

Review

Effects of Seawater Acidification on Echinoid Adult Stage: A Review

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Abstract: The continuous release of CO₂ 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. In this review, 50 articles assessing the effects of seawater acidification on the echinoid adult stage have been collected and summarized, in order to identify the most important aspects to consider for future experiments. Most of the endpoints considered (i.e., related to calcification, physiology, behaviour and reproduction) were altered, highlighting how various and subtle the effects of pH reduction can be. In general terms, more than 43% of the endpoints were modified by low pH compared with the control condition. However, animals exposed in long-term experiments or resident in CO₂-vent systems showed acclimation capability. Moreover, the latitudinal range of animals' distribution might explain some of the differences found among species. Therefore, future experiments should consider local variability, long-term exposure and multigenerational approaches to better assess OA effects on echinoids.

Keywords: ocean acidification; echinoids; sea urchin; physiology; behaviour; calcification; respiration



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1. Introduction

The usage of fossil fuels and deforestation are constantly emitting carbon dioxide (CO₂) 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 CO₂ [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 CO₂ 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 CO₂ 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 [9–13]. 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 calcifiers. 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 [20–22]. If we consider their anatomy, physiology and life cycle, they represent an ideal bioindicator for the ongoing OA [23].

In past decades, much effort was devoted to understanding the potential effects of OA on echinoids by experimentally lowering the seawater pH to one or multiple high $p\text{CO}_2$ scenarios. However, most of the studies did not consider the extent of pH variability experienced in the field by the studied animals. Coastal environments, differently from the open ocean, are subject to high physico-chemical variability, which can promote adaptive responses and different sensitivity to OA [24–27]. Overlooking the local variability may lead to misleading and contrasting results which are not useful to predict animal responses to future OA scenarios [24,27].

Since most of the articles considered in this review did not take into account local adaptation and local natural pH data on a long timescale, we will refer to the pH reduction as seawater acidification (SWA) instead of OA, as a more comprehensive term.

Here, we summarized the findings of laboratory and field experiments that considered the maintenance of adult sea urchins at low pH conditions or comparisons of sea urchin specimens collected outside and within CO_2 volcanic vent systems (i.e., naturally acidified environments). The aim of the present article is not only to update the findings reported in previous papers (e.g., [23]), but also to provide a particular focus on key aspects of the echinoid adult stage to be considered in more depth in future studies. The articles collected assess the effects of SWA on the traits of adults' biology, such as calcification, physiology, behaviour and reproduction, without examining the gamete, larval and juvenile stages. Most studies on the SWA effect on sea urchins have been carried out using gametes and larvae, fewer have considered the juvenile stage, while a few dozen have focused on the effects on the adult stage.

To search for papers on the focal topics, a systematic literature research was carried out using Web of Science and Google Scholar databases, and the following keywords: "ocean acidification", "seawater acidification", "reduced pH", "sea urchin", "echinoid", "adult", "physiology", "calcification", "behaviour", and "reproduction", and their combinations. Studies where the OA conditions were achieved with other methods than CO_2 insufflation were excluded from the review.

From the survey of the literature, 50 papers (62 experiments in total; experiments within a paper are defined as exposures carried out with different species or different duration) were included in this review. In tables reported below, studies about calcification, physiology, behaviour and reproduction are listed. Most of the experiments examined multiple effects of decreased pH on the adult sea urchin biology (on average, 3–4 endpoints per article). A total of 29 experiments used only one condition of reduced pH (plus the control), while 23 used two reduced pH values and 9 used three reduced pH values. Of all the experiments, nine were conducted using animals resident in vent systems. Of all the studies exposing animals in the laboratory, 33% considered the pH changes that are predicted for the end of the present century or sooner (from 0.1 to 0.4 units of pH reduction). In total, 44% of the articles considered both a pH reduction in the range of 0.1–0.4 and more severe scenarios that might be reached by the end of the 24th century [1]. Other

works (23%) tested only a pH reduction greater than -0.4 or a too-severe scenario that is unlikely to be reached (e.g., the case of [28,29] where the highest pH reduction compared with the control was -1.3 and -1.8 pH units). Most of the negative effects were found in studies where ΔpH was higher than 0.4 ; for each endpoint analysed, 25% and 61% of the biological responses obtained were worsened by SWA if ΔpH in the experiment was ≤ 0.4 and >0.4 units, respectively.

Although most studies have been carried out using species from either the subtropical–temperate (43%; e.g., *Paracentrotus lividus*, *Heliocidaris erythrogramma*, *Hemicentrotus pulcherrimus*) or the equatorial area (36%; e.g., *Salmacis virgulata*, *Lythechinus variegatus*, *Echinometra* sp.), the latitudinal range covered the whole globe, including subpolar–polar species (e.g., *Strongylocentrotus droebachiensis*, *Sterechinus neumayeri*; 15%) and also deep-sea species (*Strongylocentrotus fragilis*, 6%).

Among the studies considered, the vast majority of the endpoints focused on the calcification and physiology of the animals exposed to reduced pH.

2. 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 [30]. 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 [17,30–33]. The Mg-calcite content of sea urchin skeletal structures, and therefore their solubility in acidified conditions, vary with latitude, being higher in warmer waters [30]. In all the collected studies concerning test skeletal mineralogy and the related ability to tolerate mechanical stress (Table 1, line 39–69; 19 studies), 7 out of 12 species showed alterations due to low pH. Alterations were detected in both short-term and long-term exposure.

Table 1. List of studies performed on echinoid adult stage to investigate effects of SWA on calcification. “pH level” contains the value of all the conditions tested; the first value is the control. In the case that the same article tested both a realistic ($\Delta\text{pH} \leq 0.4$; based on IPCC RCP8.5) and unrealistic scenario ($\Delta\text{pH} > 0.4$), the two conditions were split. Abbreviations: Eq.-Trop. = Equatorial–Tropical; Sub.-Temp. = Subtropical–Temperate; Temp.-Pol. = Temperate–Polar.

N	Response Detail	Species	Latitudinal Range	pH Level	ΔpH	Exposure Time (Days)	ΔpH Effect	Citation
1	Growth	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.1–7.8	0.3	14	=	[34]
2	Growth	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.1–7.6–7.4	0.5–0.7	14	=	[34]
3	Growth	<i>Echinometra mathaei</i>	Eq.-Trop.	8.04–7.69	0.35	49	=	[35]
4	Growth	<i>Strongylocentrotus intermedius</i>	Sub.-Temp.	8.10–7.82	0.28	60	Altered	[36]
5	Growth	<i>Strongylocentrotus intermedius</i>	Sub.-Temp.	8.10–7.68–7.55	0.42–0.55	60	Altered	[36]
6	Growth	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.7	0.2	60	=	[37]
7	Growth	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.4	0.5	60	Slower	[37]
8	Growth	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.04–7.78	0.26	90	=	[38]
9	Growth	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.92–7.64	0.28	140	=	[39]

Table 1. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Δ pH Effect	Citation
10	Growth	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.92–7.23–6.61	0.69–1.31	140	Altered	[39]
11	Growth	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.83	0.32	140	=	[40]
12	Growth	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.33	0.82	140	altered	[40]
13	Growth	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.8	0.3	146	=	[41]
14	Growth	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.6	0.5	146	Decreased	[41]
15	Growth	<i>Echinometra mathaei</i>	Eq.-Trop.	8.09–7.63	0.46	360	=	[42]
16	Growth	<i>Echinometra</i> sp.	Eq.-Trop.	8.06–7.89–7.79	0.17–0.27	600	=	[43]
17	Growth	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.72	0.26	1200	=	[44]
18	Growth	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.52	0.46	1200	=	[44]
19	Growth	<i>Echinometra</i> sp.	Eq.-Trop.	8.0–7.48	0.52	Resident	=	[45]
20	Growth	<i>Echinometra</i> sp.	Eq.-Trop.	8.0–7.48	0.52	Resident	Increase	[45]
21	Growth (jaw size)	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.7	0.2	60	Decreased	[37]
22	Growth (jaw size)	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.4	0.5	60	Decreased	[37]
23	Growth (ossicles)	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.00–7.66	0.34	42	Reduced	[46]
24	Growth (ossicles)	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.00–7.19	0.81	42	Reduced	[46]
25	Mineral ionic content	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.06–7.69	0.37	1	Altered	[47]
26	Mineral ionic content	<i>Arbacia lixula</i>	Sub.-Temp.	8.06–7.69	0.37	1	Altered	[47]
27	Mineral ionic content	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.05–7.73	0.32	4	Altered	[47]
28	Mineral ionic content	<i>Arbacia lixula</i>	Sub.-Temp.	8.05–7.73	0.32	4	=	[47]
29	Porosity	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.01–7.6	0.39	210	=	[48]
30	Skeletal degradation	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.68	0.37	45	Higher (Spines)	[49]
31	Skeletal degradation	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.39	0.66	45	Higher (Spines)	[49]
32	Skeletal degradation	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.65	0.39	45	Higher (Spines)	[49]
33	Skeletal degradation	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.41	0.63	45	Higher (Spines)	[49]

Table 1. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Δ pH Effect	Citation
34	Skeletal degradation	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.11–7.75–7.50–7.48	0.36–0.61–0.63	Resident	Higher	[50]
35	Skeletal degradation	<i>Arbacia lixula</i>	Sub.-Temp.	8.11–7.75–7.50–7.48	0.36–0.61–0.63	Resident	Higher	[50]
36	Skeletal integrity	<i>Echinometra</i> sp.	Eq.-Trop.	8.1–7.7	0.4	330	=	[51]
37	Skeletal integrity	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	=	[52]
38	Skeletal integrity	<i>Arbacia lixula</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	Lowered	[52]
39	Skeletal mechanical properties	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.8–7.7	0.2–0.3	30	=	[53]
40	Skeletal mechanical properties	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.00–7.66	0.34	42	=	[46]
41	Skeletal mechanical properties	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.00–7.19	0.81	42	Lower force and high dissolution	[46]
42	Skeletal mechanical properties	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.8	0.3	146	=	[54]
43	Skeletal mechanical properties	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.6	0.5	146	Decreased	[54]
44	Skeletal mechanical properties	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.01–7.6	0.39	210	=	[48]
45	Skeletal mechanical properties	<i>Echinometra mathaei</i>	Eq.-Trop.	8.09–7.63	0.46	360	=	[42]
46	Skeletal mechanical properties	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.9–7.8	0.1–0.2	360	=	[55]
47	Skeletal mechanical properties	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.865–7.65	0.155–0.37	Resident	=	[55]
48	Skeletal mechanical properties	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.1–7.8	0.3	Resident	=	[55]
49	Skeletal mechanical properties	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	=	[52]
50	Skeletal mechanical properties	<i>Arbacia lixula</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	Altered	[52]
51	Skeletal mechanical properties	<i>Sterechinus neumayeri</i>	Temp.-Pol.	8.1–7.8	0.3	Resident	=	[56]

Table 1. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Δ pH Effect	Citation
52	Skeletal mineralogy	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.00–7.66	0.34	42	=	[46]
53	Skeletal mineralogy	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.00–7.19	0.81	42	Dissolution	[46]
54	Skeletal mineralogy	<i>Echinometra</i> sp.	Eq.-Trop.	8.1–7.9	0.2	70	=	[57]
55	Skeletal mineralogy	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.8	0.3	146	=	[54]
56	Skeletal mineralogy	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.6	0.5	146	=	[54]
57	Skeletal mineralogy	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.8	0.18	Resident	=	[58]
58	Skeletal mineralogy (Aristotle's lantern)	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.83	0.32	140	Thinner	[40]
59	Skeletal mineralogy (Aristotle's lantern)	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.33	0.82	140	Thinner	[40]
60	Skeletal mineralogy (FTIR-TGA)	<i>Salmacis virgulata</i>	Eq.-Trop.	8.26–8.00	0.26	14	=	[59]
61	Skeletal mineralogy (FTIR-TGA)	<i>Salmacis virgulata</i>	Eq.-Trop.	8.26–7.81–7.63	0.45–0.63	14	Loss of weight, less calcite	[59]
62	Skeletal mineralogy (gene expr.)	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.7	0.23	56	=	[60]
63	Skeletal mineralogy (gene expr.)	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.47	0.46	56	Upregulated	[60]
64	Skeletal mineralogy (gene expr.)	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	=	[52]
65	Skeletal mineralogy (gene expr.)	<i>Arbacia lixula</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	Altered	[52]
66	Skeletal mineralogy (Mg, Sr, Ca)	<i>Stomopneustes variolaris</i>	Eq.-Trop.	7.96–7.76	0.2	210	=	[61]
67	Skeletal mineralogy (Mg, Sr, Ca)	<i>Stomopneustes variolaris</i>	Eq.-Trop.	7.96–7.46	0.5	210	Altered	[61]
68	Skeletal mineralogy (Mn, Sr, Zn)	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.11–7.75–7.50–7.48	0.36–0.61–0.63	Resident	Altered	[50]
69	Skeletal mineralogy (Mn, Sr, Zn)	<i>Arbacia lixula</i>	Sub.-Temp.	8.11–7.75–7.50–7.48	0.36–0.61–0.63	Resident	Altered	[50]

Table 1. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Δ pH Effect	Citation
70	Spine development	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.1–7.8	0.3	14	=	[34]
71	Spine development	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.1–7.6–7.4	0.5–0.7	14	Impaired	[34]
72	Spine development	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.7	0.23	56	=	[60]
73	Spine development	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.47	0.46	56	Impaired	[60]
74	Spine length	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.04–7.78	0.26	90	Decreased	[38]
75	Spine mechanical strength	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.68	0.37	45	=	[49]
76	Spine mechanical strength	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.39	0.66	45	=	[49]
77	Spine mechanical strength	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.65	0.39	45	=	[49]
78	Spine mechanical strength	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.41	0.63	45	Decreased	[49]
79	Spine tips integrity	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.1–7.8	0.3	14	=	[34]
80	Spine tips integrity	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.1–7.6–7.4	0.5–0.7	14	Dissolved (7,4)	[34]
81	Spines integrity	<i>Stomopneustes variolaris</i>	Eq.-Trop.	7.96–7.76	0.2	210	=	[61]
82	Spines integrity	<i>Stomopneustes variolaris</i>	Eq.-Trop.	7.96–7.46	0.5	210	Reduced	[61]
83	Test robustness	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.04–7.78	0.26	90	=	[38]
84	Test thickness	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.04–7.78	0.26	90	Thinner	[38]
85	Test thickness	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.8	0.3	146	=	[54]
86	Test thickness	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.6	0.5	146	Decreased	[54]

S. virgulata, exposed at a pH reduced by 0.4 and 0.6 units [59], 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 Δ pH (0.81 compared with control) [46]. 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 (Table 1). 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 Δ pH was -0.5 units, and not in the case of 0.3 [54].

Alterations in calcification were present also in animals resident in CO₂ 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 (Δ pH 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 [50]. 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* [50]. 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* [52]. Nonetheless, in both studies, *A. lixula* maintained higher abundance in the vent sites compared with *P. lividus* [50,52]. 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 [57]. In addition, SWA effects are negligible in the case that the Δ pH is smaller than 0.4, and are usually more severe when Δ pH 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 [61]. 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 [49]. 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 [60]. 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 [60].

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* [46] and *P. lividus* [37] 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 [62]. 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 [34,35,42], or in animals collected in a vent system [45].

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 [54], 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 [58], and the force applied to break the skeleton was not significantly different in acidic and not-acidic conditions [55]. 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 [55]. The last two examples, in contrast with that found by Byrne and colleagues [54], 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 CO₂-vent systems [50].

Whether or not the echinoids are able to maintain the calcification rate, they may face a cost [63], as also seen for other calcifiers [64]. Indeed, other physiological processes are impacted by SWA and these may be more relevant to study than the calcification processes. Increased CO₂ concentration in seawater is associated with hypercapnia (i.e., an abnormal increase in CO₂ partial pressure in organisms) and oxygen loss [1]. This condition may generate stress, suppressing organisms’ metabolism [65] and compromising processes such as behaviour and reproduction [66–68].

3. SWA Effects on Echinoid Physiology

The increase in CO₂ concentration can impair the ion exchange between extra- and intra-cellular environments, inducing acidosis [69], which, in cascade, can lead to metabolic alterations [70]. 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 [68,71].

Echinoderms are considered hypometabolic, since they show low respiratory rates and are not efficient in balancing the concentration of ions in their extracellular fluids [65]. 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 [65,72,73]. 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 [72,74]. However, from the literature survey, the coelomic fluid of the Echinoidea seems to respond well to SWA. In 61% of the papers considered in this review where the coelomic fluid pH was assessed, no differences were found between animals maintained at low and natural pH (Table 2). The buffering capacity is maintained for animals from the equatorial to the temperate regions. Stumpp and colleagues [75] suggested that two strategies can be adopted against environmentally induced acidosis: HCO₃[−] accumulation to compensate for acid–base disruption or proton extrusion mediated through NH₄⁺ excretion.

Table 2. List of studies performed on echinoid adult stage to investigate effects of SWA on physiology. “pH level” contains the value of all the conditions tested; the first value is the control. In the case that the same article tested both a realistic ($\Delta\text{pH} \leq 0.4$; based on IPCC RCP8.5) and unrealistic scenario ($\Delta\text{pH} > 0.4$), the two conditions were split. Abbreviations: Eq.-Trop. = Equatorial–Tropical; Sub.-Temp. = Subtropical–Temperate; Temp.-Pol. = Temperate–Polar.

N	Response Detail	Species	Latitudinal Range	pH Level	ΔpH	Exposure Time (Days)	Specific Effect	Citation
1	Absorption efficiency	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.72	0.26	1200	=	[44]
2	Absorption efficiency	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.52	0.46	1200	=	[44]
3	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.06–7.69	0.37	1	Altered	[47]
4	Acid–base regulation	<i>Arbacia lixula</i>	Sub.-Temp.	8.06–7.69	0.37	1	=	[47]
5	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.05–7.73	0.32	4	Altered	[47]

Table 2. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Specific Effect	Citation
6	Acid–base regulation	<i>Arbacia lixula</i>	Sub.-Temp.	8.05–7.73	0.32	4	Altered	[47]
7	Acid–base regulation	<i>Arbacia lixula</i>	Sub.-Temp.	8.04–7.72	0.32	4	=	[76]
8	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.04–7.72	0.32	4	Altered	[76]
9	Acid–base regulation	<i>Psammechinus miliaris</i>	Sub.-Temp.	7.96–7.44–6.63–6.16	0.52–1.33–1.8	7	Altered	[29]
10	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.14–7.68	0.46	14	Altered	[77]
11	Acid–base regulation	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.98–7.51–7.11–6.65	0.47–0.87–1.33	31	Altered	[39]
12	Acid–base regulation	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.68	0.37	35	=	[78]
13	Acid–base regulation	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.39	0.66	35	=	[78]
14	Acid–base regulation	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.65	0.39	35	=	[78]
15	Acid–base regulation	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.41	0.63	35	Altered	[78]
16	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.98–7.66	0.22	35	Altered	[78]
17	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.98–7.47	0.51	35	Altered	[78]
18	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.7	0.2	60	=	[37]
19	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.4	0.5	60	=	[37]
20	Acid–base regulation	<i>Echinometra mathaei</i>	Eq.-Trop.	8.09–7.63	0.46	360	Higher	[42]
21	Acid–base regulation	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	=	[52]
22	Acid–base regulation	<i>Arbacia lixula</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	=	[52]
23	Ammonia excretion rate	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.01–7.60–7.16	0.41–0.85	45	Higher	[75]
24	Ammonia excretion rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.7	0.3	60	=	[79]
25	Ammonia excretion rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.4	0.6	60	=	[79]
26	Ammonia excretion rate	<i>Echinometra</i> sp.	Eq.-Trop.	8.1–7.9	0.2	70	=	[57]
27	Ammonia excretion rate	<i>Heliocidaris erythogramma</i>	Sub.-Temp.	8.0–7.6	0.4	84	=	[80]
28	Ammonia excretion rate	<i>Paracentrotus lividus</i> site 1	Sub.-Temp.	8.0–7.6	0.4	180	=	[25]

Table 2. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Specific Effect	Citation
29	Ammonia excretion rate	<i>Paracentrotus lividus</i> site 2	Sub.-Temp.	8.0–7.6	0.4	180	Altered	[25]
30	Ammonia excretion rate	<i>Echinometra</i> sp.	Eq.-Trop.	8.06–7.89–7.79	0.17–0.27	600	=	[43]
31	Ammonia excretion rate	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.72	0.26	1200	=	[44]
32	Ammonia excretion rate	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.52	0.46	1200	=	[44]
33	Ammonia excretion rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.8	0.18	Resident	=	[58]
34	Antioxidant capacity	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.14–7.68	0.46	14	=	[77]
35	Antioxidant capacity	<i>Salmacis virgulata</i>	Eq.-Trop.	8.26–8.00	0.26	14	Oxidative stress induction	[59]
36	Antioxidant capacity	<i>Salmacis virgulata</i>	Eq.-Trop.	8.26–7.81–7.63	0.45–0.63	14	Oxidative stress induction	[59]
37	Antioxidant capacity	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.7	0.3	60	=	[79]
38	Antioxidant capacity	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.4	0.6	60	Slight induction	[79]
39	Antioxidant capacity	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.8	0.18	Resident	Higher	[58]
40	Assimilation efficiency	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.7	0.3	60	=	[79]
41	Assimilation efficiency	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.4	0.6	60	=	[79]
42	Coelomic fluid ions concentration	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	7.89–7.44–7.16–6.78	0.45–0.73–1.11	5	Mostly =	[81]
43	Coelomic fluid ions concentration	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.83	0.32	140	Altered	[40]
44	Coelomic fluid ions concentration	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.33	0.82	140	Altered	[40]
45	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.06–7.69	0.37	1	Altered	[47]
46	Coelomic fluid pH	<i>Arbacia lixula</i>	Sub.-Temp.	8.06–7.69	0.37	1	=	[47]
47	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.05–7.73	0.32	4	=	[47]
48	Coelomic fluid pH	<i>Arbacia lixula</i>	Sub.-Temp.	8.05–7.73	0.32	4	=	[47]
49	Coelomic fluid pH	<i>Arbacia lixula</i>	Sub.-Temp.	8.04–7.72	0.32	4	=	[76]

Table 2. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Specific Effect	Citation
50	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.04–7.72	0.32	4	Altered	[76]
51	Coelomic fluid pH	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	7.89–7.44–7.16–6.78	0.45–0.73–1.11	5	Decreased	[81]
52	Coelomic fluid pH	<i>Lytechinus variegatus</i>	Eq.-Trop.	8.0–7.6	0.4	5	Decreased	[82]
53	Coelomic fluid pH	<i>Lytechinus variegatus</i>	Eq.-Trop.	8.0–7.3	0.7	5	Decreased	[82]
54	Coelomic fluid pH	<i>Echinometra lucunter</i>	Eq.-Trop.	8.0–7.6	0.4	5	Decreased	[82]
55	Coelomic fluid pH	<i>Echinometra lucunter</i>	Eq.-Trop.	8.0–7.3	0.7	5	Decreased	[82]
56	Coelomic fluid pH	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.2–7.7	0.5	7	=	[83]
57	Coelomic fluid pH	<i>Psammechinus miliaris</i>	Sub.-Temp.	7.96–7.44–6.63–6.16	0.52–1.33–1.8	7	Altered	[29]
58	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.14–7.68	0.46	14	=	[77]
59	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.1–7.7	0.4	19	Decreased	[74]
60	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.1–7.4	0.7	19	Decreased	[74]
61	Coelomic fluid pH	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.98–7.51–7.11–6.65	0.47–0.87–1.33	31	Altered	[39]
62	Coelomic fluid pH	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.68	0.37	35	=	[78]
63	Coelomic fluid pH	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.39	0.66	35	=	[78]
64	Coelomic fluid pH	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.65	0.39	35	=	[78]
65	Coelomic fluid pH	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.41	0.63	35	=	[78]
66	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.98–7.66	0.22	35	=	[78]
67	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.98–7.47	0.51	35	=	[78]
68	Coelomic fluid pH	<i>Echinometra mathaei</i>	Eq.-Trop.	8.04–7.69	0.35	49	=	[35]
69	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.7	0.2	60	=	[37]
70	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.4	0.5	60	=	[37]
71	Coelomic fluid pH	<i>Echinometra</i> sp.	Eq.-Trop.	8.1–7.9	0.2	70	=	[57]
72	Coelomic fluid pH	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.8	0.3	146	=	[41]

Table 2. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Specific Effect	Citation
73	Coelomic fluid pH	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.6	0.5	146	Decreased	[41]
74	Coelomic fluid pH	<i>Hemicentrotus pulcherrimus</i>	Sub.-Temp.	8.1–7.83	0.27	270	Decreased	[84]
75	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	=	[52]
76	Coelomic fluid pH	<i>Arbacia lixula</i>	Sub.-Temp.	7.93–7.63	0.3	Resident	=	[52]
77	Coelomic fluid pH	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.8	0.18	Resident	=	[58]
78	Energy consumed	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.72	0.26	1200	Decreased	[44]
79	Energy consumed	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.52	0.46	1200	Decreased	[44]
80	Faecal production	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.83	0.32	140	Decreased	[40]
81	Faecal production	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.33	0.82	140	Decreased	[40]
82	Food intake	<i>Echinometra lucunter</i>	Eq.-Trop.	8.23–7.75	0.48	21	Increased	[85]
83	Food intake	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.68	0.37	35	=	[78]
84	Food intake	<i>Eucidaris tribuloides</i>	Eq.-Trop.	8.05–7.39	0.66	35	=	[78]
85	Food intake	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.65	0.39	35	=	[78]
86	Food intake	<i>Tripneustes ventricosus</i>	Eq.-Trop.	8.04–7.41	0.63	35	=	[78]
87	Food intake	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.98–7.66	0.22	35	=	[78]
88	Food intake	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.98–7.47	0.51	35	=	[78]
89	Food intake	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.87–7.57	0.3	42	=	[86]
90	Food intake	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.97–7.60	0.37	42	=	[86]
91	Food intake	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.0–7.5	0.5	60	=	[72]
92	Food intake	<i>Strongylocentrotus intermedius</i>	Sub.-Temp.	8.10–7.82	0.28	60	=	[36]
93	Food intake	<i>Strongylocentrotus intermedius</i>	Sub.-Temp.	8.10–7.68–7.55	0.42–0.55	60	Decreased	[36]
94	Food intake	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.0–7.6	0.4	84	=	[80]
95	Food intake	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.92–7.64	0.28	140	=	[39]
96	Food intake	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.92–7.23–6.61	0.69–1.31	140	Decreased	[39]

Table 2. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Specific Effect	Citation
97	Food intake	<i>Anthocidaris crassispinia</i>	Temp.-Pol.	8.15–7.83	0.32	140	Decreased	[40]
98	Food intake	<i>Anthocidaris crassispinia</i>	Temp.-Pol.	8.15–7.33	0.82	140	Decreased	[40]
99	Food intake	<i>Hemicentrotus pulcherrimus</i>	Sub.-Temp.	8.1–7.83	0.27	270	Rate reduced	[84]
100	Immune system	<i>Lytechinus variegatus</i>	Eq.-Trop.	8.0–7.6	0.4	5	Altered	[82]
101	Immune system	<i>Lytechinus variegatus</i>	Eq.-Trop.	8.0–7.3	0.7	5	Altered	[82]
102	Immune system	<i>Echinometra lucunter</i>	Eq.-Trop.	8.0–7.6	0.4	5	Altered	[82]
103	Immune system	<i>Echinometra lucunter</i>	Eq.-Trop.	8.0–7.3	0.7	5	Altered	[82]
104	Immune system	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.2–7.7	0.5	7	=	[83]
105	Immune system	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.7	0.23	56	=	[60]
106	Immune system	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.47	0.46	56	=	[60]
107	Immune system	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.8	0.18	Resident	Upregulated	[58]
108	Lactate concentration	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	7.89–7.44–7.16–6.78	0.45–0.73–1.11	5	Increased	[81]
109	Metabolism enzyme activity	<i>Strongylocentrotus intermedius</i>	Sub.-Temp.	8.10–7.82	0.28	60	Altered	[36]
110	Metabolism enzyme activity	<i>Strongylocentrotus intermedius</i>	Sub.-Temp.	8.10–7.68–7.55	0.42–0.55	60	Altered	[36]
111	Metabolism enzyme activity	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.8	0.18	Resident	Upregulated	[58]
112	Oxidative damage	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.8	0.18	Resident	=	[58]
113	Respiration rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.1–7.7	0.4	19	=	[74]
114	Respiration rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.1–7.4	0.7	19	Lower	[74]
115	Respiration rate	<i>Echinometra lucunter</i>	Eq.-Trop.	8.23–7.75	0.48	21	Higher	[85]
116	Respiration rate	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.87–7.57	0.3	42	=	[86]
117	Respiration rate	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.01–7.60–7.16	0.41–0.85	45	=	[75]
118	Respiration rate	<i>Echinometra mathaei</i>	Eq.-Trop.	8.04–7.69	0.35	49	=	[35]

Table 2. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	Δ pH	Exposure Time (Days)	Specific Effect	Citation
119	Respiration rate	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.0–7.5	0.5	60	Increased	[72]
120	Respiration rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.7	0.2	60	=	[37]
121	Respiration rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.4	0.5	60	=	[37]
122	Respiration rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.7	0.3	60	=	[79]
123	Respiration rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.4	0.6	60	=	[79]
124	Respiration rate	<i>Echinometra</i> sp.	Eq.-Trop.	8.1–7.9	0.2	70	=	[57]
125	Respiration rate	<i>Heliocidaris erythrogramma</i>	Sub.-Temp.	8.0–7.6	0.4	84	Increased	[80]
126	Respiration rate	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.83	0.32	140	=	[40]
127	Respiration rate	<i>Anthocidaris crassispina</i>	Temp.-Pol.	8.15–7.33	0.82	140	Decreased	[40]
128	Respiration rate	<i>Paracentrotus lividus</i> site 1	Sub.-Temp.	8.0–7.6	0.4	180	=	[25]
129	Respiration rate	<i>Paracentrotus lividus</i> site 2	Sub.-Temp.	8.0–7.6	0.4	180	=	[25]
130	Respiration rate	<i>Hemicentrotus pulcherrimus</i>	Sub.-Temp.	8.1–7.83	0.27	270	=	[84]
131	Respiration rate	<i>Echinometra mathaei</i>	Eq.-Trop.	8.09–7.63	0.46	360	=	[42]
132	Respiration rate	<i>Echinometra</i> sp.	Eq.-Trop.	8.06–7.89–7.79	0.17–0.27	600	=	[43]
133	Respiration rate	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.72	0.26	1200	=	[44]
134	Respiration rate	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.52	0.46	1200	Increased	[44]
135	Respiration rate	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.02–7.8	0.18	Resident	=	[58]
136	Respiration rate	<i>Echinometra</i> sp.	Eq.-Trop.	8.0–7.48	0.52	Resident	=	[45]
137	Scope for growth	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.72	0.26	1200	=	[44]
138	Scope for growth	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.52	0.46	1200	=	[44]
139	Weight gain	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.97–7.60	0.37	42	=	[86]
140	Weight gain	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.7	0.23	56	=	[60]
141	Weight gain	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.47	0.46	56	=	[60]

Another effect of hypercapnia is the increase in the concentration of reactive oxygen species in animal tissues [87], 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 [58,59,79] and no oxidative damage was observed (although oxidative damage was assessed only in animals resident in CO₂ vents [58]). Overall, from the articles collected, 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 (Table 2). 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 [42,77,78], even if exposure conditions were not the same (see Table 2 for details). In another experiment carried out with *P. lividus* by Cohen-Rengifo and colleagues [37], 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 [37]. This was confirmed by the work of Marčeta and colleagues [79] 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 [79]. 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 [74]. 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 [74]. 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 [85,88,89]. 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 pCO₂ and contaminant [77]. 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 pCO₂ have been reported in both marine vertebrates [90] and invertebrates, but in the latter group, the effects are more evident, considering their poor ability to regulate extracellular pH [68,71,91]. 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 [92] and carbonate structures is required [66]. Respiration and nitrogen excretion are useful tools to assess the physiological status of an organism and have been used as such for decades [93]. The ratio between the oxygen consumed and the nitrogen excreted indicates the level of activity of oxidative and protein metabolism [93,94]. 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 [94,95].

In Table 2, 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 [40,72,74,75]. In adult sea urchins of *Strongylocentrotus droebachiensis* exposed to very low pH levels (7.60–7.16) for 45 days, the rate of NH₄⁺ excretion was significantly higher [75] 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 [75], suggesting that the catabolism of proteins was prevalent compared with the catabolism of lipids and carbohydrates [94]. 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 [25]. However, the importance of local biological adaptation was highlighted by Asnicar et al. [25] 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 [44]. 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 [72]. 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 [60,86].

Interestingly, the endpoints summarized here under the category “Food intake” (Table 2) showed more alterations in the long-term exposures (e.g., [39,40,84]) than in the short-term ones (e.g., [72,78,86]). As reported by Wang and colleagues [40], physiological responses might be time-dependent, with differences among the various endpoints considered. We can hypothesize that sea urchins kept at SWA conditions showed an unaltered feeding rate in the short-term exposures due to the high demand of energy needed to fulfil other biological requirements (e.g., building calcareous structures, gonadal growth, and immune system regulation [72,78,86]).

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 [58].

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 [82]. 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 CO₂ vents [58,83].

4. SWA Effects on Echinoid Behaviour

There is evidence that SWA also affects animals’ behaviour. The literature is still sparse, although growing fast [90,96–99]. Linked to extracellular acidosis, the altered ion gradient across the neural membrane induces membrane depolarization, neural pathway excitation and ultimately an altered behaviour [67,100]. As stated above, hypercapnia and low pH may also promote the enhanced production of adenosine in nervous tissue, which can result in behavioural alteration [68,71]. Both invertebrates and vertebrates can be influenced [96], although the impact of SWA on vertebrate behaviour seems to be weak [90,101] compared with invertebrate responses [98]. SWA effects on invertebrate behaviour have been explored in many taxa, among which are the echinoids (Table 3), and the results show a range of negative, neutral or positive responses [98]. 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.

Table 3. List of studies performed on echinoid adult stage to investigate effects of SWA on behaviour. “pH level” contains the values of all the conditions tested; the first value is the control. In the case that the same article tested both a realistic ($\Delta\text{pH} \leq 0.4$; based on IPCC RCP8.5) and unrealistic scenario ($\Delta\text{pH} > 0.4$), the two conditions were split. Abbreviations: Eq.-Trop. = Equatorial–Tropical; Sub.-Temp. = Subtropical–Temperate; Temp.-Pol. = Temperate–Polar.

N	Response Detail	Species	Latitudinal Range	Ph Level	ΔpH	Exposure Time (Days)	Specific Effect	Citation
1	Attachment	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.04–7.78	0.26	90	=	[38]
2	Feeding	<i>Stomopneustes variolaris</i>	Eq.-Trop.	7.96–7.76	0.2	210	=	[61]
3	Feeding	<i>Stomopneustes variolaris</i>	Eq.-Trop.	7.96–7.46	0.5	210	Altered	[61]
4	Foraging time	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.6–7.1	0.5	27	Longer	[102]
5	Predator-avoidance	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.04–7.78	0.26	90	Lowered	[38]
6	Resistance to flow	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.7	0.2	60	Decreased	[37]
7	Resistance to flow	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.4	0.5	60	Decreased	[37]
8	Righting response	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.97–7.60	0.37	42	=	[86]
9	Righting response	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.7	0.23	56	=	[60]
10	Righting response	<i>Lytechinus variegatus</i>	Eq.-Trop.	7.93–7.47	0.46	56	=	[60]
11	Righting response	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.7	0.3	60	=	[79]
12	Righting response	<i>Paracentrotus lividus</i>	Sub.-Temp.	8.0–7.4	0.6	60	=	[79]
13	Righting response	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.92–7.64	0.28	140	=	[39]
14	Righting response	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.92–7.23–6.61	0.69–1.31	140	Increased	[39]
15	Righting response	<i>Paracentrotus lividus</i> site 1	Sub.-Temp.	8.0–7.6	0.4	180	=	[25]
16	Righting response	<i>Paracentrotus lividus</i> site 2	Sub.-Temp.	8.0–7.6	0.4	180	=	[25]
17	Shelter seeking	<i>Paracentrotus lividus</i> site 1	Sub.-Temp.	8.0–7.6	0.4	180	Impaired	[25]
18	Shelter seeking	<i>Paracentrotus lividus</i> site 2	Sub.-Temp.	8.0–7.6	0.4	180	Impaired	[25]

Table 3. Cont.

N	Response Detail	Species	Latitudinal Range	Ph Level	Δ pH	Exposure Time (Days)	Specific Effect	Citation
19	Speed	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.6–7.1	0.5	27	=	[102]
20	Speed	<i>Paracentrotus lividus</i> site 1	Sub.-Temp.	8.0–7.6	0.4	180	=	[25]
21	Speed	<i>Paracentrotus lividus</i> site 2	Sub.-Temp.	8.0–7.6	0.4	180	Impaired	[25]
22	Tube feet characteristics	<i>Pseudocentrotus depressus</i>	Sub.-Temp.	8.2–7.56-(6.90)	0.64–1.3	48	Impaired	[28]
23	Tube feet characteristics	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.7	0.2	60	=	[37]
24	Tube feet characteristics	<i>Paracentrotus lividus</i>	Sub.-Temp.	7.9–7.4	0.5	60	=	[37]

In the literature collected in the present review, 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 [85,103–105]. 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 [102]. On the other hand, the exposure of the algae *Ulva lactuca* to high $p\text{CO}_2$ (4000 $\mu\text{-atm}$) resulted in an increase in unpalatable substances and the consequent decrease in grazing on the algae by the sea urchin *T. gratilla* [106]. The calcifying algae *Halimeda incrassata* significantly reduced its calcium carbonate content and therefore reduced its defence against grazers *L. variegatus* and *Diadema antillarum* [107]. Interestingly, in the work of Burnham and colleagues [86], 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 [86]. 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 [108]. A quick righting is linked to good physiological status, as it requires good coordinating capacities between the spines and tube feet [109], while changes in righting time are related to stress [110]. The covering behaviour consists of taking ambient elements (small rocks, shells or algae) with the tube feet to cover the aboral surface [111,112]. 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 [113–118]. 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* [38]. This, together with the reduction in defensive capacity (i.e.,

thinner plates and spines weakness [38]) 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 [25,79] and in *L. variegatus* exposed for 42 days to pH 7.60 (control pH 7.97) [86], or for 56 days to pH 7.7–7.47 (control pH 7.93) [60]. Among the five articles that investigated the righting response, this endpoint was significantly increased only in one case (Table 3). 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 [39].

The shelter-seeking behaviour in relation to environmental stressors has been poorly studied [119–121] and was assessed under reduced pH conditions in only one experiment [25]. 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 [25]. 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 [37], 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 [37]. 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 [28] found that exposure to high *pCO*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 [37].

5. SWA Effects on Echinoid Reproduction

In the present work, 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 (Table 4).

Table 4. List of studies performed on echinoid adult stage to investigate effects of SWA on reproduction. “pH level” contains the values of all the conditions tested; the first value is the control. In the case that the same article tested both a realistic ($\Delta\text{pH} \leq 0.4$; based on IPCC RCP8.5) and unrealistic scenario ($\Delta\text{pH} > 0.4$), the two conditions were split. Abbreviations: Eq.-Trop. = Equatorial–Tropical; Sub.-Temp. = Subtropical–Temperate; Temp.-Pol. = Temperate–Polar.

N	Response Detail	Species	Latitudinal Range	pH Level	ΔpH	Exposure Time (Days)	Specific Effect	Citation
1	Female fecundity	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.1–7.7	0.4	120	Decreased	[122]
2	Female fecundity	<i>Hemicentrotus pulcherrimus</i>	Sub.-Temp.	8.1–7.83	0.27	270	=	[84]

Table 4. Cont.

N	Response Detail	Species	Latitudinal Range	pH Level	ΔpH	Exposure Time (Days)	Specific Effect	Citation
3	Female fecundity	<i>Strongylocentrotus droebachiensis</i>	Temp.-Pol.	8.1–7.7	0.4	480	=	[122]
4	Gonad histology	<i>Salmacis virgulata</i>	Eq.-Trop.	8.26–8.00	0.26	14	Oocytes lesions	[59]
5	Gonad histology	<i>Salmacis virgulata</i>	Eq.-Trop.	8.26–7.81–7.63	0.45–0.63	14	Oocytes lesions	[59]
6	Gonad histology	<i>Sterechinus neumayeri</i>	Temp.-Pol.	8.12–7.8	0.32	30	Anomalies	[123]
7	Gonad histology	<i>Sterechinus neumayeri</i>	Temp.-Pol.	8.12–7.6	0.42	30	Anomalies	[123]
8	Gonad histology	<i>Echinometra</i> sp.	Eq.-Trop.	8.1–7.9	0.2	70	Male development delayed	[57]
9	Gonad histology	<i>Hemicentrotus pulcherrimus</i>	Sub.-Temp.	8.1–7.83	0.27	270	Delayed	[84]
10	Gonad histology	<i>Echinometra</i> sp.	Eq.-Trop.	8.1–7.7	0.4	330	=	[51]
11	Gonadal growth	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.72	0.26	1200	=	[44]
12	Gonadal growth	<i>Sterechinus neumayeri</i>	Temp.-Pol.	7.98–7.52	0.46	1200	=	[44]
13	Gonadal index	<i>Sterechinus neumayeri</i>	Temp.-Pol.	8.12–7.8	0.32	30	=	[123]
14	Gonadal index	<i>Sterechinus neumayeri</i>	Temp.-Pol.	8.12–7.6	0.42	30	=	[123]
15	Gonadal index	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.92–7.64	0.28	140	=	[39]
16	Gonadal index	<i>Strongylocentrotus fragilis</i>	Deep Sea	7.92–7.23–6.61	0.69–1.31	140	Decreased	[39]
17	Gonadal index	<i>Anthocardaris crassispina</i>	Temp.-Pol.	8.15–7.83	0.32	140	=	[40]
18	Gonadal index	<i>Anthocardaris crassispina</i>	Temp.-Pol.	8.15–7.33	0.82	140	=	[40]
19	Gonadal index	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.8	0.3	146	=	[41]
20	Gonadal index	<i>Tripneustes gratilla</i>	Eq.-Trop.	8.1–7.6	0.5	146	Reduced	[41]
21	Gonadal index	<i>Paracentrotus lividus</i> site 1	Sub.-Temp.	8.1–7.7	0.4	180	=	[25]
22	Gonadal index	<i>Paracentrotus lividus</i> site 2	Sub.-Temp.	8.1–7.7	0.4	180	=	[25]
23	Gonadal index	<i>Echinometra</i> sp.	Eq.-Trop.	8.1–7.7	0.4	330	=	[51]
24	Gonadal weight	<i>Echinometra</i> sp.	Eq.-Trop.	8.0–7.48	0.52	resident	Reduced	[45]

The sea urchin *S. virgulata* exposed for 14 days to reduced pH showed lesions on the oocytes at pH 7.8 and 7.6 [59]. 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 [123]. The gonadal development of males of *Echinometra* sp. was delayed when animals were maintained for 70 days at pH 7.9 [57]. 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., [122]). 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 [84]. 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 [51]. The exposure of *Echinometra* sp. was longer than that experienced by *H. pulcherrimus* [84], 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 [41]. 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 [62], where *T. gratilla* was cultured in high density and the biogenic production of CO₂ 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 [41], do sea urchins shift energy from gonadal to somatic growth. Similarly, *Echinometra* sp. sampled in a CO₂ volcanic vent system (pH 7.48) had smaller gonads compared with the control site specimens [45]. 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 [45].

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 [122]. 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 authors 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 [122].

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 [124]. To achieve fertilisation, sperm are subjected to intense selection and competition, as only a small proportion will succeed in fertilizing an egg [125] and selection will favour high-quality ejaculate [126]. It is not of interest for the present review

to delve into these matters. A recent article summarized the possible effects of SWA on gamete quality, highlighting the inter- and intra-species variability in the response [127].

6. Conclusions and Future Perspectives

According to the IPCC RCP8.5 scenario, a decrease of up to 0.4 units in pH (average surface seawater total scale pH 7.7) is expected by 2100. Data collected in this review suggest that the adult life stage of echinoids is robust against SWA when the pH reduction is smaller than 0.4 units. This is also in accordance with previous findings regarding other echinoderms [128]. However, the among-species differences in susceptibility to SWA have been highlighted, as summarized in Figure 1. Taking into account the geographical range and the variables considered (calcification, physiology, behaviour, and reproduction), some species (such as *S. intermedius* and *A. crassispina*) could be more vulnerable than others. Nonetheless, the responses obtained depend also on the exposure’s duration and the pH scenario used.

Geographical range	Species	Variables	Effect	Geographical range	Species	Variables	Effect
Equatorial-Tropical	<i>Echinometra</i> spp.	Calcification	Orange	Subtropical-Temperate	<i>Arbacia lixula</i>	Calcification	Red
		Physiology	Orange			Physiology	Yellow
		Behaviour	NA			Behaviour	NA
		Reproduction	Orange			Reproduction	NA
	<i>Eucidaris tribuloides</i>	Calcification	Orange		<i>Heliocidaris erythrogramma</i>	Calcification	Yellow
		Physiology	Orange			Physiology	Yellow
		Behaviour	NA			Behaviour	NA
		Reproduction	NA			Reproduction	NA
	<i>Iyechinus variegatus</i>	Calcification	Orange		<i>Hemicentrotus pulcherrimus</i>	Calcification	NA
		Physiology	Yellow			Physiology	Orange
		Behaviour	Orange			Behaviour	Orange
		Reproduction	NA			Reproduction	NA
	<i>Salmacis virgulata</i>	Calcification	Orange		<i>Paracentrotus lividus</i>	Calcification	Orange
		Physiology	Red			Physiology	Yellow
		Behaviour	NA			Behaviour	Orange
		Reproduction	Red			Reproduction	Orange
	<i>Stomopneustes variolaris</i>	Calcification	Orange		<i>Psammechinus militaris</i>	Calcification	NA
		Physiology	NA			Physiology	Red
		Behaviour	Orange			Behaviour	NA
		Reproduction	NA			Reproduction	NA
	<i>Triplaneustes gratilla</i>	Calcification	Yellow		<i>Pseudocentrotus depressus</i>	Calcification	NA
		Physiology	Orange			Physiology	NA
		Behaviour	NA			Behaviour	Red
		Reproduction	Orange			Reproduction	NA
<i>Triplaneustes ventricosus</i>	Calcification	Red	<i>Strongylocentrotus intermedius</i>	Calcification	Red		
	Physiology	Yellow		Physiology	Red		
	Behaviour	NA		Behaviour	NA		
	Reproduction	NA		Reproduction	NA		
Temperate-Polar	<i>Antibocidaris crassispina</i>	Calcification	Red	Temperate-Polar	<i>Strongylocentrotus droebachiensis</i>	Calcification	Orange
		Physiology	Red			Physiology	Orange
		Behaviour	NA			Behaviour	NA
		Reproduction	Orange			Reproduction	Orange
	<i>Sterechinus neumayeri</i>	Calcification	Orange	Deep Sea	<i>Strongylocentrotus fragilis</i>	Calcification	Orange
		Physiology	Yellow			Physiology	Red
		Behaviour	NA			Behaviour	Orange
		Reproduction	Yellow			Reproduction	Orange

Figure 1. Summary of the effects of seawater acidification on echinoids. For each species and variable considered, colour denotes the percentage of papers showing alterations due to the pH reduction. White: 0–10%; yellow: 10–40%; orange: 40–70%; red: 70–100%; grey: no articles on the topic.

To check whether or not differences occurred between realistic and unrealistic exposure scenarios (i.e., $\Delta pH \leq 0.4$ or >0.4 units, respectively) and whether an influence of the experiment duration was present, a generalized linear model (glm) was performed using a binomial distribution, with RStudio [129]. The whole dataset was considered, including effects on calcification, physiology, behaviour, and reproduction. Research data on CO₂

vent echinoids were excluded. For the analysis, a dummy variable was added in the dataset, assigning 0 if there were no changes compared with the control conditions, or 1 if a statistically significant change was present. A statistically significant influence of the time (Chisq = 24.914, Df = 8, $p = 0.002$) and the scenario (Chisq = 28.344, Df = 1, $p < 0.001$) was revealed, but not of the two factors' interaction (Chisq = 10.018, Df = 7, $p = 0.188$).

In Figure 2, the percentage of altered responses is reported based on the time of exposure and the realistic or unrealistic scenario used. In general, almost half (43%) of the endpoints were altered by the reduction in pH, and a considerable proportion of the studies revealed SWA alterations even in long-term experiments. As can be seen, echinoids are able to acclimate much faster to a pH reduction of less than 0.4 units (Figure 2).

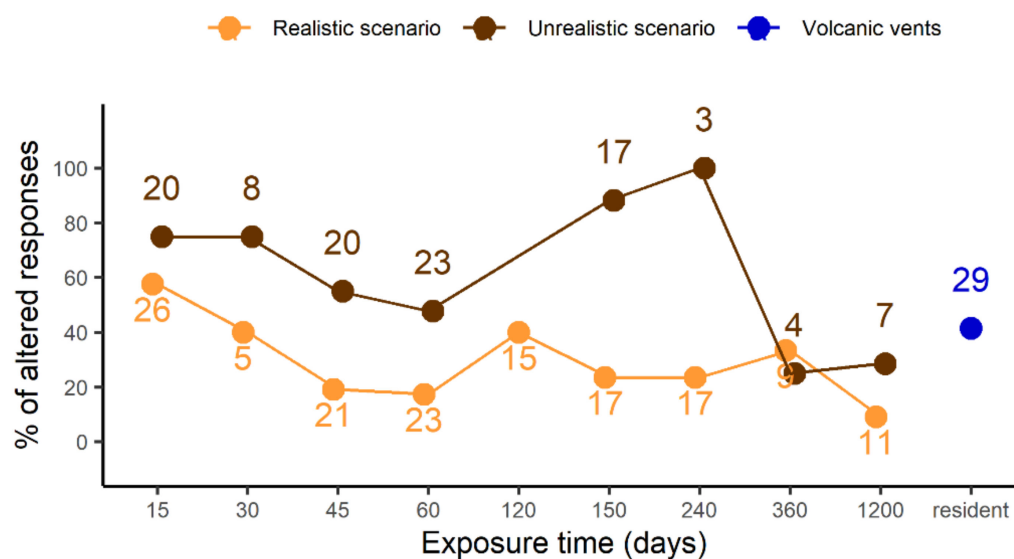


Figure 2. Percentage of altered responses compared with control conditions in sea urchins maintained under either realistic or unrealistic 2100 scenarios (IPCC RCP8.5) along time of exposure (not scaled). Close to each dot, the number of endpoints per case is reported.

After 15 days of exposure, animals are able to cope with the physico-chemical changes induced by laboratory exposure. Instead, much more time is needed for animals exposed to $\Delta\text{pH} > 0.4$ units. In this case, no signs of recovery are visible after 30 days of exposure ($>70\%$ of effects due to SWA). In the experiments that exposed echinoids for a time frame between 45 and 60 days, nearly 50–60% of the endpoints showed changes due to lower pH. Conversely, in the same time frame, the percentage of changes was $\sim 20\%$ if the ΔpH was ≤ 0.4 units. Differences compared with control conditions were also recorded after exposures lasted between 120 and 240 days in scenarios close to IPCC RCP8.5 (ΔpH 0.5 in [61]) or under more severe conditions (ΔpH 0.82 and 1.31 in [39,40]). A sensible decrease in the % of change compared with the control (suggesting the improvement in the adaptation capability of the echinoids) was detected only in experiments lasting one year or more [42,44].

Data from CO_2 vent sea urchins revealed that the percentage of change detected with respect to control sites was 41% (Figure 2).

Studies where the endpoints were analysed multiple times during the exposure highlighted the importance of this approach. For example, *P. lividus* specimens maintained at ΔpH 0.4 for six months were impacted by SWA at the beginning of the exposure but showed acclimation capability towards the end of the exposure [25]. Repeated measurements over time evidenced the subtle effects of SWA that could go unnoticed using a single-timepoint experiment. To obtain a complete picture of the SWA effects in future studies, the length of the exposure to the experimental pH levels and a repeated-measurements approach need to be considered. This is crucial to provide information of high quality and importance.

Some of the features altered by low pH might be functional for living in future OA conditions. Changes in dissolved inorganic carbon and the alkalinity of coelomic fluid are

useful for animals to maintain a stable coelomic pH value [78]. Moreover, the animals resident in vent sites showed alterations compared with animals from control sites [45,58]. For example, *P. lividus* from a vent system showed enhanced defence capability of its immune cells, with the modulation of several enzymes and proteins involved in their metabolic pathways and increased antioxidant activities. The observed changes, promoting the defensive and homeostatic abilities of the immune system, represented an adaptive response of animals to reduced pH. No alterations in biomineralization, mechanical properties, physiological responses or oxidative damage in tissues were found [52,58]. Therefore, differences in the biological traits of sea urchins living at high $p\text{CO}_2$ for a long time (both in natural and laboratory exposure) are not necessarily an impairment, as they may be functional in terms of the animal well-being, potentially without negative effects on reproduction [51,84,122]. To shed light on and sustain this hypothesis, multigenerational studies are needed, even though they are complex and difficult to complete successfully.

Further studies should also adopt a multigenerational approach in order to assess whether the calcification, physiological performances, behaviour and reproduction of sea urchin adults coping with OA would remain the same in future generations. These experiments could help to answer questions about future community structures and potential positive transgenerational effects also involving tolerance to pollutants, ocean warming, deoxygenation and other environmental stressors. Multigenerational studies take into account that gametes and early life stages are more sensitive than adults to environmental changes and the possible impact on fertilization may have strong effects at the population level [130]. An overpopulation or a depletion of sea urchins is often associated with a shift from a kelp-dominated ecosystem to barrens and vice versa [131–135]. For example, in the Mediterranean basin, variations in the grazing pressure of *P. lividus* and *A. lixula* drove changes from a complex community dominated by erect algae to a simpler one dominated by few encrusting algae [136].

Furthermore, a growing number of studies highlights intraspecific and inter-sexual variability in the animals' responses to SWA [13,25,137–142]. This implies that natural populations may be disproportionately affected and some individuals may be preadapted to future OA scenarios. Indeed, oysters of the species *Saccostrea glomerata*, whose bred lines were selected in an aquaculture facility, were found to be more resilient to OA conditions compared with a wild population [143]. OA may be emphasized in coastal areas by eutrophication and hypoxia [19,144,145], but the animals that inhabit these highly variable environments might have an inherent capacity to tolerate near-future OA scenarios [146,147]. Therefore, future studies should also consider the environmental history experienced by animals, either by pooling animals from different areas to average the results or by carrying out parallel experiments with animals from different areas. Indeed, the natural local variability in seawater chemistry can be crucial in shaping coastal population responses to climate change drivers [24,26,27,148]. In natural environments (particularly in estuarine, coastal and upwelling areas), pH and alkalinity do not have stable values and fluctuate broadly, with daily and seasonal changes and local variability [24,27,61,148]. Since variability in pH values may be present also in future OA scenarios, caging experiments in CO_2 vent systems or laboratory experiments that consider this natural variability in seawater chemistry will be useful to better model future acidification conditions. In this regard, although studies carried out with animals sampled in naturally acidified environments are outnumbered by laboratory experiments, they provide more insights into the potential adaptability of the echinoids and the evolutionary consequences of OA.

Regional range also has an influence, albeit slightly, on the susceptibility of sea urchins to OA. In a previous work, Watson and colleagues [149] compared the growth and calcification of marine invertebrates (among which echinoids) collected from the North Pole to the South Pole and found a latitudinal trend in shell morphology and composition. The authors claimed that, in a climate change scenario, this would differently affect animals and communities at different latitudinal ranges [149]. Although not statistically significant (glm with binomial distribution, excluding deep-sea and CO_2 vent experiments; factor

“latitudinal range” $\text{Chisq} = 2.149$, $\text{Df} = 2$, $p = 0.341$), our literature survey confirmed the latitudinal trend observed, since differences in the responses have been found based on the climate region of animals’ collection. In sea urchins, 38% of the endpoints analysed were affected by low pH exposure when the geographical range was between equatorial to tropical regions. For example, sea urchin growth was impaired in *S. virgulata* exposed at a pH of 7.8 and 7.6 for 14 days [59], but similar results were not obtained in *Echinometra* sp. [35,42] or in *Heliocidaris erythrogramma* [34] and growth even increased in sea urchins resident in vent systems at a pH of 7.48 [45]. In the case of sea urchins from subtropical–temperate and temperate–polar areas, 43% and 51%, respectively, of the endpoints analysed were affected by SWA conditions (Figure 3). In this case, growth was reduced in *P. lividus* [37] and *S. droebachiensis* [46] exposed to pH 7.7 and 7.4 for 60 and 42 days, respectively. Although genetic and phenotypical differences (e.g., growth and metabolic rates) are obviously present among the variety of species considered, overall observations indicate that animals collected in the equatorial–subtropical areas might be less impacted by SWA than those collected from the subtropical areas to the Poles.

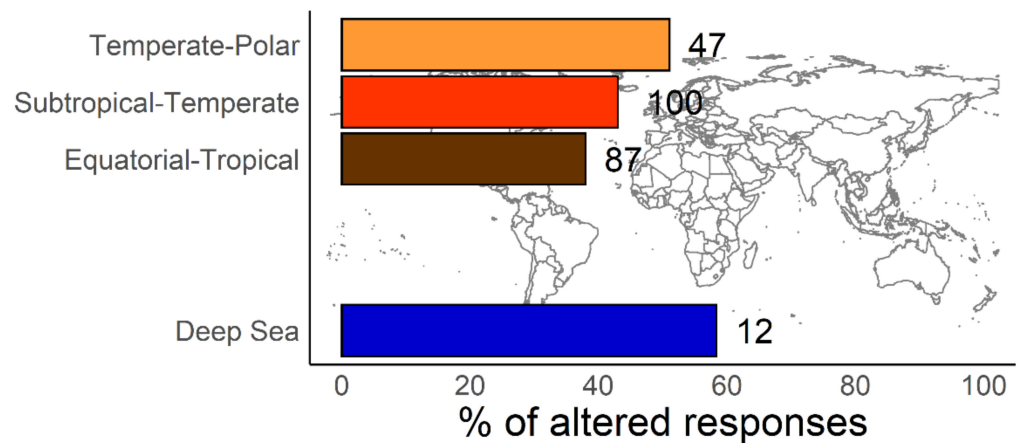


Figure 3. Percentage of altered responses in sea urchins from different latitudinal ranges and the deep sea. On the right of each bar, the number of endpoints per case is reported.

Although some echinoid species are still understudied (Figure 1), the knowledge concerning SWA effects on sea urchins has been growing in the last two decades, opening new questions to be addressed. For example, the majority of the studies in this review were performed using a stable pH value. However, in the environment, physico-chemical variables fluctuate, and it has been demonstrated that the effect of pH is different in the latter condition (e.g., [76,150]). Moreover, long-term multigenerational experiments combining SWA with other stressors will be crucial for studying the effects of climate change on echinoid populations.

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