Effects of Seawater Acidification on Echinoid Adult Stage

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Contributor: Davide Asnicar , Maria Gabriella Marin

The continuous release of CO_2 in the atmosphere is increasing the acidity of seawater worldwide, and the pH is predicted to be reduced by ~0.4 units by 2100. Ocean acidification (OA) is changing the carbonate chemistry, jeopardizing the life of marine organisms, and in particular calcifying organisms. Because of their calcareous skeleton and limited ability to regulate the acid–base balance, echinoids are among the organisms most threatened by OA.

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1. Introduction

The usage of fossil fuels and deforestation are constantly emitting carbon dioxide (CO_2) into the atmosphere, increasing its concentration [1]. This is recognized to be the most important factor causing climate change. Oceans play an important role in mitigating the greenhouse effect caused by CO_2 [2]. They have absorbed around 30–40% of the anthropogenic carbon dioxide [3][4], making the effects on land and the atmosphere milder but threatening marine organisms. Higher temperature and deoxygenation are causing the migration of animals towards other, more suitable environments, causing disruptions at the community level. Other climate change drivers are sneakier, and harder for animals to avoid. The increase in CO_2 absorbed by the ocean, due to the disruption of the carbonate system and the increase in H^+ in seawater [5], is slowly but steadily lowering the pH of the marine environment worldwide, causing ocean acidification (OA), which represents a problem to the marine biota [1][6][7]. Models (Intergovernmental Panel on Climate Change—IPCC, Representative Concentration Pathway RCP8.5) predict that the pH value of surface seawater will decrease by ~0.4 units by the end of this century if the CO_2 emissions continue in a “business-as-usual” scenario [1][8].

OA effects on marine biota have been studied broadly in the past decade, highlighting interspecific variability in the response to this stressor [9][10][11][12][13]. Different animals have different sensitivities towards stressors due to physiological, behavioural and reproductive differences, even within closely related groups [14][15]. For example, gut pH regulation was shown to differ in six Ambulacraria species and was correlated with different sensitivity to OA. In particular, the species with the best ability to regulate pH were the most sensitive towards acidification conditions in terms of both survival and growth [9].

Calcifying organisms are especially threatened by acidification, due to the reduction in calcium carbonate ($CaCO_3$) saturation and, therefore, bioavailability [7]. For example, the mortality rate of oceanic copepods increased by 50%

when animals were exposed to a reduction of 0.2 pH units [16]. However, the range of tolerance to pH variations and calcium carbonate bioavailability can vary among calcifers. Echinoderms have a calcareous skeleton mainly constituted of aragonite and calcite ($CaCO_3$ crystal forms) with a high magnesium calcite ($MgCO_3$) content [17]. $MgCO_3$ solubility is higher than $CaCO_3$, resulting in increased vulnerability of echinoderms to OA [18][19]. This is particularly evident in the Echinoidea class since sea urchins are highly calcified.

Because of their important role as a keystone species and their high sensitivity and rapid response to environmental changes, echinoids have been extensively used as model species in ecology and ecotoxicology studies to assess the effects of different stressors in the context of climate change and pollution [20][21][22].

2. Seawater Acidification (SWA) Effects on Echinoid Calcification

The mineralogical composition of sea urchins varies greatly among species, but also among individuals and among different structures of each individual [23]. In most echinoids, approximately 4% calcite has magnesium ions that substitute calcium ions. Mg-calcite is more soluble than calcite and therefore, in relation to the high Mg content, the skeletal structures of echinoids are especially weakened in a more acidic environment [17][23][24][25][26]. The Mg-calcite content of sea urchin skeletal structures, and therefore their solubility in acidified conditions, vary with latitude, being higher in warmer waters [23]. In all the collected studies concerning test skeletal mineralogy and the related ability to tolerate mechanical stress, 7 out of 12 species showed alterations due to low pH. Alterations were detected in both short-term and long-term exposure.

S. virgulata, exposed at a pH reduced by 0.4 and 0.6 units [27], after 14 days had less calcite and lost weight. *S. droebachiensis* instead showed traces of carbonate dissolution after 42 days, but only at the greatest ΔpH (0.81 compared with control) [28]. In the other four species subjected to longer exposures (from 56 days up to being resident in vent systems), low pH conditions did not cause a variation in the calcification. Only one case of long exposure (146 days) to reduced pH resulted in decreased mechanical properties of the *T. gratilla* skeleton. The force needed to break the sea urchin test was lower if animals were maintained at low pH compared with those at pH 8.1. However, the effect of SWA was significant only if the ΔpH was −0.5 units, and not in the case of 0.3 [29].

Alterations in calcification were present also in animals resident in CO_2 vents. Differences in the element composition were found in *P. lividus* and *A. lixula* specimens sampled in volcanic vent systems in the Mediterranean Sea. In particular, in the test of animals sampled in three acidified sites (ΔpH 0.36, 0.61 and 0.63 compared with the control site, pH 8.11), manganese and strontium contents were significantly higher, whereas zinc content was significantly lower [30]. Those specimens also suffered higher skeletal degradation with microfractures visible using scanning electron microscopy. Species-specific differences were found, with more severe effects in *P. lividus* than *A. lixula* [30]. However, the effect of local variability is a key point that must be considered in the response of calcification to SWA. Indeed, a similar study performed in another volcanic vent system in the Mediterranean Sea (local pH 7.63, reduced by 0.3 units compared with the control site) showed that *A. lixula* was more sensitive to SWA than *P. lividus*. Alterations in the gene expression were associated with decreased mechanical properties of the spines and test in *A. lixula* [31]. Nonetheless, in both studies, *A. lixula* maintained higher abundance in the vent sites compared with *P. lividus* [30][31]. This suggested that other factors were involved in the maintenance of the populations (e.g., larval plasticity influencing the settlement).

The duration of exposure to SWA has major relevance to the occurrence of skeletal mineralogy changes. This suggests that echinoids can maintain active calcification processes, making the carbonate bioavailability stable [32]. In addition, SWA effects are negligible in the case that the ΔpH is smaller than 0.4, and are usually more severe when ΔpH is greater than 0.4 units. For example, the sea urchin *S. variolaris* kept for 210 days at a pH reduced by 0.2 units did not show effects on the skeletal mineralogy and the spine integrity. However, if specimens were kept at a pH reduction of 0.5 units, the skeletal characteristics varied significantly compared with the control [33]. In the study of Dery and colleagues, traces of corrosion were highlighted in *Eucidaris tribuloides* exposed to pH 7.4 for 45 days, whereas no effects were observed at pH 7.7 [34]. Several experiments demonstrated that the prolongation of the exposure can lead to an improvement in the condition, resulting in a decreased acidification impact. The reduction in calcium carbonate saturation in seawater can be compensated for by modulating gene expression, as reported by Emerson and colleagues [35]. Indeed, *Lytechinus variegatus* exposed to pH 7.7 and 7.47 for 56 days showed impairment in the development of spines but the genes involved in the regeneration process were upregulated. This suggested that, with time, those animals would have been able to face SWA [35].

The difficulty of building calcareous structures in an acidified environment can lead to impairment in the growth of the skeletal parts of echinoids (test, jaws, and spines). This was the case for *S. droebachiensis* [28] and *P. lividus* [36] maintained at a pH reduced by 0.34–0.81 units for the former, and 0.2–0.5 units for the latter, for 42 and 60 days, respectively. An impairment of the growth was also found in a *T. gratilla* aquaculture system with a high density of individuals and a scarce seawater change [37]. Indeed, this led to a reduction in the pH in the tanks with an output similar to ocean acidification. The growth of *H. erythrogramma* and *Echinometra* spp., instead, was not impaired by low pH conditions, either in a laboratory exposure [38][39][40], or in animals collected in a vent system [41].

As seen above, echinoids can counteract the adverse effects of environmental acidification on calcification through compensatory mechanisms; however, the overall skeletal mechanical properties may be compromised. For example, in *T. gratilla* maintained for 146 days at pH 8.1–7.8–7.6, the mineralogy of the skeleton did not vary, but the force needed to break the skeleton was significantly lower [29], possibly due to alteration of the structure. On the other hand, *P. lividus* resident in a vent system had the same mineral composition as the outside-vent animals [42], and the force applied to break the skeleton was not significantly different in acidic and not-acidic conditions [43]. Similarly, the mechanical properties (i.e., resistance to perforation and compression, fracture force, and test stiffness) of *P. lividus* exposed to pH 7.9 and 7.8 for 360 days were not different from those of the control at pH 8.1 [43]. The last two examples, in contrast with that found by Byrne and colleagues [29], suggest again that the longer the exposure, the better the response of sea urchins to reduced pH. However, *T. gratilla* and *P. lividus* have different growth rates, being faster in the former species. This condition can make *T. gratilla* more susceptible to SWA, as it needs to deposit more calcium carbonate in less time, with negative consequences on the mechanical properties of calcareous structures. Moreover, the skeletal structure's degradation has been correlated with changes in the accumulation of essential and non-essential metals in *P. lividus* and *A. lixula* resident in CO_2-vent systems [30].

Whether or not the echinoids are able to maintain the calcification rate, they may face a cost [44], as also seen for other calcifers [45]. Indeed, other physiological processes are impacted by SWA and these may be more relevant to study than the calcification processes. Increased CO_2 concentration in seawater is associated with hypercapnia (i.e., an abnormal increase in CO_2 partial pressure in organisms) and oxygen loss [1]. This condition may generate stress, suppressing organisms' metabolism [46] and compromising processes such as behaviour and reproduction [47][48][49].

3. SWA Effects on Echinoid Physiology

The increase in CO_2 concentration can impair the ion exchange between extra- and intra-cellular environments, inducing acidosis [50], which, in cascade, can lead to metabolic alterations [51]. Most relevant effects associated with hypercapnia include (i) metabolism alteration, (ii) modification of the tissue acid–base regulation, (iii) reduced rates of protein synthesis, (iv) increase in oxygen consumption and ventilation rate, and (v) enhanced production of adenosine in nervous tissue, potentially inducing behavioural depression [49][52].

Echinoderms are considered hypometabolic, since they show low respiratory rates and are not efficient in balancing the concentration of ions in their extracellular fluids [46]. Their metabolism is influenced not only by the size and nutritional state but also by several environmental parameters, such as seasonality, oxygen tension, water temperature, salinity and pH [46][53][54]. Therefore, in sea urchins, the coelomic fluid pH might be strongly influenced by environmental pH, as they show a very low or partial compensation capability [53][55]. However, from the literature survey, the coelomic fluid of the Echinoidea seems to respond well to SWA. In 61% of the papers where the coelomic fluid pH was assessed, no differences were found between animals maintained at low and natural pH. The buffering capacity is maintained for animals from the equatorial to the temperate regions. Stumpp and colleagues [56] suggested that two strategies can be adopted against environmentally induced acidosis: HCO_3^- accumulation to compensate for acid–base disruption or proton extrusion mediated through NH_4^+ excretion.

Another effect of hypercapnia is the increase in the concentration of reactive oxygen species in animal tissues [57], thus inducing the organism to increase antioxidant defence mechanisms in order to diminish the oxidative damage. Both short- and long-term exposures showed the induction of stress-related enzymatic activities in the animal tissues [27][42][58] and no oxidative damage was observed (although oxidative damage was assessed only in animals resident in CO_2 vents [42]). Overall, the antioxidant capacity seems to be efficient in maintaining the homeostasis of the animals, even though the effects of hypercapnia have been observed in the acid–base regulation.

The acid–base balance is, indeed, one of the endpoints that are the most influenced by the pH reduction. The three sea urchin species *P. lividus*, *T. ventricosus* and *E. mathaei* showed the regulation of the dissolved inorganic carbon (DIC) and alkalinity to maintain the pH level in the coelomic fluid [40][59][60], even if exposure conditions were not the same. In another experiment carried out with *P. lividus* by Cohen-Rengifo and colleagues [36], the exposure for 60 days at a pH reduction of 0.2 and 0.5 did not cause a modification in the acid–base regulation. In addition, the pH of the coelomic fluid and the respiration rate of those animals were not altered, suggesting the acclimation of *P. lividus* for those endpoints at least [36]. This was confirmed by the work of Marčeta and colleagues [58] where *P. lividus* maintained for 60 days at pH 8.1, 7.7 and 7.4 showed no significant variations in respiration, ammonia excretion rates and assimilation efficiency [58]. In a shorter-term experiment (19 days), at pH 8.1, 7.7 and 7.4, *P. lividus* showed evidence of stress resulting in a coelomic fluid pH reduction and a respiration rate increase [55]. In particular, the oxygen uptake of *P. lividus* maintained at 10 °C at seawater pH levels of 7.7 and 7.4 was significantly higher compared with the control [55]. However, differences were not present in the experimental groups maintained at 16 °C, suggesting that the response observed varies depending on the interaction of both pH and temperature. Indeed, it is known that respiration and metabolic rates can change with temperature as well as other biological aspects, such as feeding activities [61][62][63]. Other environmental stressors instead may exacerbate SWA negative effects. Indeed, antioxidant capacity alteration was found in *P. lividus* specimens maintained in copper-spiked (0.1 µM) water at a pH reduced by 0.4 units, with additive effects due to the combination of high $p\mathrm{CO}_2$ and contaminant [59]. Thus, future studies need to use a multiple-stressor approach in order to understand how echinoids will respond to future climate change scenarios.

Metabolic modifications linked to high $p\mathrm{CO}_2$ have been reported in both marine vertebrates [64] and invertebrates, but in the latter group, the effects are more evident, considering their poor ability to regulate extracellular pH [49][52][65]. In fact, in organisms such as molluscs, corals and echinoderms, a decrease in seawater pH is often associated with elevated metabolic rates, since more energy to maintain homeostasis [66] and carbonate structures is required [47]. Respiration and nitrogen excretion are useful tools to assess the physiological status of an organism and have been used as such for decades [67]. The ratio between the oxygen consumed and the nitrogen excreted indicates the level of activity of oxidative and protein metabolism [67][68]. Moreover, O/N has been used as an index of stress related to variations in biotic and abiotic factors, such as reproductive cycle, food quality and availability, temperature, dissolved oxygen, salinity and pollution [68][69].

Results about ammonia excretion and respiration rates are summarized. Contrary to expectations, for both endpoints, minimal effects of pH or acclimation to this driver have been reported. Only a few studies showed effects linked to low pH exposure, mostly in short-term experiments that lasted a few weeks [53][55][56][70]. In adult sea urchins of *Strongylocentrotus droebachiensis* exposed to very low pH levels (7.60–7.16) for 45 days, the rate of NH_4^+ excretion was significantly higher [56] compared with the control at pH 8.01. Since the respiration rate did not change significantly in sea urchins maintained at low pH conditions, the oxygen:nitrogen atomic ratio was significantly lower [56], suggesting that the catabolism of proteins was prevalent compared with the catabolism of lipids and carbohydrates [68]. Similarly, *P. lividus* specimens maintained at pH 7.6 for 180 days showed a significantly higher ammonia excretion rate in the trials carried out after 60 and 90 days of exposure. In the following trials, instead, the values were no more significantly different from the control at pH 8.0 [71]. However, the importance of local biological adaptation was highlighted by Asnicar et al. [71] where two groups of sea urchins with different ecological backgrounds were used. The group that experienced more environmental variability was shown to be more resilient and able to acclimate to SWA sooner than the other group. *S. neumayeri* maintained for 40 months at a pH reduced by 0.26 and 0.46 units showed an increase in respiration rate and energy consumption at the lowest pH value tested [72]. However, the overall somatic and reproductive growth were not impaired. This suggests that animals may take time to acclimate to low pH conditions and that this time-frame may differ among the various species and even within the same species. *H. erythrogramma* specimens maintained at pH 7.6 for two months showed an increase in the oxygen uptake rate, compared with the control condition. Respiration was even enhanced in the exposure combination of pH 7.6 and +5 °C temperature [53]. Despite this boost in respiration rate, the feeding rate (a proxy of the ability to obtain energetic resources) was not affected by the tested SWA condition. If higher energy demand is not accompanied by higher energy uptake, somatic growth and gonad development may be compromised. This would eventually result in weaker and smaller sea urchins that could be more threatened by abiotic and biotic challenges. However, in the studies considered, sea urchin size was not affected by low pH [35][73].

Interestingly, the endpoints summarized here under the category “Food intake”showed more alterations in the long-term exposures (e.g., [70][74][75]) than in the short-term ones (e.g., [53][60][73]). As reported by Wang and colleagues [70], physiological responses might be time-dependent, with differences among the various endpoints considered.

Sea urchins were demonstrated to be able to acclimate their metabolism even under low pH conditions, if enough time is given to them. Indeed, animals sampled in a naturally acidified site (the volcanic vent site in Ischia), and therefore exposed to SWA conditions throughout their whole life, have a similar metabolism to other sea urchins sampled outside the vent site [42].

Lastly, the immune system of the sea urchins showed the ability to acclimatize to seawater acidification, but the response is species-specific. Short-term exposure (5 days) of *L. variegatus* and *E. lucunter* to pH 7.6 and 7.3 revealed the initial depression of the immunity capacity with a lowered number of haemocytes and their reduced phagocytic activity [76]. However, in another study, after an initial disruption, the recovery of the immune system was shown in *S. droebachiensis* after 7 days of exposure to a reduction of 0.5 pH units. No signs of disruption or depression were detected in the *P. lividus* immune system, when resident in CO_2 vents [42][77].

4. SWA Effects on Echinoid Behaviour

There is evidence that SWA also affects animals’ behaviour. The literature is still sparse, although growing fast [64][78][79][80][81]. Linked to extracellular acidosis, the altered ion gradient across the neural membrane induces membrane depolarization, neural pathway excitation and ultimately an altered behaviour [48][82]. As stated above, hypercapnia and low pH may also promote the enhanced production of adenosine in nervous tissue, which can result in behavioural alteration [49][52]. Both invertebrates and vertebrates can be influenced [78], although the impact of SWA on vertebrate behaviour seems to be weak [64][83] compared with invertebrate responses [80]. SWA effects on invertebrate behaviour have been explored in many taxa, among which are the echinoids, and the results show a range of negative, neutral or positive responses [80]. It must be taken into account that the magnitude of changes in behaviour, in the context of future SWA scenarios, seems to be species-specific and varies depending upon the ecosystem and the particular behaviour considered.

In literature, only 10 experiments investigated the effects of SWA on the behaviour of echinoids. Among the 24 endpoints considered, 10 were altered by lower pH. Considering the ecological relevance of sea urchins' behavioural traits, it is increasingly important to assess their modifications in relation to environmental stressors. Behavioural changes may lead to remarkable effects on the animal's fitness and at the community or the ecosystem level [61][84][85][86]. Considering behaviours such as feeding and predator avoidance, SWA can affect the population and community structure. The effects can be direct on sea urchins or indirect on their food source. For example, the exposure of the deep-sea echinoid *Strongylocentrotus fragilis* to a −0.46 pH reduction caused an increase in the foraging time [87]. On the other hand, the exposure of the algae *Ulva lactuca* to high pCO_2 (4000 μ-atm) resulted in an increase in unpalatable substances and the consequent decrease in grazing on the algae by the sea urchin *T. gratilla* [88]. The calcifying algae *Halimeda incrassata* significantly reduced its calcium carbonate content and therefore reduced its defence against grazers *L. variegatus* and *Diadema antillarum* [89]. Interestingly, in the work of Burnham and colleagues [73], the exposure of the sea urchin *L. variegatus* to a −0.3 units pH reduction for 42 days caused an alteration of the animals' feeding habits, but if the algae were also exposed to low pH, the sea urchins' preferences returned similar to those of the control [73]. Therefore, predictions about the balance between vegetation and foragers for the future are difficult and further investigation is required.

The righting is the action that a sea urchin executes to return to its natural aboral side-up position after a displacement in an inverse position [90]. A quick righting is linked to good physiological status, as it requires good coordinating capacities between the spines and tube feet [91], while changes in righting time are related to stress [92]. The covering behaviour consists of taking ambient elements (small rocks, shells or algae) with the tube feet to cover the aboral surface [93][94]. Sea urchin righting, covering and shelter-seeking behaviours enable the animal to escape from predators, reach crevices or seagrass meadows, prevent the occlusion of the apical openings of the water vascular system (madreporite) and seek protection from solar radiation and physical turbulence [95][96][97][98][99][100]. Investigating the possible impacts of acidification on behavioural endpoints could help to predict the sea urchins' responses in an acidification scenario as ecosystem engineers. A decrease in their reactions would lead to a major exposure to predators and radiation, and difficulties in finding food or reaching conspecifics for reproduction. It has been demonstrated that the exposure to low pH for 3 months led to a decrease in predator-avoidance behaviour of the sea urchin *P. lividus* [101]. This, together with the reduction in defensive capacity (i.e., thinner plates and spines weakness [101]) may compromise survival chance, with cascading effects on the benthic community.

Due to its simplicity, the righting response is the most common endpoint analysed in research aimed at evaluating sea urchin stress. The righting time was not impaired in *P. lividus* exposed for 60 or 180 days to a pH reduction of 0.3,0.4 and 0.6 units [58][71] and in *L. variegatus* exposed for 42 days to pH 7.60 (control pH 7.97) [73], or for 56 days to pH 7.7–7.47 (control pH 7.93) [35]. Among the research that investigated the righting response, this endpoint was significantly increased only in one case. Specimens of *S. fragilis* were exposed to three scenarios, with the pH reduced by 0.28, 0.69 and 1.31 units compared with the natural condition. The impairment in the righting response was significant in the two lowest pHs, which are extreme values with little relevance for near-future scenarios [74].

The shelter-seeking behaviour in relation to environmental stressors has been poorly studied [102][103][104] and was assessed under reduced pH conditions in only one experiment [71]. The experiment considered the shelter-seeking response to SWA of two sea urchin populations, both exposed for 180 days. Specimens were collected within a highly variable environment (the Lagoon of Venice) and in a coastal area, more stable in terms of physico-chemical characteristics. The two populations responded differently to the low pH condition. The shelter-seeking behaviour of lagoonal animals was impaired only slightly, particularly in the first months of exposure. Instead, the response of animals from the other site was affected by low pH, with a reduction in the number of sheltered sea urchins, distance travelled and animal speed. The lagoonal group managed to acclimate to low pH towards the end of the exposure, while the other did not [71]. Future studies should consider the shelter-seeking behaviour together with the righting, as the former might be a more sensitive endpoint.

Although it was investigated in one experiment only [36], the resistance to induced water flow seems to be another sensitive endpoint to consider. The dislodgment of *P. lividus* specimens subjected to a strong water flow was easier at low pH (7.7–7.4), suggesting lower adhesive strength in the tube feet [36]. For animals living close to the surface in the subtidal area or in intertidal pools, this would entail a greater risk of predation and the need to return quickly to a natural position. Nasuchon and colleagues [105] found that exposure to high $p\mathrm{CO}_2$ levels for 48 days caused a change in the proteomic profile of the tube feet in *Pseudocentrotus depressus*, resulting in reduced contraction force and weakened adhesion and therefore movement impairment. This was not confirmed in *P. lividus* exposed at pH 7.7 and 7.4 for 56 days, since the characteristics of the tube feet (extensibility, strength, stiffness and toughness) were similar to those in controls, suggesting that other biological features might be involved in the behavioural alteration [36].

5. SWA Effects on Echinoid Reproduction

Data concerning SWA effects on reproduction at the parental level were collected, and gonadal development, gonadal quality and female fecundity (i.e., number of eggs released) were considered.

The sea urchin *S. virgulata* exposed for 14 days to reduced pH showed lesions on the oocytes at pH 7.8 and 7.6 [27]. Gonads of *S. neumayeri* exposed to pH 7.8 and 7.6 for 30 days showed an increase in tissue damage, neoplasia and oocyte lesions [106]. The gonadal development of males of *Echinometra* sp. was delayed when animals were maintained for 70 days at pH 7.9 [32]. As seen for the previous endpoints considered, the longer the exposure, the more similar the results are between low-pH and control sea urchins (e.g., [107]). This was not the case for *H. pulcherrimus* maintained at pH 7.83 for 270 days, which showed a delay of one month in the development of the gonads compared with the control at pH 8.1 [75]. To explain this result, a reduction in food intake was hypothesized. Nonetheless, the female fecundity did not change between pH levels, suggesting that the delay was functional. The development delay may entail two detrimental effects: (i) delay of the spawning event to a less favourable period of the reproductive season; and (ii) occurrence of a spawning event with eggs in a lower amount or of lower quality. Both cases lead to unknown consequences for the filial generation, which may have to cope with unfavourable physico-chemical conditions and predation. In another experiment, Hazan and colleagues exposed *Echinometra* sp. specimens to pH 8.1 and 7.7 and checked the gonad status monthly for 330 days. The gonadal index and maturation at pH 7.7 were not different compared with the control [108]. The exposure of *Echinometra* sp. was longer than that experienced by *H. pulcherrimus* [75], but even considering the same time of exposure under experimental conditions, in the former case the gonadal maturation was not delayed under the SWA scenario.

In *T. gratilla*, the gonadal index, expressed as the ratio of gonad weight to animal weight, revealed significantly smaller gonads in specimens kept at low pH (7.8 and 7.6) for 146 days [109]. Although animals were fed ad libitum, even their total body weight was lower at reduced pH, but not significantly. A similar outcome was found in the work by Mos and colleagues [37], where *T. gratilla* was cultured in high density and the biogenic production of CO_2 led to effects similar to SWA with a reduction in gonad production. However, in this case, a reduction in somatic growth was also documented, after 42 days of exposure at pH 7.8 and 7.6. Overall, these results suggest that only after longer exposure to reduced pH, as in the work of Dworjanyn and Byrne [109], do sea urchins shift energy from gonadal to somatic growth. Similarly, *Echinometra* sp. sampled in a CO_2 volcanic vent system (pH 7.48) had smaller gonads compared with the control site specimens [41]. Interestingly, this was the only negative effect of pH noticed in the work of Uthicke and colleagues. As for the other parameters considered in that study, animals from the vents performed better than their counterparts at pH 8.0. Indeed, after a 17-month monitoring period, the average growth of the animals was significantly higher at the vent site [41].

Female fecundity is an important endpoint to consider in order to understand if a shift in energy allocation happened. As seen in the paragraph concerning SWA effects on physiology, the disruption of metabolism and therefore the reallocation of resources towards survival and growth rather than reproduction might take place in a short–medium-term exposure. This trend can change with the prolongation of the exposure, reallocating energy towards reproduction, as observed in *S. droebachiensis* exposed to pH 7.7 in a long-term exposure [107]. Indeed, the number of eggs released by a female was significantly lower after 120 days of exposure, but it was no longer different from control conditions (pH 8.1) after 480 days of exposure. The researchers concluded that after 480 days, animals were fully acclimated to the low pH and were able to use the energy stored to develop eggs, since they did not need it for other biological necessities [107].

Other aspects linked to reproduction success may be affected by SWA, enlarging the variety of endpoints to be studied. Many papers explored the effects of reduced pH on gametes, fertilization success, embryo and larval quality and fitness. In external fertilizers, SWA may have an important effect due to the limited buffering capacity of internal pH in sperm [110]. To achieve fertilisation, sperm are subjected to intense selection and competition, as only a small proportion will succeed in fertilizing an egg [111] and selection will favour high-quality ejaculate [112].

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