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Baseline

Stress response to trace elements mixture of different embryo-larval stages of *Paracentrotus lividus*

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ABSTRACT

This study investigated for the first time the oxidative biomarkers responses in all larval stages of sea urchin. The contamination effects were reproduced by using contaminated seawater to concentrations measured in the area adjacent to an old asbestos mine at factors of 5 and 10. The results suggested that the concentrations were not sufficiently high to induce a major oxidative stress. The biometric differences make this method a more sensitive approach for assessing the effects on sea urchin larvae. Measurements of specific activities of antioxidant enzymes at each stage suggested a high capacity of the larvae to respond to oxidative stress. This normal activity of the organism must be considered in future research. This work also highlighted the importance of spawners provenance in ecotoxicological studies. These data are essential to better understand the stress responses of sea urchin larvae and provide baseline information for later environmental assessment research.

The intensification of anthropogenic practices such as agricultural, urban and industrial discharges can lead to high levels of pollution in coastal habitats and affect marine ecosystems (Islam and Tanaka, 2004; Mostofa et al., 2013). These increasing discharges of pollutants of different kinds cause pressure on the marine ecosystem, disrupting its natural balance (Halpern et al., 2007; Benedetti et al., 2015). Due to their continuous inputs, persistence, toxicity, numerous discharge routes and ability to accumulate in organisms, trace elements are a major issue in the marine environment (Spencer et al., 2006; Ali et al., 2013).

Within the Mediterranean Sea, Corsica Island has long been considered as a site subject to low anthropic pressure, in contrast to other Mediterranean coasts (Gobert et al., 2017). Nevertheless, concerning levels of trace elements were measured in the north-west of Corsica, near an old asbestos mine (Cary et al., 2013; Ternengo et al., 2018; El Idrissi et al., 2020). Studies have shown high concentrations of chromium (Cr), cobalt (Co), and nickel (Ni) in the area adjacent to the old mine due to the release of 4.5×10^6 m^3 of solid waste rock into the sea during the active mining period between 1950 and 1965 (BRGM, 1997; Andral et al., 2004; Cary et al., 2013). An accumulation of these trace elements has been recorded in several organisms implanted in this area (*e.g.* mussels, sea urchin, Mediterranean tapeweed (seagrass) *Posidonia oceanica*; Lafabrie et al., 2007; Kantin et al., 2015; El Idrissi et al., 2020). A variety of methods are used to assess the levels of contamination in marine organisms and ecosystems. Quantification of chemicals by analytical tools can measure the extent and significance of environmental contamination (Guendouzi et al., 2017; Rouane-Hacene et al., 2017). However, analytical techniques are not adequate to assess the effects of the presence of contaminants on organisms or on the health of the ecosystem (Lagadic et al., 1998; Ramade, 2007). Indeed, the effects of trace elements on organisms vary considerably depending on their forms (Xian, 1989) and the synergistic or antagonistic actions that may occur in the environment (Fernandez and Beiras, 2001; Nogueira et al., 2021), but also on the organism considered, its stage of development or its physiological state (Paredes and Bellas, 2015).

In recent years, bioassays have been used more frequently to better predict the effects of contaminants on organisms exposed to pollutants (*e.g.* Ruocco et al., 2020; Nogueira et al., 2021; Rendell-Bhatti et al., 2021). It has been widely demonstrated in controlled experiments that biomarkers can be used to assess the effects of xenobiotics on the organism's vital structures and functions (*e.g.* Roccheri et al., 2004;

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Richardson et al., 2021). Marine organisms are very sensitive to many environmental stresses, and therefore the analysis of their response to different stressors is crucial for our understanding of defence mechanisms (Roccheri et al., 2004). Numerous studies suggest that exposure to various trace elements can cause the production of reactive oxygen species (ROS) resulting in irreversible damage in marine organisms (Nieto et al., 2010). One of the predominant mechanisms for the toxicity of trace elements is interference with cellular redox regulation and induction of oxidative stress (Beyersmann and Hartwig, 2008). It is therefore of interest to consider the activities of antioxidant enzymes such as catalase (CAT), glutathione peroxidase (GPX), glutathione-s-transferase (GST), superoxyde dismutase (SOD), acting against oxidative stress.

The choice of bioindicators for bioassays must take into account many factors such as sensitivity and reliability but also distribution and environmental relevance (Chapman, 2002a). Besides its key role in structuring benthic communities through grazing activity, the sea urchin is one of the most suitable test organisms for acute bioassays of marine pollution (Boudouresque and Verlaque, 2013). Indeed, sea urchin larvae have many advantages: widespread geographical distribution, rapid development, ease of handling and rearing under laboratory conditions (Geraci et al., 2004; Salvo et al., 2015). Consequently, bioassays on embryo-larval stages are frequently used in the determination of the availability of chemicals and assessment of their toxicity (*e.g.* Migliaccio et al., 2014; Ruocco et al., 2020; Nogueira et al., 2021). The sensitivity of the sea urchin larvae and morphological abnormalities due to pollutants exposure have been reported under controlled laboratory conditions or in natural marine-polluted ecosystems (Saco-Álvarez et al., 2010; Beiras et al., 2012; Gharred et al., 2021). While larvae have been used to assess trace elements contamination, no study has examined induced oxidative stress over the entire larval cycle. It is therefore essential to improve the understanding of biomarker responses to environmentally relevant concentrations for all larval stages.

The overall aim of this study is to assess the capacity of larval stages to respond to stress induced by trace elements concentrations of concern (levels measured near the old asbestos mine at Canari (Corsica, France)). This study has also assessed the responses according to the stage of development, the origin of the spawners and also the pre-exposure of the fertilized eggs to contamination. These data, combined with the monitoring of larval development, will allow a better understanding of the effects of contaminants on aquatic organisms and also a better use of sea urchin larvae as bioindicators.

Adult sea urchins, *Paracentrotus lividus* (Lamarck, 1816), were collected in April by scuba diving in Corsica (France, Mediterranean Sea) at two specific stations: (i) Albo (42°46.313 N, 9°20.150 E), a contaminated site due to its proximity to the old asbestos mine at Canari, and (ii) Calvi (42°34.916 N, 8°43.589 E), a reference site characterized by very low levels of trace elements contamination (Fig. 1; Ternengo et al., 2018; Gobert and Richir, 2019; El Idrissi et al., 2020). Directly after the field sampling, individuals were transported in an insulated box to the laboratory. For each site, 30 males and 30 females were spawned. Concentrated sperm was collected dry, mixed and kept on ice until use. In order to optimize the genetic mixing, equal amounts of eggs from each female were mixed and suspended in natural filtered seawater. A concentrated sperm was added and after 45 min, fertilization success was checked (fertility rate above 90 %; Pétinay et al., 2009; Buttino et al., 2016). The number of fertilized eggs was assessed and distributed in the rearing tanks. Temperature was adjusted at the beginning of the experiments (20 °C) and was continuously monitored using HOBO TidbiT® v2 loggers (accuracy: ± 0.21 °C). All animal procedures were in compliance with the guidelines of the European Union (Directive 609/86/CEE).

Bioassays were performed to assess the impact of the contamination measured in the seawater column in front of the old asbestos mine at Canari (Fig. 2). The effects on the embryo-larval stages were reproduced by using synthetic polluted seawater characterized by a mixture of seven trace elements selected for distinct purposes: (i) cobalt (Co), chromium (Cr) and nickel (Ni) are measured at high concentrations in the study area (Ternengo et al., 2018); (ii) iron (Fe), copper (Cu) and zinc (Zn) are essential trace elements usually recovered at high levels in sea urchin gonads (El Idrissi et al., 2020), and (iii) mercury (Hg) has been frequently discussed for several years in the scientific community in view of its potential impact (*e.g.* Streets et al., 2019; Zheng et al., 2019). Two treatments were tested using the average concentrations measured in the seawater column in front of the old asbestos mine multiplied by 5 (treatment 1) and multiplied by 10 (treatment 2; Table 1). Trace element stock solutions diluted in deionized water were prepared using the following analytical grade solutions (1 g L^{-1} Certipur®, Merck, Germany): $Co(NO_3)_2$, $Cr(NO_3)_3$, $Cu(NO_3)_2$, $Fe(NO_3)_3$, $Hg(NO_3)_2$, $Ni(NO_3)_2$, $Zn(NO_3)_2$. Synthetic polluted seawater was prepared by adding trace elements into control seawater to reach the desired concentrations.

Two experiments were carried out using larvae produced by sea urchins from Albo and Calvi and were conducted simultaneously so as to have the same experimental conditions. Fertilized eggs from each site were placed in rearing tanks filled with filtered seawater and in contaminated water (treatment 1; Fig. 2). After 48 h, the pre-exposed larvae were transferred to rearing tanks with filtered seawater. The seawater was renewed daily and food, composed of a mixture of phytoplankton, was provided *ad libitum*.

In total, four rearing tanks of 80 L were used (two rearing tanks for the larvae from the spawners of each site). For each population, one of the two rearing tanks received pre-exposed larvae and the other, non-exposed larvae (Fig. 2). About 20,000 larvae from each rearing tank were collected at different stages (fertilized eggs; 4-arms; 6-arms; 8-arms) and placed in contaminated water at different concentrations (treatments 1 and 2; Fig. 2). After 48 h of exposure to contaminants, larvae were frozen in liquid nitrogen and immediately stored at −80 °C for biochemical analyses. Duplicates were performed for each treatment and a control was carried out for each experiment.

Samples were homogenized using a Potter-Elvehjem homogenizer in chilled phosphate buffer (100 mM, pH 7.4; 25 mg w/w per mL of buffer) containing 20 % glycerol and 0.2 mM phenylmethylsulfonyl fluoride as a serine protease inhibitor. The homogenates were centrifuged at 15,000 ×*g* for 30 min at 4 °C and the supernatant was used for biochemical assays. Protein concentration was measured as described in Bradford (1976) and was used to normalize the final unit for biomarker responses. Biomarkers including catalase (CAT), superoxide dismutase (SOD), glutathione peroxidase (GPX) and glutathione-S-transferase (GST) were assessed in whole body tissues of *Paracentrotus lividus* larvae as described by Greani et al. (2017). All enzyme activities were expressed in units mg^{-1} protein (specific enzymatic activities). Antioxidant enzyme activity was determined using a Specord 205 spectrophotometer (Analytic Jena, Wembley, UK).

In order to have a better understanding of the effects of contaminants, at each stage studied, sixty larvae from each treatment were photographed under a stereomicroscope. The larvae were then measured using ImageJ software to determine the total length, body width and length and arm length.

All statistical analyses and graphical representations were conducted using XLSTAT® software. The results were expressed as mean ± standard error (SE). Data were transformed when conditions of normal distribution and homogeneity of variance were not met and were analyzed using analysis of variance (ANOVA) followed by post-hoc Tukey's honestly significant difference (HSD) tests. The relationship between enzymatic activities was measured by Pearson correlation coefficient. Differences were considered statistically significant at $p < 0.05$.

Recent studies suggest that exposure to different contaminants, including trace elements, may cause a cascade of physiological events such as the production of ROS (Roccheri et al., 2004; Benedetti et al., 2015; Chan and Wang, 2019). When ROS production exceeds the cellular antioxidant defences, it results in oxidative stress, involved in

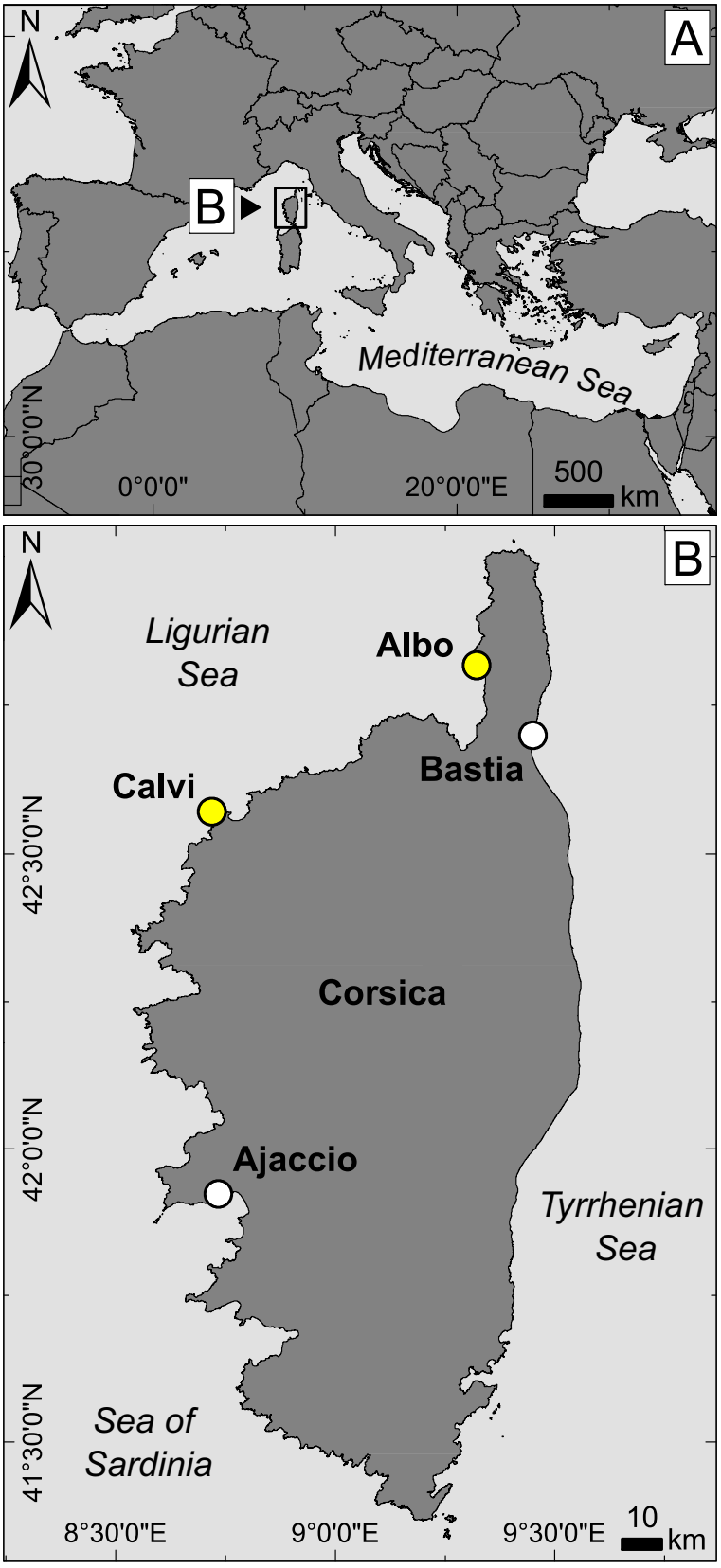

Fig. 1. Location of study coastal areas in Corsica Island (A; NW Mediterranean) and the sampling sites (B).

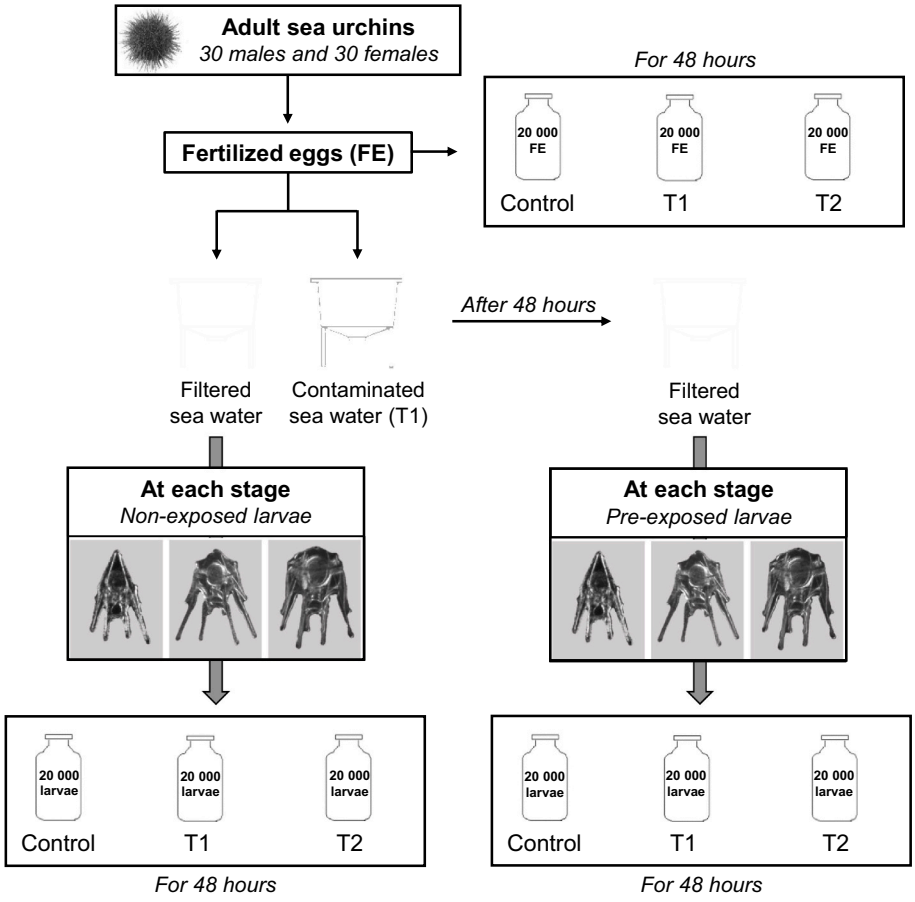

Fig. 2. Schematic overview of the experimentation performed with sea urchins from each site. All embryolarval stages studied (fertilized eggs (FE), 4-arm; 6-arm and 8-arm) were exposed for 48 h to a treatment 1 (T1) and 2 (T2).

Table 1
Average concentration recorded near an old asbestos mine at Canari, Corsica, France (μg L^{-1}; El Idrissi et al., 2022) and trace elements concentration tested from larvae produced by sea urchins sampled at Calvi and Albo.

	Co	Cr	Cu	Fe	Hg	Ni	Zn
Average concentration (μg L^{-1})	0.02	0.15	0.30	1.10	0.40	1.38	1.30
Treatment 1: 5-fold concentration (μg L^{-1})	0.1	0.75	1.5	5.5	2	6.9	6.5
Treatment 2: 10-fold concentration (μg L^{-1})	2	1.5	3	11	4	13.8	13

DNA damage, protein oxidation, lipid peroxidation impacting the survival of marine organisms (Winston and Di Giulio, 1991; Nieto et al., 2010; Halliwell and Gutteridge, 2015; Chan and Wang, 2019). In order to offset molecular and cellular damages, aerobic organisms have developed mechanisms including an assortment of antioxidant enzymes (Valavanidis et al., 2006; Vlahogianni and Valavanidis, 2007; Ighodaro and Akinloye, 2018). Some studies reported biomarker responses of oxidative stress in organisms to trace elements contamination (Farombi et al., 2007; Sappal et al., 2009; Liu and Wang, 2016; Chan and Wang, 2019). Interference with cellular redox regulation is a major mechanism for the toxicity of trace elements (Beyersmann and Hartwig, 2008; Benedetti et al., 2015). For example, Cu and Fe are widely known to actively mediate ROS production through Fenton and Haber-Weiss reactions and could alter cellular redox balance (Chan and Wang, 2018). However, the results of this study show that there is no significant difference in the specific activity of antioxidant enzymes depending on the concentrations used (Fig. 3A). Thus, these concentrations are probably not high enough to create oxidative stress in *Paracentrotus lividus* larvae, although they are 5 to 10 times higher than those at the contaminated sites (Table 1; Ternengo et al., 2018; El Idrissi et al., 2022). A recent study has shown that the number of trace elements also plays an important role in the effects on sea urchin larvae (El Idrissi et al., 2022). A mixture with higher diversity of trace elements would probably have had a greater impact on the mechanism against oxidative stress in sea urchin larvae.

Despite the absence of significant differences in enzymatic response to the various treatments, biometrics differences have been reported (Fig. 4). This method of measuring larvae is therefore probably more suitable and sensitive when concentrations are low. Larvae are significantly lengthier when they are contaminated (Fig. 4). This could be justified by the fact that the mixture used in this study is composed for the most part by essential trace elements, fundamental for most physiological processes of living organisms (Janssens et al., 2009; Yamaguchi et al., 2009; Ghribi et al., 2020). A phenomenon of hormesis characterized by an improvement of the biological aptitude at low dose had been assumed in the study of El Idrissi et al. (2022). This is a response, generally favorable, to low-dose exposures to contaminants or stress-generating phenomena (Mattson, 2008). Thus, the biological response to organic or inorganic stress would not necessarily lead to a negative effect on short-term growth (Chapman, 2002b; Pétinay et al., 2009). In this study, this hypothesis can be refuted because there is no difference in specific stress biomarker activity when the larvae were contaminated or not (Fig. 3A). Several authors reported the sensitivity of the

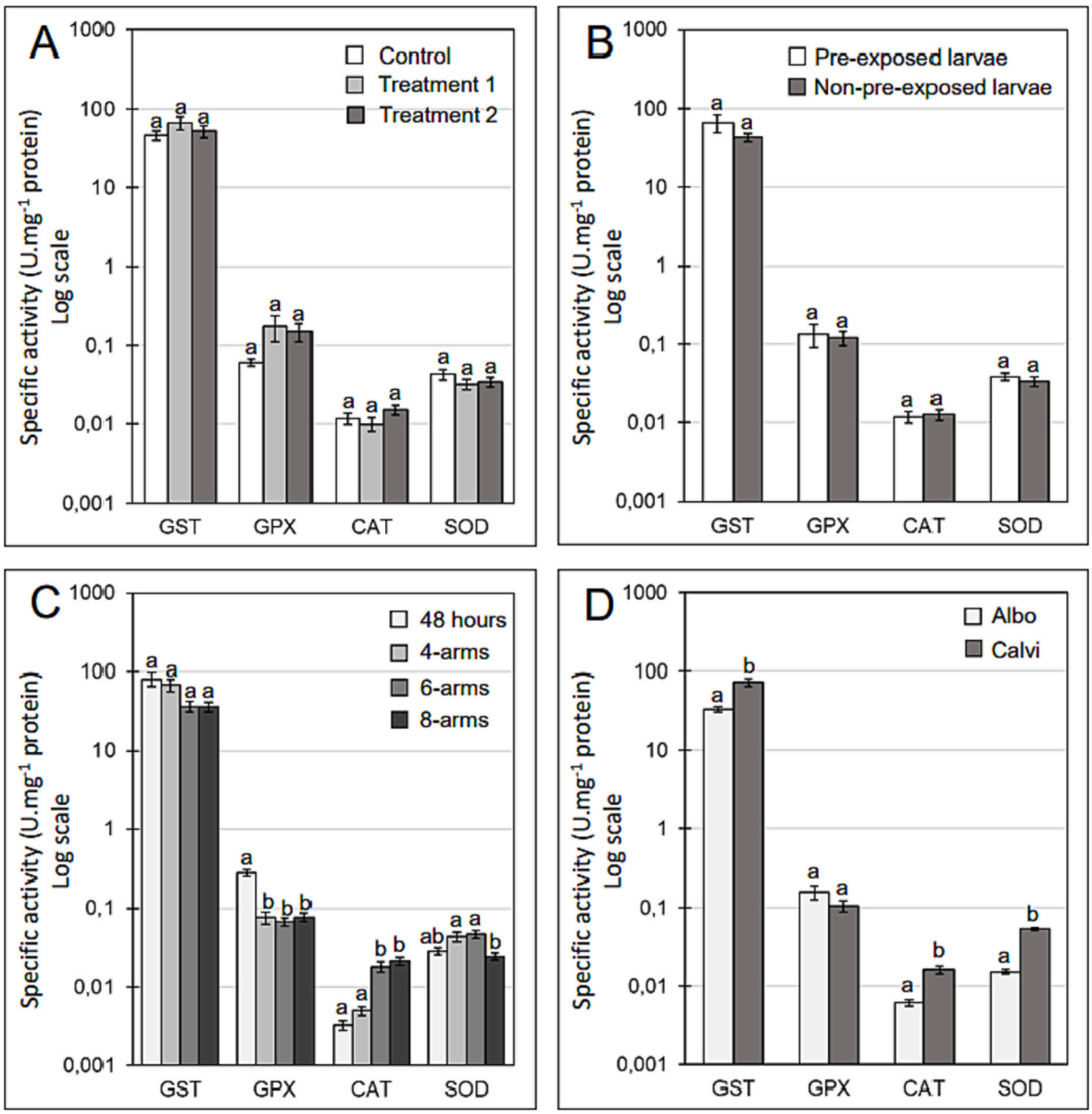

Fig. 3. Changes in specific activities in *Paracentrotus lividus* larvae according to (A) contaminant concentrations, (B) pre-exposure of the fertilized eggs, (C) developmental stage and (D) the origin of the spawners. Dissimilar letters denote significant differences between groups (p-value < 0.05).

morphology of sea urchin larvae, especially with abnormalities, during different exposures to pollutants (Kobayashi and Okamura, 2004; Beiras et al., 2012; Migliaccio et al., 2014; Gharred et al., 2016). However, in this work, there was no malformation as described by Carballeira et al. (2012). The concentrations used in this research are probably not sufficient to induce a stress biomarker response and therefore malformation of the larvae. Transcriptional responses might be more sensitive but these do not necessarily correspond to contaminant effects and are more useful as biomarkers of exposure (Giuliani and Regoli, 2014; Benedetti et al., 2015).

A first stressor may precondition the species to be less sensitive to a second stressor (Crain et al., 2008). However, it appears that pre-exposure had no effect on sea urchin larvae in this investigation (Fig. 3B). Indeed, there is no variation of the specific activity of the four studied enzymes involved in oxidative stress when the larvae are in contact or not with contaminants at the embryonic stage (Fig. 3B). This seems to confirm the hypothesis that the contaminations used in these experiments are insufficient to induce an increase in oxidative stress.

The larvae were contaminated for only 48 h at each stage to determine whether there were different responses depending on the stage (Fig. 3C). This short period prevents organisms from acquiring resistance to contamination through physiological acclimatization (Benedetti et al., 2015). The embryonic development of sea urchin is characterized by crucial successive stages from fertilization to organogenesis (Byrne et al., 2009; Gharred et al., 2021). This early stage is therefore likely to be more sensitive than later stages and could explain a significantly higher GPX specific activity (Fig. 3C). SOD has a higher specific activity in stage 4 and 6-arms (Fig. 3C). The latter is a metalloenzyme using trace elements such as Cu and Fe as cofactor (McCord and Fridovich, 1969; Li et al., 2009; Zhang et al., 2010). Santon et al. (2003) and Zhang et al. (2010) demonstrated that Zn contamination at an environmentally relevant concentration can support SOD activity and thus play a protective role in delaying oxidative processes. This enzyme detoxifies the superoxide radical and thus provides protection against damage induced by free radicals (Zhang et al., 2010). This mechanism is one of the first lines of defence against oxygen toxicity (Winston and Di Giulio, 1991). Stages 4 and 6-arms probably have a better ability to respond to early signs of oxidative stress by catalyzing the conversion of

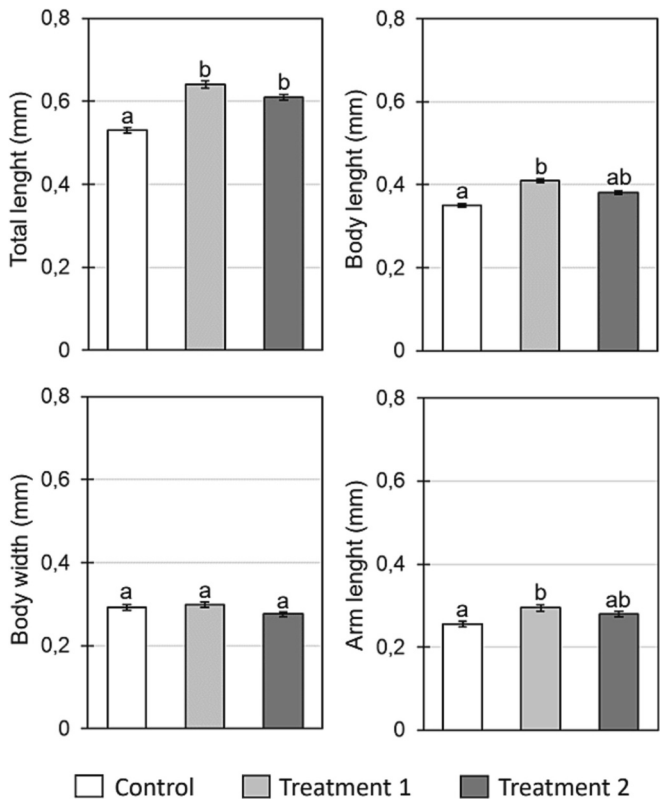

Fig. 4. Effects of exposure to different concentrations of a mixture of trace elements on development of *Paracentrotus lividus* larvae. Dissimilar letters denote significant differences between groups (p-value < 0.05).

the superoxide radical to hydrogen peroxide. The latter is also an important ROS (Rojkind et al., 2002) and leads to the formation of the hydroxyl radical in the presence of transition metals *via* the Fenton and Haber-Weiss reactions (Haber and Weiss, 1932; Winterbourn, 1995). It is important to underline that the hydroxyl radical is the most powerful oxidant of ROS with a high rate constant (Di Giulio et al., 1989; Gligorovski et al., 2015). It is therefore essential to eliminate hydrogen peroxide by metabolizing it into water and oxygen using certain enzymes such as CAT in order to avoid potential damage (Roméo et al., 2000; Ko et al., 2000). The results exhibited an increasingly higher CAT activity during larval development with 0.0032 ± 0.0004 U.mg^{-1} proteins at the embryonic stage and 0.2139 ± 0.0065 U.mg^{-1} proteins at the 8-arm stage (Fig. 3C). In this way, hydrogen peroxide potentially metabolized by SOD during stages 4 and 6-arms can be eliminated by CAT activity in order to limit or eliminate the potential impacts due to ROS. This suggests the ability of the larvae to respond to oxidative stress. Moreover, the specific activity of CAT is positively correlated with the specific activity of SOD (0.228; p-value 0.002). It is important to take this information into account in future works studying the responses of sea urchin larvae to different stresses. Indeed, ROS are produced during normal aerobic metabolism, and organisms use a number of enzymes to trap them, even in the absence of stress (Del Río et al., 2006; Mittler et al., 2004; Navrot et al., 2007). Moreover, ROS not only indicates the presence of deleterious oxidative stress but is also involved in the regulation of metabolic processes (Levine, 2002; Migdal and Serres, 2011). Consequently, it is necessary to interpret the responses of the stress biomarkers with prudence, taking into account the normal activity of the organism studied. It would be interesting to reproduce the experiment with higher concentrations in order to verify the hypotheses expressed in this study regarding the ability of the larvae to resist stress.

Several authors have indicated the importance of considering spawners quality in studies of the effects of contaminants on larvae (*e.g.* Bougis et al., 1979; Pétinay et al., 2009). El Idrissi et al. (2022) demonstrated significant differences in development and size between the larvae obtained by the spawners from Albo and those produced by spawners from Calvi. These size differences are confirmed in this work with significantly larger larvae when they are obtained by sea urchins from Albo (Fig. 5). Durkina and Evtushenko (1991) observed an acceleration in development in the descendants of individuals exposed to Cu. It is likely that larvae from Albo spawners develop more rapidly and are lengthier due to the contamination of the spawners (Ternengo et al., 2018; El Idrissi et al., 2020).

The specific activity of GST, CAT and SOD is significantly higher in larvae produced by sea urchins from Calvi (Fig. 3D). El Idrissi et al. (2022) has mentioned that Calvi is exposed to other sources of pressure than trace elements inducing spawners with lower quality gametes, explaining the slower development and smaller larvae. The quality of gametes is known to be greatly influenced by different environmental factors such as temperature, quality of the seawater (*e.g.* chemical quality, bacteriological quality) and also spawners feeding condition (*e.g.* Zhao et al., 2015; Gallo et al., 2020). This potential pressure, unknown at this time, may lead to larvae more sensitive to stressors with higher specific antioxidant enzyme activity (Fig. 3D). According to Benedetti et al. (2015), the difference in the ability to resist the environmental conditions would indicate the occurrence of adaptive mechanisms in chronically exposed organisms. The possibility of a genetic adaptation has already been demonstrated in long-term exposure (Uthicke et al., 2019; Ruocco et al., 2020) and it is now widely accepted that offspring inherit epigenetic information from their parents (Benedetti et al., 2015; Crean and Immler, 2021). This may provide some protection (Amiard-Triquet et al., 2011; Munday et al., 2013; Foo and Byrne, 2016) but the effects are not necessarily adaptive and epigenetic inheritance may also increase negative consequences of environmental change if parents transmit stress to future generations (Bonduriansky and Crean, 2018; Crean and Immler, 2021). In accordance with Lawrence (1990), biological stress would result in a decrease in production. This suggests that energy will be used in priority to metabolize enzymes against oxidative stress and less for growth. Therefore, sea urchins are characterized by high levels of phenotypic plasticity (Zhadan et al., 2017; Ruocco et al., 2020) and their morphological and physiological characteristics are subject to changes during the adaptation to selected environmental conditions (Ruocco et al., 2020).

The lower specific activity in larvae produced by spawners from Albo may also be attributed to an inhibition caused by contaminants. While some defences can be induced, others might be inhibited, or induced as the first phase of a response and then depleted at longer periods (Benedetti et al., 2015). These larvae are susceptible to being more impacted by oxidative stress, because less protected, while those produced by the spawners from Calvi have a better defence with a higher specific activity. In order to confirm or refute these hypotheses, it would be interesting to reproduce this experiment with higher concentrations of trace elements, to explore the level of expression of key genes in the adaptation of the stress response and also to undertake an extensive study in the Calvi area.

Sea urchins are key species in the structuring of marine ecosystems (Boudouresque and Verlaque, 2013). Their larval stage constitutes a critical period in their life cycle because the decrease in their survival rate can reduce the long-term viability of adult populations (Martin et al., 2011; Richardson et al., 2021). Consequently, it is necessary to improve our understanding of the effects of stress responses to different biotic and abiotic parameters. To our knowledge, this is the first time that a study has assessed stress responses over the entire larval cycle. Hence, this study provides baseline information for future investigations assessing the effects of environmental stress on sea urchin larvae.

CRediT authorship contribution statement

O. El Idrissi: Formal analysis, Investigation, Writing – original draft,

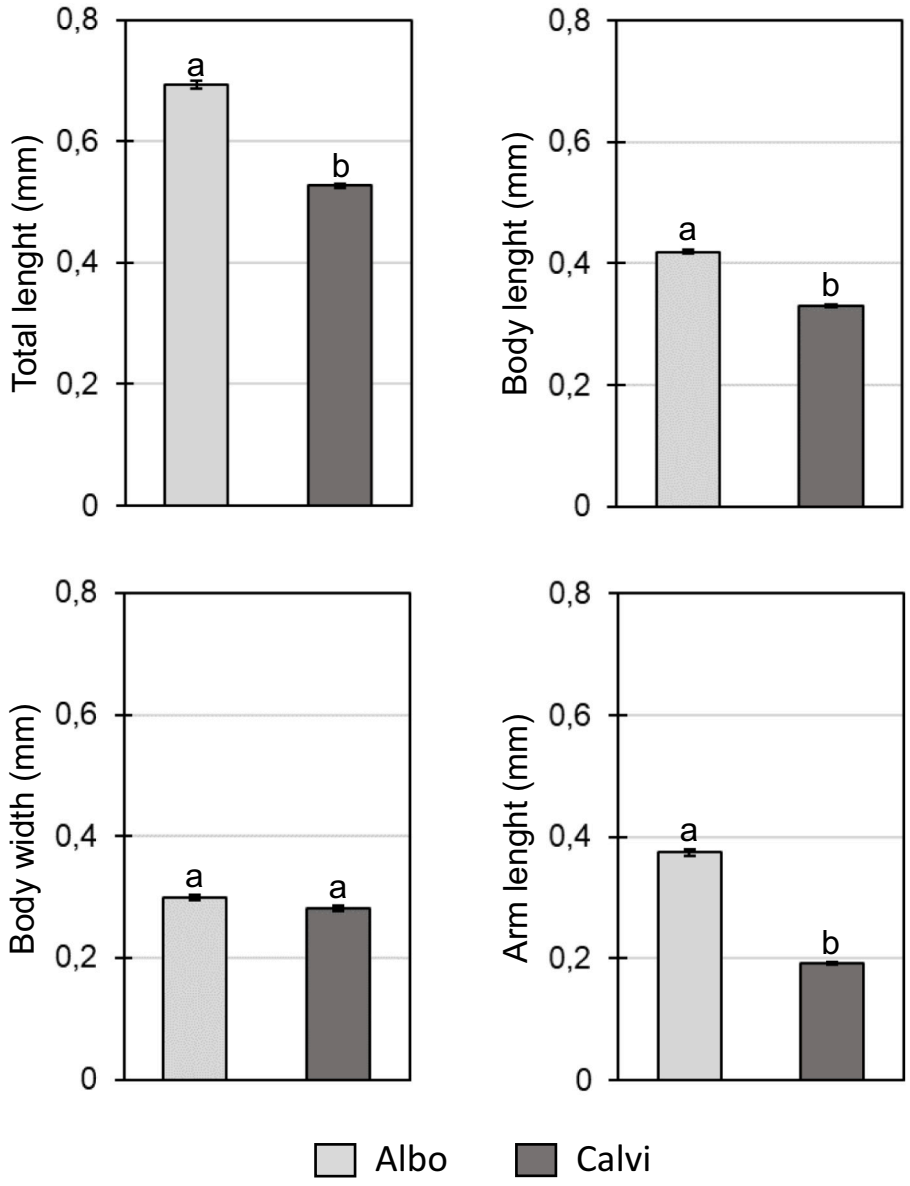

Fig. 5. Morphological measurements of larvae from spawners harvested at Albo and at Calvi. Dissimilar letters denote significant differences between groups (p-value < 0.05).

Writing – review & editing. **J. Santini:** Writing – review & editing, Funding acquisition, Resources. **M. Bonnin:** Investigation. **M. Demolliens:** Investigation. **A. Aiello:** Funding acquisition, Resources. **S. Gobert:** Writing – review & editing, Funding acquisition, Resources. **V. Pasqualini:** Writing – review & editing, Funding acquisition, Resources. **S. Ternengo:** Writing – review & editing, Funding acquisition, Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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