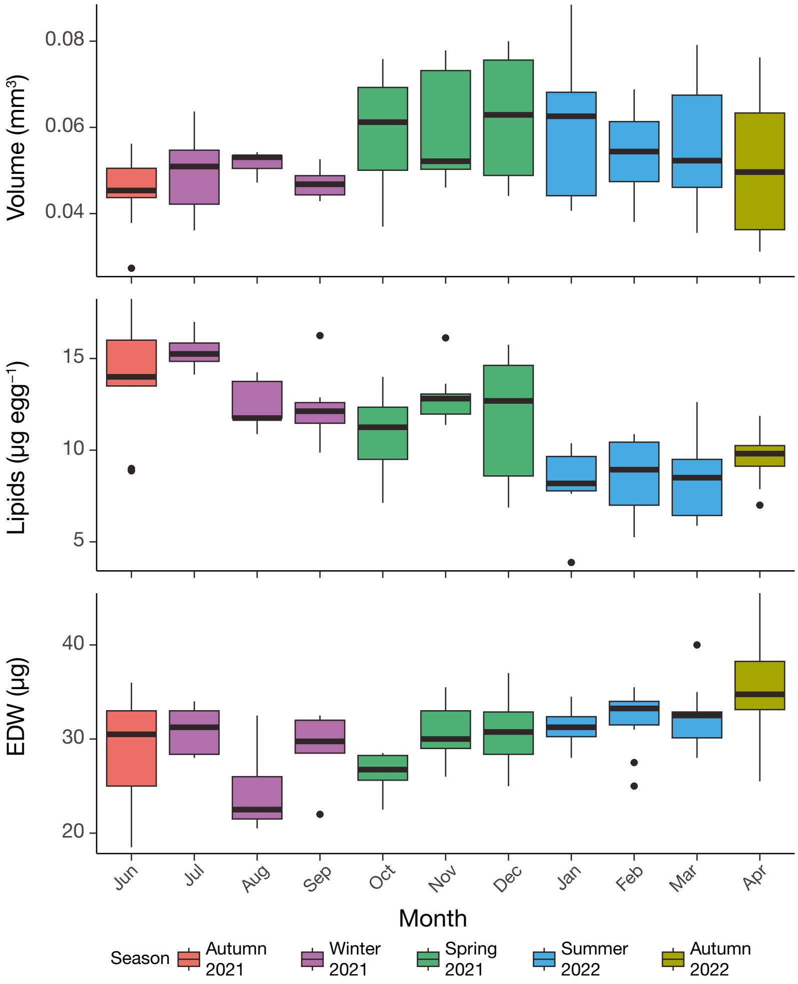

Fig. 3. Temporal variation in maternal investment traits of *Taliepus dentatus*. The boxplots show the monthly variation in (A) embryo volume, (B) lipid content and (C) embryo dry weight (EDW). Box: interquartile range; horizontal and vertical lines: median and the entire data range, respectively; black dots: outliers. Data are grouped by season

3.3. FAs of early embryos of *Taliepus dentatus*

A total of 25 FAs were detected, of which 10 were saturated FAs (SFAs), 6 were monounsaturated FAs (MUFAs), and 9 were polyunsaturated FAs (PUFAs). The sum of SFAs decreased during the sampling period, from 44–48% in Autumn and Winter 2021 to 38% in Summer and Autumn 2022 (Table S3). Within the SFAs, C16:0 (palmitic acid) was the most abundant, followed by C18:0 (stearic acid) and C14:0 (myristic acid). The MUFAs showed steady percentage values throughout the sampling period (25–29%; Table S3). The most represented MUFAs were C18:1n9 (oleic acid) and C16:1 (palmitoleic acid). The PUFAs showed highly variable percentages during the sampling period (Table S3). Specifically, the n3-PUFAs were most abundant during Spring 2021, and Summer and Autumn 2022 (Table S3). The sum of n6-PUFAs in Autumn and Winter 2021 was 26.87 and 23.08, respectively, while it was higher in Spring 2021 (35.30), and increased in Summer and Autumn 2022 (36.28 and 36.32, respectively) (Table S3). The PERMANOVA on FAs revealed significant differences in FA composition among months (pseudo-$F_{10,87}$ = 21.03; p = 0.001). The PCoA showed that most of the variance was explained by PCo1 (74.5%), while PCo2 only explained 12.7% (Fig. 4). A separation of FAs between 2 blocks was found along PCo1, which was related to a seasonal differentiation (Spring 2021/Summer 2022 vs. Autumn 2021/Winter 2021) in the production of FAs in early embryos. FAs in Autumn 2022 differentiated from those in Autumn 2021 and were grouped with the Spring 2021/Summer 2022 block (Fig. 4). The FAs that most contributed to the Autumn 2021/Winter 2021 block were the PUFAs C22:6n3 (docosahexaenoic acid, DHA), C20:5n3 (eicosapentaenoic acid, EPA) and C20:2 (eicosadienoic acid) and the MUFAs 14:1 (tetradecanoic acid) and 15:1 (pentadecanoic acid). The FAs that most contributed to the Spring 2021/Summer 2022 block were the PUFAs C20:4n6 (arachidonic acid, ARA), C18:2n6 (linoleic acid) and C22:2 (docosadienoic acid); the MUFAs C20:1 (eicosenoic acid) and C17:1 (heptadecanoic acid); and the SFAs C21:0 (heneicosanoic acid) and C23:0 (tricosanoic acid). According to the SIMPER analyses, the average contribution of FAs was less even for the following combinations: (1) Autumn 2021 vs. Spring 2021, (2) Autumn 2021 vs. Summer 2022, (3) Autumn 2021 vs. Autumn 2022, (4) Winter 2021 vs. Spring 2021, (5) Winter 2021 vs. Summer 2022 and (6) Winter 2021 vs. Autumn 2022. In terms of single FAs, the SIMPER analysis found that C16:0 (palmitic acid), C20:4n6 (ARA) and C20:5n3 (EPA) were the FAs that contributed with the highest average to the separation between blocks (Fig. S2, Table S4).

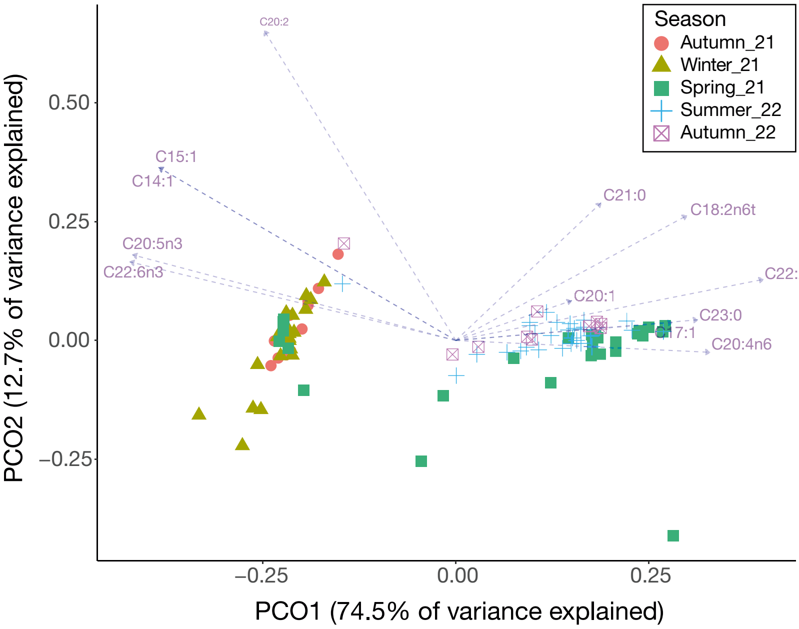

Fig. 4. Multivariate analysis (principal coordinates analysis, PCoA) of the fatty acid (FA) composition. Each point represents the averaged FA composition. The shape and colour of each point represent the season in which the sample was collected. Dashed arrows represent the factorial charge, and the FAs with higher (>015) factorial charge are presented

3.4. Effects of environmental means, variance and monthly predictability on embryo volume, lipid content and EDW

Five models best described the relationship between the mean, variance and predictability of the environmental variables (T, DO and S) and MI traits (embryo volume, lipid content and dry weight). In terms of mean values, the best model was the one considering the single effect of T on embryo volume, with T positively related to embryo volume (Fig. 5A, Table 1). In terms of variance, the best models were the ones considering (1) the single effect of T on embryo lipid content (Fig. 5B, Table 1), with T being negatively related to embryo lipids, and (2) the concurrent effect of T+DO on embryo volume (Fig. 5B, Table 1), with T and DO being positively related to embryo volume. In terms of predictability, the best models were the ones considering (1) the single effect of DO on embryo lipids (Fig. 5C, Table 1), with increasing predictability of DO negatively related to embryo lipids, and (2) the concurrent effect of DO+S on embryo volume (Fig. 5C, Table 1), with positive effects of DO and negative effects of S.

3.5. Effects of environmental means, variability and predictability on FAs

The GLM analysis showed overall significant effects of the mean, variance and predictability of the environmental variables (T, DO and S) on FA composition (Table 2). When decomposing the variance of FAs using single GLMs (Table S5), T, DO and S affected FAs differently, depending on whether the mean, variance or predictability were considered (Fig. 6). Specifically, when looking at T, almost all FAs were significantly related to changes in its mean and variance, while only 2 FAs (C20:5n3 and C17:1) were related to changes in the predictability of T fluctuations (Fig. 6).

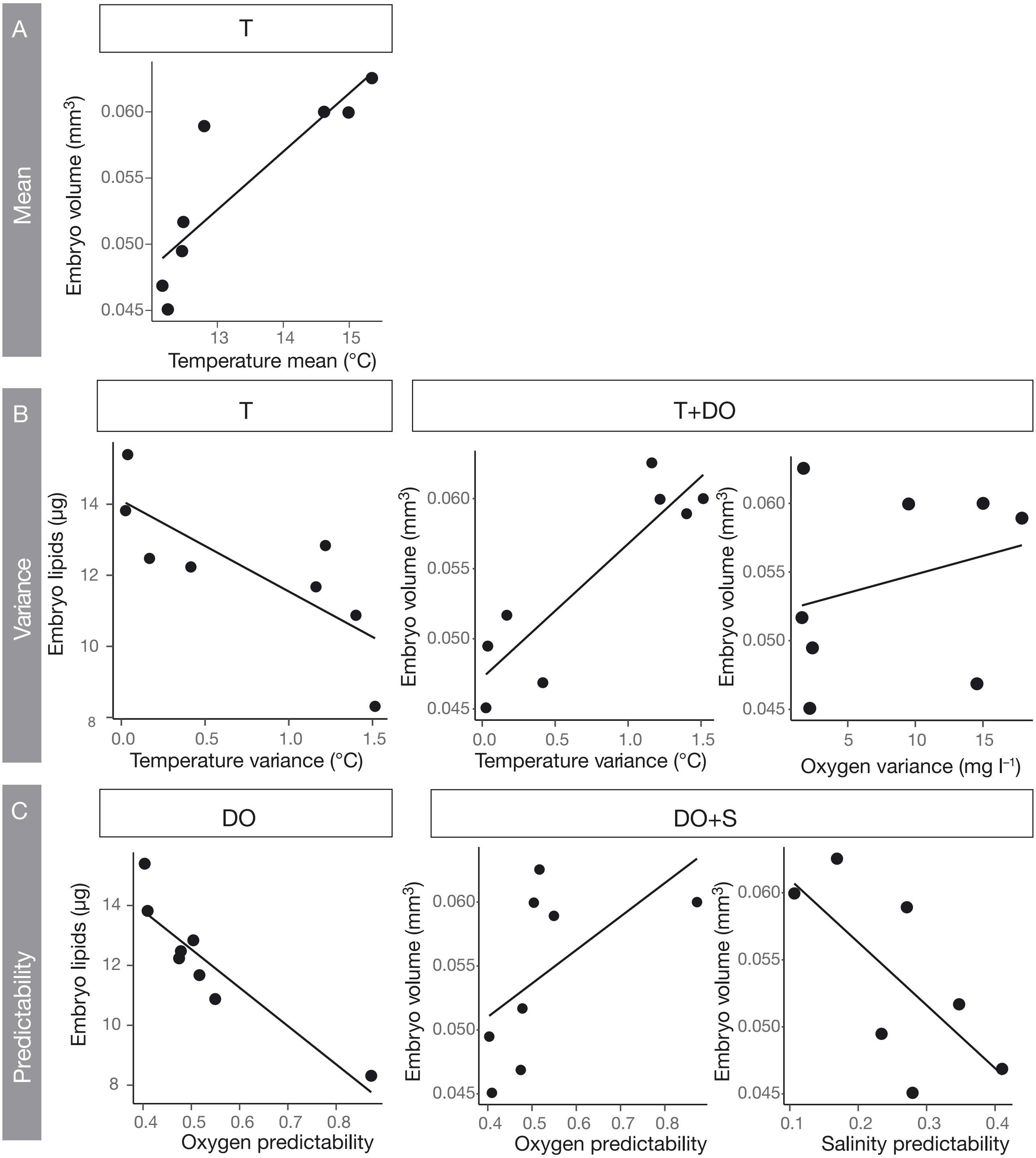

Fig. 5. Linear regression models between maternal investment traits (embryo volume and lipids) and the environmental data (T: temperature, DO: dissolved oxygen, S: salinity) considering (A) mean, (B) variance and (C) predictability values. The best single and additive effects based on multiple linear regression models are shown based on the highest *F*-statistic among the significant models (see Section 2 for details)

Considering DO, most FAs were significantly related to changes in the variance and predictability, while only 2 FAs (C18:3n3 and C17:1) were related to changes in the mean DO (Fig. 6). With regard to S, only 1 FA (C14:0) was related to changes in its variance, while all remaining FAs were related to either the changes in the mean or the predictability of S fluctuations (Fig. 6).

Table 1. Best linear models describing the effects of the environmental components (mean, variance and predictability) of dissolved oxygen (DO), temperature (T) and salinity (S) on kelp crab *Taliepus dentatus* embryo lipids, volume and dry weight. **Bold** variables and values represent significant results ($p < 0.05$)

Response variable	Explanatory variable	Mean			Variance			Predictability		
		Residuals	*F*	p	Residuals	*F*	p	Residuals	*F*	p
Embryo lipids	**DO**	1,11	1.84	0.223	1,11	4.18	0.087	**1,11**	**36.15**	**0.002**
	T	1,11	1.63	0.249	**1,11**	**9.78**	**0.020**	1,11	7.38	0.035
	S	1,11	0.82	0.404	1,11	1.00	0.362	1,11	0.04	0.841
	T + S	2,11	0.44	0.670	2,11	2.72	0.180	2,11	0.26	0.778
	T + DO	2,11	2.33	0.193	2,11	4.73	0.070	2,11	12.91	0.011
	S + DO	2,11	0.34	0.729	2,11	0.92	0.467	2,11	25.22	0.005
	T + S + DO	3,11	0.26	0.851	3,11	1.38	0.397	3,11	12.93	0.032
Embryo volume	DO	1,11	0.31	0.602	1,11	0.49	0.510	1,11	2.98	0.138
	T	**1,11**	**18.79**	**0.005**	1,11	25.99	0.002	1,11	1.9	0.217
	S	1,11	1.45	0.281	1,11	0.00	0.960	1,11	4.7	0.082
	T + S	2,11	7.11	0.048	2,11	13.23	0.017	2,11	2.68	0.182
	T + DO	2,11	9.04	0.022	**2,11**	**52.72**	**<0.001**	2,11	1.22	0.370
	S + DO	2,11	2.91	0.217	2,11	0.10	0.901	**2,11**	**35.44**	**0.003**
	T + S + DO	3,11	5.96	0.088	3,11	22.05	0.015	3,11	21.47	0.016
Embryo dry weight	DO	1,11	0.34	0.882	1,11	0.00	0.962	1,11	0.43	0.536
	T	1,11	2.36	0.176	1,11	0.38	0.559	1,11	0.7	0.424
	S	1,11	0.00	0.972	1,11	0.84	0.399	1,11	2.09	0.207
	T + S	2,11	0.58	0.601	2,11	0.45	0.662	2,11	0.84	0.494
	T + DO	2,11	1.03	0.422	2,11	0.24	0.791	2,11	0.31	0.745
	S + DO	2,11	0.09	0.910	2,11	0.48	0.649	2,11	1.65	0.299
	T + S + DO	3,11	0.29	0.831	3,11	0.25	0.852	3,11	0.85	0.551

Table 2. Results of multivariate generalized linear modelling to test for the effects of mean, variance and predictability of temperature, dissolved oxygen and salinity on the fatty acid composition of early eggs of *Taliepus dentatus*. All p-values were significant ($p < 0.05$)

	Mean		Variance		Predictability	
	Deviance (df)	p	Deviance (df)	p	Deviance (df)	p
Temperature (T)	472.4 (1,76)	0.002	1554 (1,76)	0.002	85.65 (1,76)	0.005
Dissolved oxygen (DO)	80.92 (1,76)	0.005	510.3 (1,76)	0.002	304.6 (1,76)	0.002
Salinity (S)	1308 (1,56)	0.002	72.81 (1,56)	0.007	177.6 (1,56)	0.002

4. DISCUSSION

The present study showed a significant temporal (11 mo) variation in MI traits (embryo volume, EDW, embryo lipid content and FA composition) in a population of the Chilean kelp crab *Taliepus dentatus*, which were associated with changes in the mean, variance and predictability of fluctuations in DO, water temperature and salinity. Embryo volume, lipids and dry weight varied non-linearly with time, suggesting within-population phenotypic flexibility (sensu Piersma & Drent 2003) shaped by changes in environmental conditions and characteristics of the study site. Significant linear relationships (both positive and negative) were found between the MI traits and the *in situ* characterisation of DO concentrations, water temperature and salinity that crabs experienced several days before embryo collection. Importantly, our analysis included an in-depth characterisation of the environmental drivers affecting the MI of kelp crabs, including the mean, the variance and the predictability of environmental fluctuations that improved our understanding of (1) how diel variation in environmental conditions can be perceived by benthic organisms (see Bernhardt et al. 2020) and (2) how this perception can be incorporated into important ecological traits of a population, such as MI in offspring (Baldanzi et al. 2022). Furthermore, this study showed that different environmental variables emerged as main drivers of MI traits depending on which environmental parameter (mean, variance or predictability of the fluctuations) was considered for characterising the environment. For instance, when average values were considered to explain the effects of the environ-

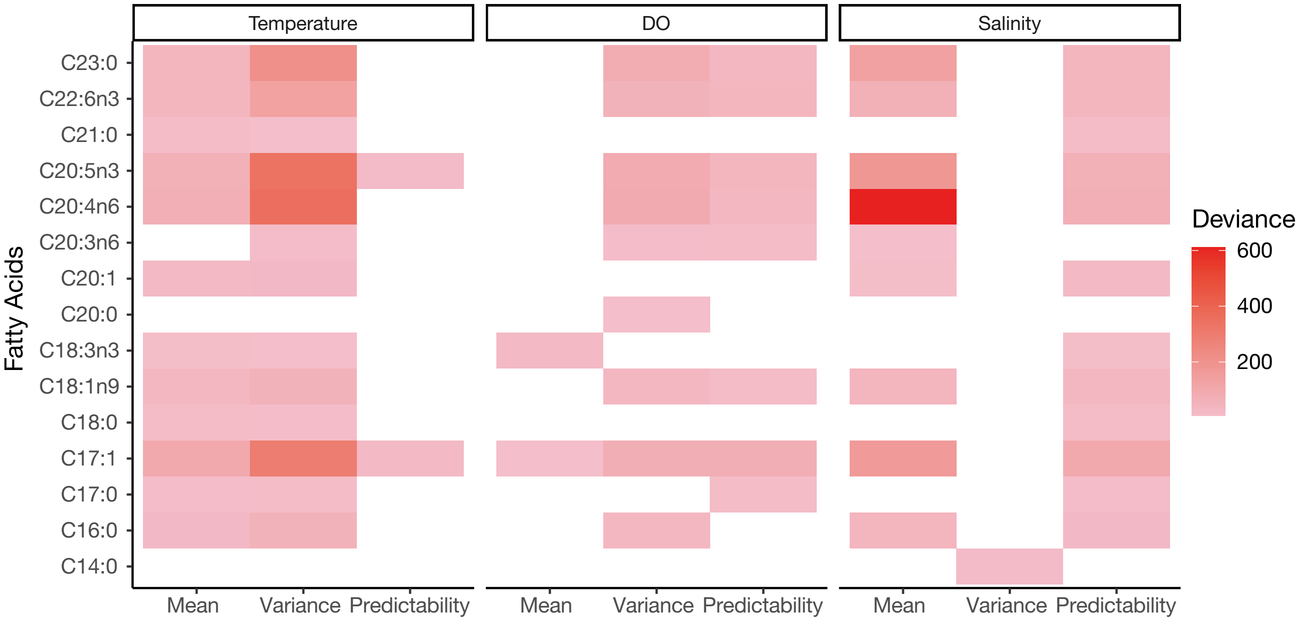

Fig. 6. Univariate results of the multivariate generalized linear model (manyGLM) analysis on the effects of the mean, variance and predictability of the fluctuations in temperature, dissolved oxygen (DO) and salinity on the fatty acid (FA) composition of *Taliepus dentatus* embryos. The heatmap shows only significant results of the manyGLM of each FA. The deviance (given in the colour legend) quantifies the FA compositions that are best explained by either the mean, the variance or the predictability of the fluctuations in temperature, DO and salinity. High (low) deviance is represented by darker (lighter) colours. Blank cells are not statistically significant

ment on MI traits, temperature appeared to be the most important driver, but when adding the variance and predictability as additional components of the environmental characterisation, the DO concentration and salinity contributed to explain the complex relationships between the environment and MI traits.

The general increase in embryo volume from Winter to Summer 2021 (with a peak around November 2021) was well predicted by an increase in the mean and the variance of water temperatures, especially during the spring—summer transition and a concurrent effect of increasing DO mean and variance. While the positive relation of embryo volume with temperature contrasts with many studies showing greater volumes at lower temperatures (as predicted by the Rule of Rass; see Lardies & Castilla 2001, Brante et al. 2003, Wehrtmann & López 2003, Laptikhovsky 2006), it confirmed the findings of Baldanzi et al. (2018), who reported larger volumes of early embryos of *T. dentatus* at lower latitudes (higher temperatures) on the coast of Chile. We interpreted this result as a direct consequence of temperature on the biochemical composition of embryos, which in turn affected embryo size (McAlister & Moran 2012). The size of an embryo is one of the most important aspects of the life history of free-spawning marine organisms; however, little is known about how embryo size relates to its composition and how this interplay is affected by the environment (Moran & McAlister 2009). Baldanzi et al. (2018) found that the lipid content of early embryos of *T. dentatus* increased significantly at higher latitudes, where cold waters slowed down metabolic activity and thus required a high amount of energy stored. The concurrent positive effect of increasing variances of temperature and DO on embryo volume can be explained in terms of optimal allocation strategy (sensu Levins 1968). Increasing variance of temperature and DO conditions induced females to invest in larger (but less lipid-rich) embryos to better cope with this environmental variability. The decrease in lipid content and a concurrent increase in embryo volume suggests that other temperature- and oxygen-dependent biochemical components of early embryos, such as proteins, were produced to meet the energetic demand for faster development at higher and more variable temperatures (Navarro et al. 2014) and can substitute lipids as energy storage (Moran & McAlister 2009). Nevertheless, since this study investigated early-staged embryos only (so that a decrease in nutrient concentration due to embryo development is excluded), the interplay between MI in biochemical components of embryos and the environment could be key in determining inter-individual variability in MI (Pavanelli et al. 2010, Baldanzi et al. 2022).

Interestingly, we found a strong negative relationship between lipid concentration of early embryos and (1) the predictability of the fluctuations in DO concentrations and (2) the temperature variance. On average, female *T. dentatus* invested in more lipid-rich embryos when fluctuations in DO concentrations measured days before embryo collections were less predictable, but the temperature values were less variable, adopting an optimal allocation strategy (sensu Levins 1968) and showing an average increase in MI. In contrast, during more predictable fluctuations in DO concentrations (towards austral summer), but more variable temperatures, decreasing investment in lipids could allow females to save energy to future reproductive events (Foster et al. 2015) or to deal with stress (Marshall & McQuaid 2011). For example, during summer months, environmental conditions in our study area (i.e. temperature, DO and salinity) showed increased mean temperatures, hyper- and hypoxic events, and a marked decrease in salinity, although more predictable, which could have affected crab activity and metabolism. By lowering the investment in energy-rich embryos, females could optimise the energy allocation to adjust the offspring phenotype to the prevailing environmental conditions. These findings agree with previous studies on the effects of environmental predictability on invertebrate physiology. For example, Baldanzi et al. (2015) found that natural populations of south African sandhoppers increased their thermal sensitivity (the slope of the reaction norm) when local temperatures showed a more predictable variability, suggesting that predictable fluctuations can improve the energy allocation to the overall animal metabolism under thermal stress (Sokolova 2021).

The seasonal differentiation in FAs found in early embryos suggests that females invested differently in the quality (FA composition) of their offspring and not only in the quantity (lipid concentration), depending on the conditions experienced during the year. The FAs that best represented this seasonal effect were the long-chain PUFAs C20:4n6 (ARA) found during spring/summer months and C22:6n3 (DHA)/C20:5n3 (EPA) found primarily during autumn/winter. Given that long chain PUFAs cannot be synthesized de novo and are transferred conservatively from mothers to offspring (Steinberg 2022), the presence of PUFAs in the diet, especially DHA and EPA, is fundamental. Changes in diet quality within our study area and specifically for *T. dentatus* is not expected, as these animals feed mainly on kelp (see Jofré Madariaga et al. 2013 for the congeneric species *T. marginatus*). However, changes in diet quality of other invertebrate species driven by environmental conditions are common in the Humboldt Current System and are associated with seasonal changes in upwelling (Lazo-Andrade et al. 2021). While we did not assess the effect of diet on seasonal changes in the FA composition, we demonstrated that the environmental conditions during embryogenesis played a non-marginal role in determining maternal allocation and energy transfer to embryos, potentially affecting the quantity/quality of food available for kelp crabs, adding a certain degree of complexity when interpreting the link between MI, embryo quality and the multivariate environment.

Overall, temperature, DO and salinity were significantly correlated with FA differentiation in early embryos of *T. dentatus* during our sampling period; however, this depended on whether we considered the mean, the variance or the predictability of the fluctuation. For instance, FA composition of early embryos was mostly explained by the mean and variance, but not the predictability, of temperature fluctuation, whereas the predictability of oxygen and salinity fluctuations well explained FA differentiation, much more than changes in average values. These results can be interpreted in terms of oxidative stress and homeoviscous adaptation.

The results suggested that periodical and predictable fluctuations in DO are associated with the differentiation in many FAs, particularly the long-chain PUFAs, which are vulnerable to reactive oxygen species during oxidative stress (Rivera-Ingraham & Lignot 2017). Therefore, predicting changes in DO could be fundamental during oogenesis, allowing females to invest in the quality of the offspring according to the degree of fluctuating conditions perceived, contributing to an optimal allocation strategy (Levins 1968). Similarly, this may apply to situations where salinity changes. Many marine coastal invertebrates are osmoconformers and are abundant in coastal areas where salinities do not fluctuate frequently and periodically. Our environmental data, however, showed that *T. dentatus* may experience hypoosmotic stress due to sudden decreases in salinity in the study area, which receives seasonal (although low) riverine discharges from the Aconcagua semi-closed estuary (Masotti et al. 2018). *T. dentatus* may benefit from a certain level of predictability of the salinity conditions to avoid oxidative stress (Rivera-Ingraham & Lignot 2017) as, during salinity stress, radical and non-radical reactive species are generated by mitochondrial respiration and other processes.

Low temperature can affect developmental FAs by acting on the membrane fluidity (Ernst et al. 2016), supporting the theory of homeoviscous adaptation (Sinensky 1974), the idea that greater unsaturation of the fatty acyl chains decreases the melting point, resulting in more fluid structure in membranes. For example, Pacific cod embryos increased n3-PUFA content during exposure to cold temperatures (decreasing temperatures from 8 to 2°C) (Laurel et al. 2012). The magnitude of temperature changes necessary to activate membrane lipid regulation pathways and, therefore, its fluidity, are more associated with changes in mean and variance at a seasonal rather than daily scale. Changes in mean and variance in our sampling periods between seasons could be responsible for the differentiation in FA production between seasons and the transfer of energy from mother to offspring through diet incorporation. In this context, the Chilean coastal habitats generally show poor availability of PUFAs, especially EPA and DHA, during autumn/winter (Guzmán-Rivas et al. 2021, Viña-Trillos & Urzúa 2021). Therefore, in coastal species such as *T. dentatus*, these FAs must be obtained from lipid reserves that the females have previously stored in the hepatopancreas, subsequently deposited in the eggs and finally preserved during the embryogenesis until the first larval feeding stage is reached (Jeffs & O'Rorke 2020). This may explain why the content of essential PUFAs (autumn/winter: EPA, DHA; spring/summer: ARA) in early embryos of *T. dentatus* show a marked seasonality associated with the mean and variance of temperature as revealed by the present study. In addition to selective storage and preservation of these biomolecules, selectively enhanced maternal storage of essential long-chain PUFAs in the embryos is also likely to occur but needs scrutiny in future experimental studies to reveal association with these environmental factors (temperature, food, DO, salinity).

In conclusion, the present study revealed a significant correlation between environmental fluctuations and their predictability on females' per-offspring investment, improving our understanding of the effects of the environment on the ecology of benthic species. These findings are promising to inform future laboratory-based studies to disentangle the link between environmental fluctuation and species biological traits. Our results suggest new insights regarding how species may perceive, integrate and process environmental fluctuations and generate responses that may be transferred to subsequent generations (latent effects of maternal allocation on larvae), an important and overlooked aspect in the ecology of marine coastal invertebrates. Considering that recent climate predictions forecast an increase in weather variability (IPCC 2023), such as more frequent and unpredictable extreme events (Harris et al. 2018), investigating the overlooked relationship between maternal effects and environmental predictability will improve our understanding of the impacts of rapid climate change on coastal marine species (Crean & Marshall 2009).

Acknowledgements. We thank many students of the Universidad de Valparaíso and the Universidad Católica de la Santísima Concepción for their help during animal collection and analysis of embryo volume, lipid content and fatty acids. The present work was part of F.F.'s undergraduate thesis at the Universidad de Valparaíso. The research was fully funded by the FONDECYT project (n°11221161) from the Agencia Nacional de Investigación y Desarrollo (ANID — Chile) assigned to S.B. and partially supported by the research centre Centro de Observación y Análisis del Ambiente Costero (COSTA-R, CIDI UV 12, Universidad de Valparaíso) through student scholarship. The research also received partial support from the project RED21992, 'Sistema articulado de investigación en cambio climático y sustentabilidad de zonas costeras de Chile' (MINEDUC, Chile). M.F. was supported by his baseline funding grant from the School of Natural and Environmental Science of Newcastle University.

LITERATURE CITED

Aparicio-Rizzo P, Masotti I (2019) Inter-annual variability of oceanographic conditions and phytoplankton in Valparaíso Bay (~33° S), central Chile. Rev Biol Mar Oceanogr 54:70–81

Aparicio-Rizzo P, Masotti I, Landaeta MF (2020) Influence of coastal upwelling on micro-phytoplankton variability at Valparaíso Bay (~33° S), central Chile. Rev Biol Mar Oceanogr 55:11–25

Baldanzi S, McQuaid CD, Porri F (2015) Temperature effects on reproductive allocation in the sandhopper *Talorchestia capensis.* Biol Bull (Woods Hole) 228:181–191

Baldanzi S, Storch D, Navarrete SA, Graeve M, Fernández M (2018) Latitudinal variation in maternal investment traits of the kelp crab *Taliepus dentatus* along the coast of Chile. Mar Biol 165:37

Baldanzi S, Storch D, Fusi M, Weidberg N, Tissot A, Navarrete SA, Fernández M (2020) Combined effects of temperature and hypoxia shape female brooding behaviors and the early ontogeny of the Chilean kelp crab *Taliepus dentatus.* Mar Ecol Prog Ser 646:93–107

Baldanzi S, Saldías GS, Vargas CA, Porri F (2022) Long term environmental variability modulates the epigenetics of maternal traits of kelp crabs in the coast of Chile. Sci Rep 12:18806

Bascur M, Guzmán-Rivas F, Mora S, Urzúa Á (2017) Seasonal changes in the biochemical composition of females and offspring of red squat lobster, *Pleuroncodes monodon* (Decapoda, Munididae), from the Southeastern Pacific. Mar Ecol 38:e12419

Bernhardt JR, O'Connor MI, Sunday JM, Gonzalez A (2020) Life in fluctuating environments. Philos Trans R Soc Lond B 375:20190454

Bitter MC, Kapsenberg L, Silliman K, Gattuso JP, Pfister CA (2021) Magnitude and predictability of pH fluctuations shape plastic responses to ocean acidification. Am Nat 197:486–501

Boero F (1994) Fluctuations and variations in coastal marine environments. Mar Ecol 15:3–25

Brante A, Fernández M, Eckerle L, Mark F, Pörtner HO, Arntz W (2003) Reproductive investment in the crab *Cancer setosus* along a latitudinal cline: egg production, embryo losses and embryo ventilation. Mar Ecol Prog Ser 251:221–232

Burgess SC, Marshall DJ (2014) Adaptive parental effects: the importance of estimating environmental predictability and offspring fitness appropriately. Oikos 123:769–776

Cequier-Sánchez E, Rodríguez C, Ravelo ÁG, Zárate R (2008) Dichloromethane as a solvent for lipid extraction and assessment of lipid classes and fatty acids from samples of different natures. J Agric Food Chem 56:4297–4303

Clarke A (1988) Seasonality in the antarctic marine environment. Comp Biochem Physiol B 90:461–473

Crean AJ, Marshall DJ (2009) Coping with environmental uncertainty: dynamic bet hedging as a maternal effect. Philos Trans R Soc Lond B 364:1087–1096

Dierschke V, Marra S, Parsons M, Fusi M, French G (2022) Marine bird abundance. OSPAR 2023: the 2023 quality status report for the North-East Atlantic. OSPAR Commission, London. https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/marine-bird-abundance/ (accessed on 28 March 2024)

Ernst R, Ejsing CS, Antonny B (2016) Homeoviscous adaptation and the regulation of membrane lipids. J Mol Biol 428:4776–4791

Fariña JM, Palma AT, Ojeda FP (2008) Subtidal kelp associated communities off the temperate Chilean coast. In: McClanahan T, Branch GM (eds) Food webs and trophic dynamics of marine benthic ecosystems. Oxford University Press, New York, NY, p 79–102

Fernández M, Brante A, Baldanzi S (2020) Costs and benefits of brooding among decapod crustaceans: the challenges of incubating in aquatic systems. In: Cothran RD, Thiel M (eds) The natural history of the Crustacea, Vol 6. Oxford University Press, New York, NY, p 86–144

Fields JT, Mullen HK, Kroenke CM, Salomon KA, Craft AJ, Conrad IE, Baeza JA (2020) Reproductive performance in a phyletic dwarf, the spider crab *Petramithrax pygmaeus* (Bell, 1836) (Decapoda: Brachyura: Mithracidae). J Crustac Biol 40:325–329

Folch J, Lees M, Stanley GHS (1957) A simple method for the isolation and purification of total lipides from animal tissues. J Biol Chem 226:497–509

Foster SA, Wund MA, Graham MA, Earley RL, Gardiner R, Kearns T, Baker JA (2015) Iterative development and the scope for plasticity: contrasts among trait categories in an adaptive radiation. Heredity 115:335–348

Fox J, Weisberg S, Price B, Adler D and others (2019) car: companion to applied regression. R package version 3.1-3. https://CRAN.R-project.org/web/packages/car/index.html

Fusi M, Marasco R, Ramond JB, Barausse A, Baldanzi S (2022) Editorial: Fluctuating habitats: ecological relevance of environmental variability and predictability on species, communities, and ecosystems. Front Ecol Evol 10:907622

Gill RL, Collins S, Argyle PA, Larsson ME, Fleck R, Doblin MA (2022) Predictability of thermal fluctuations influences functional traits of a cosmopolitan marine diatom. Proc R Soc B 289:20212581

Giménez L, Anger K (2001) Relationships among salinity, egg size, embryonic development, and larval biomass in the estuarine crab *Chasmagnathus granulata* Dana, 1851. J Exp Mar Biol Ecol 260:241–257

Gulyas L, Powell JR (2019) Predicting the future: parental progeny investment in response to environmental stress cues. Front Cell Dev Biol 7:115

Guzmán-Rivas F, Quispe-Machaca M, Queirolo D, Ahumada M, Urzúa Á (2021) Latitudinal changes in the lipid content and fatty acid profiles of juvenile female red squat lobsters (*Pleuroncodes monodon*) in breeding areas of the Humboldt Current System. PLOS ONE 16: e0253314

Harris RMB, Beaumont LJ, Vance TR, Tozer CR and others (2018) Biological responses to the press and pulse of climate trends and extreme events. Nat Clim Change 8: 579–587

Helmuth B, Broitman BR, Blanchette CA, Gilman S and others (2006) Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. Ecol Monogr 76:461–479

Hernáez P, Palma S (2003) Fecundidad, volumen del huevo y rendimiento reproductivo de cinco especies de porcelánidos intermareales del norte de Chile (Decapoda, Porcellanidae). Investig Mar 31:35–46 (in Spanish with English Abstract)

IPCC (2023) Climate change 2023: synthesis report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, p 35–115. https://www.ipcc.ch/report/ar6/syr/ (accessed on 14 April 2024)

Jeffs A, O'Rorke R (2020) Feeding and nutrition of crustacean larvae. In: Anger K, Harzsch S, Thiel M (eds) Developmental biology and larval ecology: the natural history of the Crustacea, Vol 7. Oxford University Press, New York, NY, p 309–324

Jofré Madariaga D, Ortiz M, Thiel M (2013) Demography and feeding behavior of the kelp crab *Taliepus marginatus* in subtidal habitats dominated by the kelps *Macrocystis pyrifera* or *Lessonia trabeculata*. Invertebr Biol 132:133–144

Kroeker KJ, Bell LE, Donham EM, Hoshijima U, Lummis S, Toy JA, Willis-Norton E (2020) Ecological change in dynamic environments: accounting for temporal environmental variability in studies of ocean change biology. Glob Change Biol 26:54–67

Kuijper B, Hoyle RB (2015) When to rely on maternal effects and when on phenotypic plasticity? Evolution 69:950–968

Laptikhovsky V (2006) Latitudinal and bathymetric trends in egg size variation: a new look at Thorson's and Rass's rules. Mar Ecol 27:7–14

Lardies M, Castilla J (2001) Latitudinal variation in the reproductive biology of the commensal crab *Pinnaxodes chilensis* (Decapoda: Pinnotheridae) along the Chilean coast. Mar Biol 139:1125–1133

Laurel BJ, Copeman LA, Parrish CC (2012) Role of temperature on lipid/fatty acid composition in Pacific cod (*Gadus macrocephalus*) eggs and unfed larvae. Mar Biol 159: 2025–2034

Lazo-Andrade J, Guzmán-Rivas FA, Espinoza P, García-Huidobro MR, Aldana M, Pulgar J, Urzúa Á (2021) Temporal variations in the bioenergetic reserves of *Concholepas concholepas* (Gastropoda: Muricidae) in contrasting coastal environments from the Humboldt current system. J Sea Res 167:101970

Levins R (1968) Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton, NJ

Lorioux S, DeNardo DF, Gorelick R, Lourdais O (2012) Maternal influences on early development: preferred temperature prior to oviposition hastens embryogenesis and enhances offspring traits in the Children's python, *Antaresia childreni.* J Exp Biol 215:1346–1353

Maraun D, Kurths J (2004) Cross wavelet analysis: significance testing and pitfalls. Nonlinear Process Geophys 11: 505–514

Marshall DJ, McQuaid CD (2011) Warming reduces metabolic rate in marine snails: Adaptation to fluctuating high temperatures challenges the metabolic theory of ecology. Proc R Soc B 278:281–288

Masotti I, Aparicio-Rizzo P, Yevenes MA, Garreaud R, Belmar L, Farías L (2018) The influence of river discharge on nutrient export and phytoplankton biomass off the central Chile coast (33°–37° S): seasonal cycle and interannual variability. Front Mar Sci 5:423

McAlister JS, Moran AL (2012) Relationships among egg size, composition, and energy: a comparative study of geminate sea urchins. PLOS ONE 7:e41599

Melbinger A, Vergassola M (2015) The impact of environmental fluctuations on evolutionary fitness functions. Sci Rep 5:15211

Montecinos A, Balbontín F (1993) Indices de surgencia y circulación superficial del mar: implicancias biológicas en un área de desove de peces entre Los Vilos y Valparaíso, Chile. Rev Biol Mar 28:133–150

Moran AL, McAlister JS (2009) Egg size as a life history character of marine invertebrates: Is it all it's cracked up to be? Biol Bull (Woods Hole) 216:226–242

Navarro JC, Monroig Ó, Sykes AV (2014) Nutrition as a key factor for cephalopod aquaculture. In: Iglesias J, Fuentes L, Villanueva R (eds) Cephalopod culture. Springer, Dordrecht, p 77–95

Oksanen J, Kindt R, Legendre P, O'Hara B, Stevens MHH (2007) vegan: community ecology package. R package version 1.8-8. https://CRAN.R-project.org/web/packages/vegan/index.html

Paradis E, Schliep K (2019) Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528

Parichy DM, Kaplan RH (1992) Maternal effects on offspring growth and development depend on environmental quality in the frog *Bombina orientalis.* Oecologia 91:579–586

Pavanelli C, Mossolin E, Mantelatto F (2010) Maternal investment in egg production: environmental and population-specific effects on offspring performance in the snapping shrimp *Alpheus nuttingi* (Schmitt, 1924) (Decapoda, Alpheidae). Anim Biol 60:237–247

Piersma T, Drent J (2003) Phenotypic flexibility and the evolution of organismal design. Trends Ecol Evol 18:228–233

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rilov G, Mazaris AD, Stelzenmüller V, Helmuth B and others (2019) Adaptive marine conservation planning in the face of climate change: What can we learn from physiological, ecological and genetic studies? Glob Ecol Conserv 17: e00566

Rivera-Ingraham GA, Lignot JH (2017) Osmoregulation, bioenergetics and oxidative stress in coastal marine invertebrates: raising the questions for future research. J Exp Biol 220:1749–1760

Roesch A, Schmidbauer H (2018) WaveletComp: computational Wavelet analysis. R package version 1.1. https://CRAN.R-project.org/web/packages/WaveletComp/

Shumway RH, Stoffer DS (2017) Time series analysis and its applications: with R examples, 4th edn. Springer, Cham

Sinensky M (1974) Homeoviscous adaptation — a homeostatic process that regulates the viscosity of membrane lipids in *Escherichia coli*. Proc Natl Acad Sci USA 71: 522–525

Sokolova I (2021) Bioenergetics in environmental adaptation and stress tolerance of aquatic ectotherms: linking physiology and ecology in a multi-stressor landscape. J Exp Biol 224:jeb236802

Steinberg CEW (2022) Biosynthesis of polyunsaturated fatty acids — 'Many can, some can't.' In: Steinberg CEW (ed) Aquatic animal nutrition: organic macro- and micro-nutrients. Springer, Cham, p 723–752

Tapia FJ, Navarrete SA, Castillo M, Menge BA and others (2009) Thermal indices of upwelling effects on inner-shelf habitats. Prog Oceanogr 83:278–287

Trivers RL (ed) (1972) Parental investment and sexual selection. In: Campbell BG (ed) Sexual selection and the descent of Man. Routledge, London, pp 136–179

Urzúa Á, Anger K (2013) Seasonal variations in larval biomass and biochemical composition of brown shrimp, *Crangon crangon* (Decapoda, Caridea), at hatching. Helgol Mar Res 67:267–277

Vargas LM (1995) Descripción del desarrollo embrionario de *Cancer polyodon* Poepping 1836 (Crustacea: Decapoda: Brachyura) y efectos de la temperatura, bajo condiciones de laboratorio. BSc thesis, Universidad Católica del Norte, Coquimbo

Vásquez JA, Buschmann AH (1997) Herbivore-kelp interactions in Chilean subtidal communities: a review. Rev Chil Hist Nat 70:41–52

Viña-Trillos N, Urzúa Á (2021) Comparison of lipids and fatty acids among tissues of two semiterrestrial crabs reveals ecophysiological adaptations in changing coastal environments. Comp Biochem Physiol A Mol Integr Physiol 259:111012

Wang Y, Naumann U, Eddelbuettel D, Wilshire J, Warton D (2022) mvabund: statistical methods for analysing multivariate abundance data. R package version 4.2.1. https://CRAN.R-project.org/package=mvabund

Wehrtmann IS, Graeve M (1998) Lipid composition and utilization in developing eggs of two tropical marine caridean shrimps (Decapoda: Caridea: Alpheidae, Palaemonidae). Comp Biochem Physiol B Biochem Mol Biol 121:457–463

Wehrtmann IS, López GA (2003) Effects of temperature on the embryonic development and hatchling size of *Betaeus emarginatus* (Decapoda: Caridea: Alpheidae). J Nat Hist 37:2165–2178

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, NY

Wickham H, Bryan J (2023) R packages: organize, test, document, and share your code, 2nd edn. O'Reilly Media, Sebastopol, CA. https://r-pkgs.org/

Editorial responsibility: Rochelle D. Seitz,
Gloucester Point, Virginia, USA
Reviewed by: F. B. Ribeiro and 2 anonymous referees

Submitted: May 24, 2024
Accepted: January 10, 2025
Proofs received from author(s): February 24, 2025