AQUACULTURE, FISH and FISHERIES   WILEY

How ocean warming and acidification affect the life cycle of six worldwide commercialised sea urchin species: A review

Thomas Uboldi[1] ⬤ | Frédéric Olivier[2] | Laurent Chauvaud[1] | Réjean Tremblay[3]

[1]Institut Universitaire Européen de la Mer, Unité Mixte de Recherche 'Laboratoire des sciences de l'environnement marin' (LEMAR, UMR 6539), Centre National de la Recherche Scientifique, Institut de Recherche pour le Développement, Université de Bretagne Occidentale; Technopôle Brest-Iroise, Plouzané, France

[2]Laboratoire de 'Biologie des Organismes et Écosystèmes Aquatiques' (BOREA), Muséum national d'Histoire naturelle, Sorbonne Université, Université de Caen Basse-Normandie, Université des Antilles, Centre National de la Recherche Scientifique, Institut de Recherche pour le Développement-207, Paris, France

[3]Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski, Rimouski, Québec, Canada

Correspondence
Thomas Uboldi, Institut Universitaire Européen de la Mer, Unité Mixte de Recherche 'Laboratoire des sciences de l'environnement marin' (LEMAR, UMR 6539), Centre National de la Recherche Scientifique, Institut de Recherche pour le Développement, Université de Bretagne Occidentale; Technopôle Brest-Iroise, rue Dumont d'Urville, 29280 Plouzané, France.
Email: thomas.uboldi@icloud.com.

Abstract

Ongoing global changes are expected to affect the worldwide production of many fisheries and aquaculture systems. Because invertebrates represent a relevant industry, it is crucial to anticipate challenges that are resulting from the current environmental alterations. In this review, we rely on the estimated physiological limits of six commercialised species of sea urchins (*Loxechinus albus, Mesocentrotus franciscanus, Paracentrotus lividus, Strongylocentrotus droebachiensis, Strongylocentrotus intermedius* and *Strongylocentrotus purpuratus*) to define the vulnerability (or resilience) of their populations facing ocean warming and acidification (OW&A). Considering that coastal systems do not change uniformly and that the populations' response to stressors varies depending on their origin, we investigate the effects of OW&A by including studies that estimate future environmental mutations within their distribution areas. Cross-referencing 79 studies, we find that several sea urchin populations are potentially vulnerable to the predicted OW&A as environmental conditions in certain regions are expected to shift beyond their estimated physiological limit of tolerance. Specifically, while upper thermal thresholds seem to be respected for *L. albus* along the SW American coast, *M. franciscanus* and *S. purpuratus* southern populations appear to be vulnerable in NW America. Moreover, as a result of the strong warming expected in the Arctic and sub-Arctic regions, the local productivity of *S. droebachiensis* is also potentially largely affected. Finally, populations of *S. intermedius* and *P. lividus* found in northern Japan and eastern Mediterranean respectively, are supposed to decline due to large environmental changes brought about by OW&A. This review highlights the status and the potential of local adaptation of a number of sea urchin populations in response to changing environmental conditions, revealing possible future challenges for various local fishing industries.

KEYWORDS
aquaculture, ecophysiology, fishery, ocean acidification, ocean warming, sea urchin

1 | INTRODUCTION

In the actual context of global changes, ocean warming and acidification (OW&A) are both closely related to increased atmospheric CO_2 concentration and are expected to deeply impact biological communities through generalised effects on the entire oceanic system (Hale et al., 2011; Occhipinti-Ambrogi, 2007). Since 1993, the rate of ocean warming (OW) has more than doubled, and in the last decades, through a massive CO_2 output, human activities have already resulted in a global temperature increase of 1.0°C and pH reduction by 0.1 point compared with the beginning of the industrial era (IPCC, 2021). If the 'business-as-usual' scenario continues, predictions raise concerns about the near-future sustainability of several fisheries and aquaculture systems around the globe (Froehlich et al., 2018; Maulu et al., 2021; Wallhead et al., 2018). Indeed, environmental changes may challenge the growth and stability of various marine productions due to the emerging consequences associated to OW&A (Froehlich et al., 2018; Reid et al., 2019). For instance, Froehlich et al. (2018) estimated that the extension of suitable waters to bivalve cultures are expected to globally decline by the end of the century. Among commercialised marine species, echinoids are observed to undergo a variety of physiological, transcriptomic and immunological changes as a result of the conditions imposed by OW&A (Byrne & Hernàndez, 2020), raising questions about the future management of several populations.

In addition to their importance in terms of ecological services (Matranga et al., 2005; Pearse, 2006; Sweet et al., 2016), sea urchins are widely exploited for commercial purposes, supporting a growing market of considerable wealth: a global production of 73,000 metric tons with an estimated value of 208 million US$ (FAO, 2016; Sato et al., 2018). Although recent studies emphasise the growing importance of echinoid farming within integrated multitrophic aquaculture (IMTA) systems (Grosso et al., 2021; Shpigel et al., 2018), sea urchin fisheries account for more than 99.9% of total sold per year, with aquaculture providing the remainder (Stefánsson et al., 2017). Worldwide, the greatest demand of sea urchins occurs in Japan (80–90%), France and Korea, while the main consumers in Europe include France, Italy and Spain. Actually, the whole sector relies on a few marketable species that are mainly exploited and sold. Approximately, 50% of global landings are accounted by the Chilean sea urchin (*Loxechinus albus*) harvested on the Pacific coast of South America and distributed as a culinary product in Japan and many European countries. Other countries showing a high level of sea urchin productivity include United States, Canada, Japan and Russia, the most harvested species belonging to the *Mesocentrotus* and *Strongylocentrotus* genus (i.e., *M. franciscanus*, *S. intermedius*, *S. purpuratus*, *S. droebachiensis*). While *M. franciscanus* and *S. purpuratus* constitute two most valuable species on the North-West American coasts, *S. droebachiensis* is distributed in many regions of the northern hemisphere, where it is also widely harvested. In northern Japan, *S. intermedius* covers a large part of the local catches, constituting with *Mesocentrotus nudus* two species of highest local demand. Finally, *Paracentrotus lividus* is the most historically fished sea urchin of the Mediterranean Sea and is frequently exported to other external markers. The *P. lividus* fisheries are putting large pressure on wild stocks and it is estimated that many natural reserves are now highly depleted (Shpigel et al., 2018).

Today, most of such species' main exploitation area are expected to dramatically change in the near future as a consequence of global changes (Darmakari et al., 2019, Fujii et al., 2021, Valera et al., 2018), redefining the regional species' abundance and availability for commercial fishing (Feng et al., 2021; Kawana et al., 2019; Wallhead et al., 2018). As a result, it is critical to anticipate new opportunities and challenges in marine production systems so that involved industries can implement viable and long-term adaptation strategies (Froehlich et al., 2018; Reid et al., 2019). Aquaculture and fisheries can clearly benefit from defining the tolerance limits of target species when confronted to global change consequences. Specific investments and stressor mitigation policy can then be deployed to limit the negative effects imposed by the OW&A. Overall, a deeper understanding of how stressors affect sea urchins' life cycle will facilitate the implementation of effective fisheries management strategies. In particular, for poikilothermic organisms like echinoids, OW constitutes a major environmental factor controlling their development, physiology and genetic expression (O'Donnel et al., 2009; Byrne, 2011; Manrìquez et al., 2019; Wong & Hofmann, 2020). Generally, OW increases the development speed during early life stages, leading to mutations in the skeletal growth, calcification process and several physiological patterns (Byrne & Hernàndez, 2020; Byrne et al., 2014; Dworjanyn & Byrne, 2018; Garcia et al. 2018; Sheppard Brennand et al., 2010). In parallel to rising temperatures, ocean acidification (OA) is observed to affect several living aspects of various echinoids species, especially in their early, most vulnerable developmental stages (Dupont & Thorndyke, 2009). Lowering pH leads to large calcification and skeletogenesis complications in sea urchins, as well as to severe alterations in their initial development, physiology and reproductive success through hypercapnia, deregulated gene expression and reduced carbonate availability (Byrne, 2011; Byrne & Hernàndez, 2020; Ross et al., 2011; Wong & Hofmann, 2020). Thus, the combined effects of OW&A can have significant implications for the development and fitness of individuals in a population, regulating their distribution across different geographical areas (Clemente et al., 2014; Girard et al., 2012; Wallhead et al., 2018).

Although predictions suggest a general rise in temperature and lowering pH, oceans and seas do not warm and acidify uniformly (Goyet et al., 2016; Lima & Wethey, 2012; Valera et al., 2018). While some coastal areas are expected to experience intense warming, others are cooling due to specific local conditions (e.g., increased upwelling events; Lima & Wethey, 2012). Consequently, populations of the same species will face significantly different environmental challenges depending on their geographical location (Evans et al., 2015; Gaitan-Espita et al., 2017). Over the long time period, unique conditions of specific areas allow adaptive phenotypic mutations, resulting in distinct evolutionary trajectories among isolated populations (Broitman et al., 2020). Understanding how acclimatisation and phenotypic plasticity differ across populations is critical for characterising and

predicting evolutionary adaptation in the face of ongoing environmental alterations (Whitehead 2012). Thermal tolerance, for example, differs between populations based on their origin, influencing their geographical distribution and defining their acclimation potential to cope with thermal challenges (Broitman et al., 2020). Observing the effect of OW&A in individuals from different populations is extremely valuable because it infers transgenerational plasticity or local adaptation, as well as a possible means of genetic adaptation to future altered conditions (Byrne et al., 2020; Evans et al., 2015; Kapsenberg et al., 2017). Consequently, populations rather than species have been favoured in this review, as expected tolerances and sensitivities to OW&A may vary depending on the original living conditions.

Within this context, the present review synthesises the scientific literature focusing on the impacts of OW&A on several life stages (i.e., planktonic and benthic post-metamorphic stages) of the most economically relevant sea urchins' species (*L. albus*, *Mesocentrotus franciscanus*, *P. lividus*, *Strongylocentrotus droebachiensis*, *Strongylocentrotus intermedius* and *Strongylocentrotus purpuratus*). Based on experimental studies and field observations, we define a series of physiological, immunological and transcriptomic alterations in different populations facing expected environmental conditions. One main objective of this review is to establish the potential vulnerability of populations exposed to OW&A conditions that fall behind their limit of tolerance in order to inform local fishing industries to the incoming challenges enforced by the current global changes.

2 | METHODS

Selected studies focus on the effects of OW&A expected in the next future on the entire life cycle of six sea urchin species (see above). In order to select species of greatest economical interest, we relied on two reports reviewing the sea urchin harvesting activity in the last two decades (James et al., 2016, Stefánsson et al., 2017). The literature search was conducted from 06/2020 to 06/2022 on both Google Scholar and Web of Science, comprising only peer-reviewed papers for the investigation section.

The search keywords included 'warming temperature', 'lowering pH', 'increasing pCO_2' and the expression 'ocean warming effect on', 'ocean acidification effect on', 'combined effect of ocean warming and acidification on' with the scientific name of the target species. From all the resulting works, we selected 61 studies (10 field observations and 51 experimental studies) that included the target species as well as warming and/or lowering pH consistent with the IPCC predictions. Particularly, by 2100, the temperature of the upper ocean (0–2000 m) is very likely to increase by five to seven times as much under high emission scenarios (Representative Concentration Pathway RCP8.5) and by two to four times as much for low emission scenarios (RCP2.6) compared with 1970 (i.e., between +0.73 and 2.58°C by the end of the century; IPCC, 2021). Concerning OA, IPCC (2021) states that it is virtually certain that surface ocean pH will decline by 0.036–0.042 or 0.287–0.29 pH units in 2081–2100, relative to 2006–2015, for the RCP2.6 or RCP8.5 scenarios, respectively. As long as temperature and pH changes were consistent with the IPCC predictions, we included both laboratory and aquaculture-aimed studies to improve our understanding of the warming and acidification effects on sea urchins' phenotypic plasticity and acclimation potential. Especially, studies must apply thermal excursions within 3/4°C from the annual average maximum temperature and a lowering pH up to 0.3/0.4 units on individuals collected from a known location in order to also consider the environmental particularities of specific geographical areas (see below). We include field observations that evaluated the effects of recurring warming and acidification events on wild resident individuals to highlighting the potential for local adaptation of populations from naturally altered sites (e.g., CO_2 vents, upwelling areas). When available, we also relied on direct surveys to define any shifts in the distribution of different sea urchins species to determine whether they are gradually replacing the considered populations.

Because environmental mutations occur at different rates depending on location, the review also includes 18 studies considering small-scale spatial events in order to precisely assess the regional environmental alterations imposed by OW&A. In particular, the reported studies examine the local physical–chemical changes that take place on different coastal systems, predicting thermal and pH shifts that will affect a number of areas where the considered species are typically found. As a result of cross-referencing a total 79 studies concerning both sea urchin tolerance limits and environmental alterations, it has been possible to assess the vulnerability of distinct sea urchin populations in different geographical areas.

3 | RESULTS

3.1 | *L. albus* (Molina, 1782) – South-East Pacific

The Chilean Sea urchin *L. albus* native to the west coast of South America is distributed from Peru to southern Chile, where it is also most exploited. Catches of this worldwide commercialised species account presently for approximately 50% of the echinoid's global landings (Stefánsson et al., 2017). In 1995, fisheries peaked with 54,609 t, then catches declined to an average of 18,077 t per year between 2010 and 2016 (James et al., 2016).

Individuals primarily inhabit rocky shores on the intertidal zone between 0 and 20 m depth, although they can reach significant depths of several hundred meters (Molinet et al., 2013). According to its large latitudinal and bathymetric distribution, populations are exposed to a wide range of temperature and pCO_2 gradients along the Chilean coast: northernmost waters are warmer (22°C) than southern (5°C) and pCO_2 concentrations are higher at depth (>800 μatm) than at surface (500 μatm; Manrìquez et al., 2019).

3.1.1 | Planktonic life stages

Although planktonic stages constitute the most sensitive phase of the whole sea urchin life cycle (Dupont & Thorndyke, 2009), one sole study

focuses on the effects of OA on *L. albus* larvae. Gaitan-Espita et al. (2017) showed that predicted high pCO_2 (1200 μatm; 7.7 pH) leads to significant effects on the total larval length, shifting from ~410 to ~380 μm in some populations. Moreover, post-oral arm length also decreases by 12.5% (i.e., from 160 to 140 μm). In *echinoplutei* stages, the appropriate sizes and proportions among body components, such as oral arms, are essential for feeding, swimming and protection from predators (Byrne et al., 2010). Shorter arms larvae display reduced food capture and swimming capabilities (O'Donnell et al., 2010). Consequently, *echinoplutei* took longer to reach the final 4-armed pluteus stage and success was significantly reduced (Gaitan-Espita et al., 2017). However, phenotypic plasticity confers a potential tool to counteract acidification across generations as the extent of these effects varies across sampling sites. Particularly, populations of CO_2-supersaturated subregions (latitudes 18–39°S) were less affected by water acidification (1200 μatm; 7.7 pH) than those of CO_2-undersaturated subregions (i.e., more than 40°S; Gaitan-Espita et al., 2017). Such results reflect contrasting selective pressures along the spatial distribution of *L. albus*, with highly plastic phenotypes and greater tolerance to OA in larvae of populations from central and northern Chile (Gaitan-Espita et al., 2017).

3.1.2 | Benthic life stages

After primary settlement on the seabed, post-settlement development begins, involving several morphological changes to finally reach the juvenile stage. At this stage, calcification, expansion and creation of internal tissues lead to significant changes in mass, diameter and the body shape (Ebert, 2001). Manrìquez et al. (2017) analysed the effect of OW (19°C) and acidification (945 μatm; 7.63 pH) on juveniles originated from northern Chile (29°S) for a period of 7 months (i.e., until the adult phase is reached). When compared to control (16°C and 430 μatm; 7.88 pH), increasing temperature and pCO_2 affect the individuals' development, with sea urchins showing a significantly reduced body mass (~0.15 weight loss % d^{-1}). Altered conditions also increased the rate of test dissolution and decreased the structural tenacity, resulting in easier skeletal failure. Indeed, warming increases Mg incorporation within sea urchin skeletons, improving hardness and test strength (Byrne et al., 2014; Dworjanyn & Byrne, 2018). However, when exposed to acidification, it also increases carbonate dissolution, resulting in major structural complications (Byrne et al., 2013).

In terms of feeding, *L. albus* consumption was observed to be largely temperature and pH dependent: grazing rate increased by 22% at elevated temperature (19°C) and pCO_2 (1310 μatm; 7.48 pH) compared with control (16°C and 453 μatm; 7.84 pH; Manrìquez et al. 2017). Such change in feeding most likely relates on metabolic changes and may explain the reduced growth of some juveniles, with serious consequences for productivity.

The internal coelomic fluid of sea urchins contains coelomocytes cells that are involved in many physiological aspects and determines the immunological capacity (Ramirez-Gomez & Garcia-Arraràs, 2010). One central feature of such cells is the ability to synthesise heat shock proteins (HSPs), which recognise and interact with denatured proteins arising from intense warming stresses, minimising the probability of their interaction with further metabolites (Tomaken & Somero, 2000). In *L. albus*, the capacity to synthesise HSPs and other molecular compounds is considerably influenced by temperature and pH, as well as their interaction. According to Vergara-Amado et al. (2017), the expression of particular molecular markers (HSPs, detoxification proteins and osmoregulatory proteins) increased in individuals from central Chile (39°S) exposed to warmer conditions (18°C) than control (14.5°C). However, such increase occurred only during the first 12 h of exposure, as levels returned to normal after 48 h indicating a good potential for acclimation. In Manrìquez et al. (2019), temperature did not affect the HSP production in Chilean individuals from the North regions (29°S), whereas HSP concentrations increased up to 75-fold under high temperatures (20°C) and pCO_2 levels (1400 μatm; 7.45 pH). This final example illustrates how temperature and pCO_2 interact to potentially alter the thermal stress response of *L. albus*, reducing individuals' heat tolerance and acclimation capacity.

3.1.3 | *L. albus* facing OW&A

When considering the data reported here, *L. albus* appears to be able to withstand large temperature changes without serious metabolic consequences in the medium to long term. Warming waters (from 7 to 14°C) are not a threat to the survival and growth of individuals collected from the species' southern distributional margin (53°S; Detrée et al., 2020). In northern regions, 18–20°C constitute a threshold beyond which both development and physiology processes degrade (Table 1). The wide thermal tolerance range could be attributed to the widespread distribution along the East Pacific coastline, where *L. albus* is exposed to various temperature conditions. However, the interaction between OW&A plays a fundamental role in defining the degree of tolerance in different sea urchins populations (Manrìquez et al., 2017, 2019). In central and northern Chile, settled individuals are particularly sensitive to high temperatures (19–20°C) and low pH (7.45–7.6 pH), with major effects on their development and physiology.

The coast of Chile is expected to cool in the next future as upwelling events intensify (Lima & Wethey, 2012; Valera et al., 2018). In contrast to the overall thermal increase of oceans, Falvey and Garredau (2009) claim that central and northern coasts (17–37°S) cooled by −0.20°C per decade from 1979 to 2006. As a result, the upper thermal tolerance limits observed for *L. albus* may be respected in the near future, though no experimental studies consider the lower limits. However, northern regions are also predicted to experience lower pH of their surrounding waters due to increased upwelling events (Cai et al., 2021). Although Gaitan-Espita et al (2017) showed a high potential for adaptation of local populations to such particular conditions concerning the larval phenotypic plasticity, studies on the long-term consequences of transgenerational plasticity and/or genetic adaptation of resident individuals are still lacking when considering such integrated stressors (i.e., lowering temperature and pH).

TABLE 1 Summary table of the most valuable reported studies on the effects the effects of OW&A on the different life stages of the considered sea urchin species (GE, gamete exposure; LE, larval exposure; AD, adult exposure; pH, NBS scale; temperature, °C)

Species	Life stage	Population	Control cond. pHnbs/T	Tested pHnbs	Tested T	Tested pHnbs/T	Time	Effects	References
L. albus	Larvae	S Chile (40°S)	8/14°C	7.7			84 h LE	Increase of abnormal larvae compared with northern populations	Gaitan-Espita et al. (2017)
	Juvenile	N Chile (29°S)	7.88/16°C			7.63/19°C	7 month	Altered test structure/altered grazing behaviour/reduced body mass	Manriquez et al. (2017)
	Juvenile	Central Chile (39°S)	14.5°C		18°C		48 h	No significant difference in HSPs production	Vergara-Amado et al. (2017)
	Adults	N Chile (29°S)	7.82/16°C			7.45/20°C	30 days	Altered HSPs production	Manriquez et al. (2019)
	Adults	S Chile (53°S)	7°C		14°C		60 days	No significant effects on survival and growth	Détrée et al. (2020)
M. franciscanus	Fertilisation	SW Canada (48°)	8/7–11°C	7.8			21 days AE	Increased unsuccessful fertilisation	Reuter et al. (2011)
	Larvae	SW USA (34°N)	8/13°C			7.67/17°C		T° increase buffers lowering pH	Wong and Hofmann (2020)
	Larvae	SW USA (34°N)	8/15–18°C			7.87/15°C	48 h LE	Lower expression of HSP 70	O'Donnell et al. (2009)
	Adult	SW (36°N)	8.1/13°C	7.4			3 months	Growth, grazing and calcification rate decline	Doham et al. (2022)
	Adult	N Mexico (28°N)	15°C		21°C		7 days	Higher mortality	Hernandez et al. (2004)
S. purpuratus	Fertilisation	SW USA (34°N)	8/15°C	7.76			4 h GE	Unsuccessful fertilisation compared with northern population (44°N)	Kapsemberg et al. (2017)
	Larvae	SW USA (34°N)	8.1/14°C	7.7			21 days LE	Postponed development/altered larval morphology	Stumpp et al. (2011)
	Larvae	SW USA (34°N)	8/14°C			7.6/18°C	5 days LE	Altered morphology and genomic responses	Padilla-Gamiño et al. (2013)
	Adult	SW Canada (48°N)	13°C		16°C		3 months	Increased body weight	Azad et al. (2011)
S. intermedius	Fertilisation	Yellow sea (China)	9.8–20°C		21°C		15 months AE	Increased unsuccessful fertilisation	Zhao et al. (2018a)
	Larvae	Yellow sea (China)	9.8–20°C		21°C		15 months AE / 9 days LE	Increased abnormal larvae and mortality/negative transgenerational effects	Zhao et al. (2018a)
	Larvae	Yellow sea (China)	8/20°C	7.7			70 h LE	Delayed cleavage and reduced larval survival	Zhan et al. (2016)
	Larvae	Yellow sea (China)	7.99/20°C	7.7			70 h LE	Altered metabolism/increased larval mortality	Li et al. (2020)
	Juvenile	Yellow sea (China)	18.5°C		21°C		15 months AE	No significant transgenerational effects	Chi et al. (2021)
	Adult	Yellow sea (China)	18.5°C		23°C		10 months	Growth and survivorship decrease	Zhao et al. (2018b)
	Adult	Yellow sea (China)	18.5°C		22°C		6 weeks	Gonad growth decrease	Zhao et al. (2015)

(Continues)

TABLE 1 (Continued)

Species	Life stage	Population	Control cond. pHnbs/T	Tested pHnbs	Tested T	Tested pHnbs/T	Time	Effects	References
	Adult	Yellow sea (China)	8.1/20°C	7.7			2 months	Decreased growth and altered genetic expression	Zhan et al. (2020)
	Adult	Yellow sea (China)	8/21°C			7.6/24°C	29 days	Unsustainable bioenergetics state	Zhang et al. (2022)
S. droebachiensis	Fertilisation		8/12°C	7.7			16 months AE	No significant difference in fertilisation success	Dupont et al. (2012)
	Fertilisation	Svalbard islands	8/3°C	7.8			1 h GE	Increased percentage of unfertilised eggs	Bogner et al. (2014)
	Larvae	SW Canada (49°N)			17°C		22 days LE	Higher mortality when coupled with low-quality food	Feehan et al. (2018)
	Larvae		8/12°C	7.7			16 months AE	No significant difference in larval survival and development	Dupont et al. (2012)
	Larvae	S Norway (57°N)	8/9°C	7.6			29 days	No significant difference in larval morphology	Dorey et al. (2022)
	Adult	N Norway (70°N)	6–10°C		10°C		11 weeks	Gonad growth increase	Siikavoupio et al. (2008)
	Adult	NE Canada (45°N)	1–17°C		17°C			Mobility and grazing activity decrease above 17°C	Lauzon-Guay/Scheibling (2007)
	Adult	S Norway (57°N)	8/10.5°C	7.6			45 days	Accumulation of bicarbonate to compensate extracellular low pH	Stumpp et al. (2012)
P. lividus	Fertilisation	Canary islands	8.1/19°C			7.7/25°C	3.5 h	No significant difference in fertilisation success	Garcia et al. (2018)
	Fertilisation	Canary islands	8.1/19°C			7.7/22.5°C	200 min	No significant difference in fertilisation success	Cohen-Rengifo et al. (2013)
	Fertilisation	S France		7.7			46 h GE	No significant difference in fertilisation success	Martin et al. (2011)
	Larvae	Canary islands	8.1/19°C			7.7/25°C	3 days	Larval mortality increases considerably	Garcia et al. (2018)
	Larvae	Canary islands	8.1/19°C			7.7/22.5°C	10 days	No significant difference in larval body length and settled larvae	Garcia et al. (2015)
	Larvae	NW France	8/11–14°C	7.6			3 days	Positive transgenerational effects – larvae from intertidal pools are more resistant to low pH	Moulin et al. (2011)
	Larvae	NE Italy	8/18°C	7.7			2 months AE	Negative transgenerational effects	Mačeta et al. (2022)
	Juvenile	Canary islands	8/19.5°C	7.6			100 days	Decreased test robustness	Rodriguez et al. (2017)
	Adult	S Italy	8.2/20°C	7.8		7.8/+2°C	12 months	No significant difference in test integrity	Collard et al. (2016)
	Adult	Portugal	18°C		24°C		90 days	Reduced somatic and gonad growth	Santos et al. (2020)
	Adult	W Mediterranean	20°C		24°C		50 days	Reduced somatic and gonad growth	Yeruham et al. (2019)

3.2 | *M. franciscanus* (Agassiz, 1863) and *S. purpuratus* (Stimpson, 1857) – North-East Pacific

Due to similar geographical range, red (*M. franciscanus*) and purple (*S. purpuratus*) sea urchins' biology and ecology have been frequently compared in past decades (Tegner & Dayton, 1981; Miller & Elmet, 1999; Rogers-Bennett & Okamoto, 2020). While the spatial distribution of *M. franciscanus* spans the entire Pacific coast of North America (from northern Mexico to Alaska), *S. purpuratus* is restricted between northern Mexico and the Canadian northwest coast. On the other hand, purple sea urchins have a wider (5 –160 m) distribution along the shore than red sea urchins (0–90 m). This last species grows faster, reaching a relatively larger size and a higher commercial value (Rogers-Bennett & Okamoto, 2020). Red sea urchins are thus mostly commercially traded, with sales reaching up to $50 million in 2004 in the United States (the species' most important supplier); then, total catches have gradually declined along the entire west coast of North America (Rogers-Bennett, 2007).

3.2.1 | Planktonic life stages

OW&A effects on fertilisation process remain understudied, especially for red sea urchins. As many other sea urchin species, sperm performance of both *M. franciscanus* and *S. purpuratus* is strongly inhibited by lower pH conditions, reducing the fertilisation benefit (Reuter et al., 2011; Kapsenberg et al., 2017). Particularly, when sperms are exposed to a slight lowering pH (7.95), fertilisation success of some echinoids drops to values of $45 \pm 5\%$ (compared with $90 \pm 7\%$ of current conditions; i.e., 8.0 pH; Sung et al., 2014). Despite such findings, Kapsenberg et al. (2017) stated that the influence of acidification on the fertilisation success of *S. purpuratus* varies according to the state of acclimatisation to sudden changes in water pH, potentially leading to local population adaptation. In particular, fertilisation in individuals exposed to strong seasonal upwelling events (resulting in most frequent exposure to low pH; 7.8) in the northern US regions (44°N) was more resilient to tested lowering pH (7.76). Instead, individuals from southern US regions (38°N and 34°N) less exposed to upwelling episodes showed greatest pH sensitivity, reducing their fertilisation success.

Moderate warming improved larval growth of red sea urchins from southern California (34°N), as the body size of the embryo prism stage was 20.8% greater at high (17°C) than at low temperature (13°C; Wong & Hofmann, 2020). Furthermore, warming temperature during early developmental stages buffered the negative effects of acidification (i.e., reduced body size) and slightly extended the individual thermal tolerance (Wong & Hofmann, 2020). Same authors also demonstrated that the sole acidification (7.67 pH) had no effect on individual thermal tolerance, contrasting previous findings on the same population at similar temperatures (15°C; O'Donnell et al. 2009). In this last case, elevated pCO_2 levels (7.87 pH) lowered the expression of the molecular chaperone HSP 70, making larvae more vulnerable to thermal stress. The observed disparities between studies may result from a weak differ-

ence in the examined developmental stage (i.e., prism vs. pluteus larvae) and/or transgenerational effects caused by environmental history of the selected parents.

The larval developmental rate of *S. purpuratus* of southern California populations also increases linearly with rising temperature (18°C; i.e., IPCC temperature projection during spawning season in southern California) while it decreases with acidification (Stumpp et al, 2011; Padilla-Gamiño et al., 2013). In particular, whereas larvae reared under control conditions (8.1 pH) spent 78–80% of available energy on growth, those reared under high pCO_2 (7.7 pH) spent 39 to 45% of available energy in buffering the physiological changes caused by acidification (Stumpp et al., 2011). This acclimation effort leads to developmental postponement and alters several morphological parameters, such as body, arms and skeleton length (Stumpp et al., 2011; Padilla-Gamiño et al., 2013). Similar to fertilisation, embryos transcriptomic response to high pCO_2 was strongly correlated to the magnitude of pH changes naturally perceived along the mosaic of the Northeast Pacific Coast, with northern groups (44°N) being more resilient to acidification (Evans et al., 2015). Concerning southern populations (32°N), Lee et al. (2019) showed severe impacts on larval development only below 7.2 pH, indicating a wide range of tolerance. However, animals were collected in a site where high daily pH variation operates (0.36 pH units), demonstrating that the population may have adapted to such particular conditions. Finally, simultaneous exposure to warming (18°C) and acidification (7.6 pH) trigger metabolic depression and transcriptomic downregulation responses in *S. purpuratus* larvae from southern California (Padilla-Gamiño et al., 2013), significantly extending the time for a complete development with potential subsequent cascading effects on individuals' fitness and populations' stability (Okamoto et al., 2018).

3.2.2 | Benthic life stages

When considering benthic stages, OW&A can affect the metabolic rate (Donham et al., 2022; Ulbricht & Pritchard, 1972), mobility (Hernandez et al., 2004) and growth (Azad et al., 2011; Donham et al., 2022) of both species. Although gonad production of Californian *M. franciscanus* was unaffected by an increase in temperature (from 13 to 16°C) in the presence of an adequate food supply (McBride et al., 1999), warming can still play a significant role in the survival of some populations. Red sea urchin thermal tolerance limits reach 21°C in northern Mexico populations (28°N; i.e., the species' southern distributional margin), as mortality was significantly higher (+20.8%) after 1 week of acclimation compared with 15 and 18°C rearing conditions (Hernandez et al., 2004). Donham et al. (2022) also contended that more frequent upwelling events (contributing to local lowering pH at 7.4) expected in central California (36°N; Garcia-Reyes & Largier, 2010) would have a negative impact on the physiology of local red sea urchins. Indeed, as the upwelling intensity increases over time, adult individuals' rates of respiration, grazing, growth and calcification decrease, with potential serious consequences for the fitness.

Thermal optimum of Canadian populations of *S. purpuratus* (48°N) has been assessed between 12 and 16°C as individual's weight increases after 12 weeks of such thermal exposure, recommending that culture operations should be made at 12°C to optimise gonad profitability (Azad et al., 2011). There is, however, a lack of experimental studies analysing physiological changes under both warming and acidification on settled individuals.

3.2.3 | *M. franciscanus* and *S. purpuratus* facing OW&A

According to studies, OW&A have a major influence on all life stages of both *M. franciscanus* and *S. purpuratus*. Particularly, high temperatures (18–20°C) associated with low pH (7.6–7.7 pH) alter the development and physiology of both species (Table 1). Sensitivity of individuals to OA constitutes a crucial factor in defining the resilience of populations to current environmental changes. In the Northeast Pacific, models predict persistent and widespread acidification episodes within the local coastal habitat (Gruber et al., 2012). Specifically, the California Current System (CCE) is particularly vulnerable to OA since it is increasingly exposed to waters with abnormally low surface pH compared with the system's historical state (Brady et al., 2020). Because of the presence of regular upwelling events, the northern communities of the Northwest American coast experience much lower pH conditions than the southern communities (Hofmann et al., 2014; Evans et al., 2015). In particular, 20% of pH values measured in Oregon fell below 7.8, compared with less than 2% of pH values recorded in California (Hofmann et al., 2014). Consequently, according to Evans et al. (2015), northern populations of *M. franciscanus* and *S. purpuratus* should be locally adapted to OA, being more tolerant to natural pH variations and thus more resilient to increasing upwelling events.

With regard to OW, the thermal optimum of both species remains relatively narrow (between 12 and 18°C) and warming temperatures have large consequences on the individuals' fitness and survivorship (Table 1). In particular, while coastal cooling trends are observed in northern areas due to increasing upwelling events (−0.2°C/decade; Valera et al., 2018), southern regions are expected to experience a massive thermal increase before the end of the century (+4/7°C; Lima & Wethey, 2012; Sanchez-Cabeza et al., 2022). As a result, the northern populations will have their thermal tolerance limits respected, though their concerns remain about their ability to withstand the regional increasingly upwelling events (especially in benthic life stages). On the other hand, the regional warming of southern coastal systems in combination with increased local acidification raise concern about the stability of sea urchin populations at their distributional margin. Interestingly, observations reveal that during warm periods on the southern California coast, *M. franciscanus* is replaced by the Coronado sea urchin (*Centrostephanus coronatus*; Kawana et al., 2019). The latter species is originally found in subtropical areas but reported in recent years to gradually shifts towards northern regions (Freiwald et al., 2016). Such works well describe the potential vulnerability of

southern populations of red sea urchins to the conditions imposed by OW&A. According to Sato et al. (2018) *Strongylocentrotus fragilis* could be a valuable candidate to fill potential production gaps of *M. franciscanus* in southern California. This species is well adapted to low oxygen levels (11.7–16.9 mmol kg^{-1}) and low pH (<7.44) as it lives mainly at great depths (500 m). Despite these characteristics, the clear technological limitations for fishing and the relatively low profitability of its gonads (e.g., 80% reduced gonad size by weight; Sato et al., 2018) limit the potential future marketability of this species.

3.3 | *S. intermedius* (Agassiz, 1864) – North-West Pacific

With regards to the high consumption and production of echinoids in the north-west Pacific, associated aquaculture and fisheries may be the most exposed to the consequences of global changes (Ohgaki et al., 2019). Six species of sea urchins are harvested in the sole Japan, *S. intermedius* and *M. nudus* accounting for 80% of total landings in the northern regions. *S. intermedius* is a well-regarded species in oriental fisheries and aquaculture production systems (particularly in Hokkaido Island; Hu et al., 2020) and can be found in both intertidal and subtidal rocky shores (mostly between 0 and 15 m) along Asia's eastern coasts: primarily in the Okhotsk Sea, in Japan Sea and Japanese Pacific coast. Over the last decade, the species has also been successfully introduced from Japan into Chinese waters, becoming an important resource for the local aquaculture industry (Lawrence et al., 2018).

3.3.1 | Planktonic life stages

Despite its economic relevance, few studies are available on *S. intermedius*' tolerance to OW&A-related stressors, particularly on their interaction (Table 1). Fertilisation success was only slightly impaired in adults collected in the Yellow Sea (China) and exposed to high temperatures (21°C) during 15 months (Zhao et al., 2018b). However, warming significantly increased the percentage of abnormal larvae, lowering larval survival after 9 days exposure (i.e., −20% of the survival rate compared to control at 18°C). In a complementary study, Chi et al. (2021) did not detected any significant carryover effects between parents and juveniles, implying that newly settled sea urchins were less susceptible to the carryover effects under warming temperatures (15 months at 21°C) than planktonic life stages.

Although acidification had no effect on fertilisation rate (7.6 pH; Zhan et al., 2016), several larval body characters were altered when exposed to lowering pH (from 7.7 to 7.5; Li et al., 2020): higher proportion of abnormal larvae with asymmetrical post-oral arms, major corrosion of spicules (Zhan et al., 2016; Li et al., 2020) and increasing mortality after 70 h of post-fertilisation exposure (i.e., ~15.6, ~34.8 or ~53.2% at either control/8.0, intermediated/7.7, or lowest/7.5 pH respectively; Li et al., 2020).

3.3.2 | Benthic life stages

At higher temperatures (+3°C) than control (20°C), the test diameter of Yellow Sea's adults decreased by 2 mm as did the mean body weight by about 3 g after 10 months of exposure (Zhan et al., 2016; Zhao et al., 2018a). The mortality rate also increased linearly with increasing temperature (+9% mortality vs. control), indicating a relevant stress condition (Zhang et al., 2017; Zhao et al., 2018a). After 6 weeks of exposure at 22°C, gonad weight and gonad index significantly decreased from an average of 13–9.5 g compared with control (20°C; but not after 10 months in Zhao et al., 2018a), most likely due to a lower food conversation ratio at high temperatures (Zhao et al., 2016).

Acidification has general negative effects not only on individual growth but also on its genetic regulation (Zhan et al., 2020). Indeed, growth rate and intestinal morphology of settled adults were significantly affected after 60 days of incubation in low pH conditions (7.7 pH). As a consequence, the individual's food intake also decreased, resulting in metabolic changes that altered the animals' fitness. Concerning transcriptomic processes, lowering pH (from 7.7 to 7.5 pH) causes changes in the expression of two immune-related genes (SiTNF14 and SiTGF-) that play important roles in inflammation and repairing mechanisms (Zhan et al., 2020), making individuals potentially more vulnerable to diseases and mass mortality events. Interestingly, *S. intermedius* from the Yellow Sea exhibit a lower ability to adapt to OW&A than the tropical *Tripneustes gratilla* sea urchin (Zhang et al., 2022). As expected, after 29 days of exposure to high temperatures (24°C) and low pH (7.6), antioxidant activity increased while cellular energy allocation decreased, indicating an unsustainable bioenergetic state compared to *T. gratilla* (control at 21°C; Zhang et al., 2022).

3.3.3 | *S. intermedius* facing OW&A

S. intermedius is associated to water temperatures ranging between 13 and 22°C throughout the year, with a thermal optimum below 20°C (Zhao et al., 2018b). The juvenile's tolerance threshold is equal to 23°C, above which high mortality rates are observed (see Zhao et al., 2016). Consequently, the combined action of the regional warming and acidification could seriously decrease the resilience of certain harvested populations. In the northern Yellow Sea, bottom-waters (40 m) warm at a rate of 0.0314 ± 0.142°C/year since 1976, and lowering pH is expected to decrease of 0.0018 units per year (Li et al., 2022). In Japan, Valera et al. (2018) report a larger increase in sea surface temperature, with values of +0.5°C per decade since 1982 along the Japanese coasts. In particular, Fujii et al. (2021) well describe the future projection of physical and biogeochemical conditions of the Hokkaido Island (northern Japan) where the expected annual-average temperature should increase between 2.2 and 5.5°C at the end of the century, while the associated pH value would decrease by 0.06/0.38 (for RCP 2.6 and RCP 8.5, respectively). Combining these projections with the current temperature and pH values (up to 24.3°C and 7.86 pH recorded

in 2018; Fujii et al., 2021), we find estimations fall beyond the tolerance thresholds expected for *S. intermedius* (Table 1). Consequently, we hypothesise that the impact of regional OW&A in northern Japan is becoming an extremely important factor recommending the establishment of appropriate adaptation strategies for Japanese industries. In recent years, the distributional range of the temperate *Heliocidaris crassispina* has shifted northward (Feng et al., 2021). Usually found in the southern region of Japan, populations of *H. crassispina* moved to the Oga Peninsula (northern Honshu, Japan), where they replaced the native *M. nudus* (Feng et al., 2019). Compared with *S. intermedius*, *H. crassispina* better tolerate seawater chemical and physical variations, being more used to tropical conditions (Dorey et al., 2018; Feng et al. 2021; Minuti et al., 2020; Mak and Chan, 2018). *H. crassispina* should thus be favoured by future conditions imposed by the local OW&A, becoming a species of major interest in the sea urchin trade of such fishing areas.

3.4 | *S. droebachiensis* (Müller, 1776) – Circumpolar-North

The temperate-cold green sea urchin *S. droebachiensis* shows a circumpolar distribution within the northern hemisphere, being found in the shallow subtidal zone (mostly between 0 and 50 m) of North Atlantic and North Pacific oceans. The species' geographic range spans the Atlantic from Greenland to Cape Cod (USA) and northern Europe including Spitzbergen, as well as the Pacific from the east coasts of Siberia and the Okhotsk Sea in Asia and from Alaska to Oregon in North America.

At the scale of global trade, it is considered as a lower quality resource than previously reported species because of its lower gonadal content (i.e., gonads index below 10%; Siikavoupio et al., 2006). Due to its large distributional area, however, *S. droebachiensis* is commonly exploited along the coasts of Eastern United States and Canada, Russia and Norway and it appeared to be a good candidate for marine cold water aquaculture (Siikavoupio et al., 2012; Stefánsson et al., 2017).

3.4.1 | Planktonic life stages

Although considerable responses are observed in literature, *S. droebachiensis* planktonic stages show a high potential for acclimation under OW&A conditions. Fertilisation success was 4.5 times lower in adults subjected to high pCO$_2$ (1270 μatm; 7.7 pH) during 4 months, but no differences to control were observed under longer period of exposure (16 months; Dupont et al., 2013). Bögner et al. (2014) demonstrated that in individuals collected from Arctic populations, the percentage of unfertilised eggs increases considerably at high pCO$_2$ concentrations (550–800 μatm; ~7.85 pH), although eggs were physiologically able to dampen the effects of acidification up to 7.8 pH (770 μatm). Consequently, Chen and Li (2018) suggested a generalised

10% reduction in fertilisation success in individuals exposed to reduced pH (7.7/7.8), with costly compensation processes compromising the energy budget for subsequent development stages.

S. droebachiensis larvae reared in southern British Columbia (49°N, 125°W; Canada) developed faster during the first planktonic life phase when reared in warmer conditions (17° compared with 9°C; Feehan et al. 2018). At 14°C, larvae produced by adults from Nova Scotia (45°N, 61°W; Ca) experienced a similar process (Hart & Scheibling, 1988). Feenhan et al. (2018), however, observed slower development and higher mortality of larvae fed with low-quality food (i.e., kelp detritus) at 17°C, most likely due to a synergetic negative effect of thermal stress and altered food resources. As a result, larvae may require adequate nutritional supply and energy efficiency to compensate the metabolic increase caused by warming waters.

When parents were previously exposed to lowering pH during 4 months (pCO$_2$ 1270 μatm; 7.7 pH; Dupont et al., 2013), 5–9 fewer offspring reached the juvenile stage at the end of the experiment. However, when adults were pre-exposed for 16 months, elevated pCO$_2$ during larval development had no significant direct effect on settlement success (Dupont al. 2013). In a study conducted in the Kattegat Sea (southern Norway), Dorey et al. (2022) confirmed the presence of a tipping point for *S. droebachiensis* larvae at 7.6 pH, below which larval body growth was significantly lower after 29 days of exposure: 103 m/log day in 7.2 pH compared to 141 and 139 m/log day in 7.6 and 8.0 pH. Chen and Li (2018) found that larval growth and mortality in green sea urchins collected in subarctic regions were also resilient to OA, highlighting the phenotypic plasticity of larvae that maintained a great swimming ability even at 7.6 pH (Chan et al., 2015).

3.4.2 | Benthic life stages

Warming waters typically accelerate juvenile growth to the adult stage after settlement. In *S. droebachiensis* the increase in growth rate is most noticeable when thermal transition remains smooth (from 6 to 10°C; Siikavoupio et al., 2012). The most favourable temperature for optimal post-settlement development ranges between 9 and 13°C in northern Norway (70°N), before major metabolic costs occur (Pearce et al., 2005; Siikavoupio et al., 2012). Similarly, adults developed larger gonads (+9%) after 11 weeks of exposure to warming temperatures (i.e., from 6 to 12°C), with no further increase in the range between 10 and 14°C (Siikavoupio et al., 2006; Siikavoupio et al., 2008). The tolerable thermal maximum appears to be 17°C in certain populations of the Northeast Canadian coasts (45°N), above which individuals significantly reduce their grazing activity and mobility (Lauzon-Guay and Scheilbing, 2007).

When considering acidification, green sea urchins exposed to natural seasonal hypercapnia conditions displayed a remarkable resistance to increasing pCO$_2$ concentrations (1000–1430 μatm; 7.6 pH) by actively compensating the extracellular lowering pH with the accumulation of bicarbonate (Stumpp et al., 2012). However, the energy costs associated with this regulation can also be a major source of repro-

ductive disturbance, possibly reducing the individual's fitness (Stumpp et al., 2012).

3.4.3 | *S. droebachiensis* facing OW&A

Throughout its life cycle, *S. droebachiensis* shows a great acclimation potential to cope with near future OW&A. Under moderate acidifying conditions both larvae and adults display a good degree of tolerance (Dorey et al., 2022; Stumpp et al., 2012; Table 1). This finding is consistent with the results of Byrne et al. (2013), who found that body development in cold water species is less influenced by acidification, due to their adaptation to the low carbonate saturation levels found in polar waters. However, although the tolerance range appears to be wide (down to 7.6/7.7 pH), the ocean surface pH is expected to decline by 0.287–0.29 pH units before 2100 in the RCP8.5 scenario (IPCC 2021), raising concern about the long-term resilience of a number of southern populations that are less adapted to endure waters with low carbonate concentrations.

Regarding the thermal challenge, this species can withstand a wide range of temperatures depending on the population (Table 1). Specimens can be found in both cold (−1°C) and temperate (17°C) waters, the thermal tolerance limit reaching up to 22°C in laboratory conditions (Lauzon-Guay & Scheilbing, 2007). In economic terms, because maximum yield is reached when summer temperatures do not exceed 12°C (Siikavoupio et al., 2006; Siikavoupio et al., 2008), fishing and commercialisation of *S. droebachiensis* should be highly efficient along coasts of northern regions. However, as the rate of oxygen consumption linearly increase with rising temperatures (Siikavoupio et al., 2008), it is questionable at what point the metabolic balance would shift towards an unsustainable state with subsequent drop in productivity. In particular, sub-Arctic and Arctic regions (i.e., Nordic Sea, Barents Sea, Bering Sea and St. Lawrence Gulf) are all considered as warming hotspots, exhibiting some of the largest temperature increases on the globe before the end of the century (between 2 and 4.5°C according to scenarios; Khosravi et al., 2022). In such areas, *S. droebachiensis* is also the most fished and sold sea urchin species (Stefánsson et al., 2017). Based on the studies reported here, such intense warming temperatures are likely to bring instability to many southern populations, with the combined action of OW&A potentially redefining the populations' tolerance limits and leading to important consequences on local industries sustainability. Actually, the species is retreating northward along the Norwegian coasts (Nyhagen et al., 2018). In southern fjords, where special hydrographical conditions allow the maintenance of local populations, animals become smaller (5–3 cm average) and higher density of individuals move to deeper waters over time (from 10/15 to 20 m between 1992 and 2013; Nyhagen et al., 2018). According to predictions, the yield of *S. droebachiensis* in northern Norway will decline significantly over the next 30 years due to altered conditions imposed by OW&A (Wallhead et al., 2018). Despite the high acclimatisation potential and phenotypic plasticity of *S. droebachiensis*, observations suggest that environmental conditions

in many areas are becoming less suitable to the harvesting of several green sea urchin populations.

3.5 | *P. lividus* (Lamark, 1816) – Mediterranean and North-West Atlantic

P. lividus inhabits the Mediterranean Sea and part of the north-eastern Atlantic, from Ireland to southern Morocco, including the archipelagos of Macaronesia. Individuals are typically found on sublittoral rocky seafloors at greater depths than its commonly associated species *Arbacia lixula*, ranging between the intertidal plan and 30 m depth (Garcia et al., 2018). The species is mainly harvested on the Eastern European coast and in the Mediterranean basin where fishing has become increasingly attractive due to the high prices of gonads (up to €150 per kg; Grosso et al., 2021). Nowadays, because intensive harvesting depleted several wild stocks (Sphigel et al., 2018), some studies are carried out to assess the feasibility of using *P. lividus* in aquaculture in order to improve the system sustainability (Grosso et al., 2021; Sphigel et al., 2018).

3.5.1 | Planktonic life stages

Several studies dealing with the simultaneous effects of OW&A on early life stages are available (Table 1). In the Canary Islands, fertilisation rates did not differ when gametes were exposed for 210 min to rising temperature (from 19 to 25°C) and lowering pH (7.7, 7.4; Garcia et al., 2018). Similarly, Cohen-Rengifo et al. (2013) stated that fertilisation was not affected by coupled warming (from 19 to 22.5°C) and acidification (7.7, 7.4 pH). Such antagonistic effect could be due to the stimulating effect of moderate warming, which usually increases fertilisation success and buffers the adverse effects of lowering pH (Garcia et al., 2018). Alternatively, the sole acidification did not alter the fertilisation success, as gametes remain intact after an 8.1–7.7 pH exposure over a 3-day period (Martin et al., 2011).

Considered individually, OW and OA have a significant impact on the development of *P. lividus*' planktonic stages. Warming temperatures increase the proportion of eggs in the advanced division phase, whereas low pH delays the general development (Moulin et al., 2011; Cohen-Rengifo et al., 2013; Garcia et al., 2018). When both factors co-occur, a slight thermal increase dampens the impacts of acidification on larval morphology (Garcia et al., 2015; 2018): body and post-oral arm length are reduced in *P. lividus* larvae exposed to low pH (7.4) and 19°C, while such parameters result unaffected at 20.5°C in same pH conditions. Interestingly, the negative effects of coastal pollutants (i.e., gadolinium) on larval physiology were also reduced in experimental conditions of near-future temperature projections (+3°C, 21°C; Martino et al., 2021). Nonetheless, when warming was excessive (22.5/24°C) such dampening effect disappeared, with an increase of malformed larvae in both experiences (Garcia et al., 2015; Martino et al., 2021). After 3 days of exposure, larval mortality increased in 7.7 pH condition in all temperature treatments (except the control

temperature 19°C; Garcia et al., 2018), indicating a threshold in their acclimation potential. Similarly, the tolerance limit of 7.7 pH (at 20°C) is also validated for southern France's *P. lividus* larvae: post-oral arms and body length were similar from 8.1, to 7.7 pH after 3-day exposure, then decreased considerably at 7.5 pH. In a complementary study, Moulin et al. (2011) observed a potential transgenerational plasticity to buffer the acidification influence, suggesting that larvae originating from pre-exposed adults to lower pH (7.8) were more resilient to future OA. By contrast, additive negative effects of 2-month parental exposure to low pH (7.7) were found on larval survival (Marčeta et al., 2022). Because sea urchins tested in Moulin et al. (2011) lived in tidal pools naturally exposed to daily pH variations, the observed differences in acclimation between both studies could be attributed to different parents' life history.

3.5.2 | Benthic life stages

Hermans et al. (2010) observed that the Mg/Ca ratio of post-settled juvenile skeleton raises under warming (13–24°C) until it reaches a plateau, assuming that it results from a saturation of the magnesium transport system during skeletogenesis. Generally, higher Mg content improves hardness and strength of sea urchin tests exposed to rising temperatures (e.g., *Tripneustes gratilla* in Dworjanyn and Byrne, 2018). However, enhanced Mg concentration in the ossicles also leads to higher dissolution of skeletal compounds, increasing the vulnerability of echinoids to OA (Byrne et al., 2013). After 100 days exposure, test robustness of *P. lividus* juveniles from Canary Islands decreased when exposed to reduced pH conditions (7.6; Rodriguez et al., 2017). Similarly, in the Ligurian Sea (NW Mediterranean), juvenile tests became gradually more fragile under lowering pH (from 7.9 to 7.7 pH; Asnaghi et al., 2013). However, once adult stage is reached, test integrity was not altered after 1-year laboratory exposure to OW&A (+2°C and 7.9/7.8 pH; Collard et al., 2016). Still, *P. lividus* density often decreases at marine CO_2 vent sites, where seawater pCO_2 is constantly high (1000–1525 μatm; Baggini et al., 2015; Calosi et a., 2013). Such field observations suggest a low ability to regulate extracellular acid–base balance over long periods compared with other species (i.e., *Arbacia lixula*), possibly due to the elevated costs of maintaining high bicarbonate concentrations to buffer the seawater acidification (Calosi et al., 2013).

Individuals' energy budgets are also temperature dependent, affecting both sea urchin morphology and growth potential. In Portugal, individuals with higher gonads index (+1.93%) were obtained at 22°C compared with other tested temperatures (18, 20 and 24°C) after 90 days exposure (Santos et al., 2020). By contrast, because 24°C drastically reduces somatic and gonad growth, such temperature constitutes a limit of tolerance for productivity of populations harvested in the same region (Santos et al., 2020). Such results reinforce the work of Yeruham et al. (2019) conducted over 50 days in the Eastern Mediterranean which showed that 20–22°C temperatures induce a more efficient energy expenditure ratio, resulting in a higher scope for growth (+10%) when compared with warmer treatments (24–26°C).

Beyond this threshold, the productivity of P. lividus is likely to decrease, influencing the organism's energy investment priorities.

3.5.3 | P. lividus facing OW&A

The productivity and yield of wild P. lividus is optimal when waters do not exceed 22°C during the harvesting period (May–July) in the Mediterranean Sea. In the eastern part of the basin, severe mortality events have been reported when summer temperatures exceed 30.5°C, resulting in the collapse of many local populations (Yeruham et al., 2015). Under OW&A, a number of models consider the Mediterranean Sea as a warming hotspot, predicting a generalised increase in surface temperatures between 1.5 and 3°C relative to present day levels (Corrales et al., 2018; Darmakari et al., 2019). The coasts of the north-east Africa and Middle East are showing the greatest seawater warming (0.05°C/year since 1982; Shaltout & Omstedt, 2014), also increasing the frequency of marine heatwaves (Shaltout & Omstedt, 2014; Darmakari et al., 2019). If this trend is confirmed in the next future, summer coastal temperatures should exceed 30°C over long periods (Darmakari et al., 2019), far beyond the bearing limits of local P. lividus. Moreover, a generalised acidification of the Mediterranean Sea is expected before 2100, with a predicted pH decrease of 0.245 in the western and 0.242 in the eastern basins, according to the RCP2.6 scenario (0.462 and 0.457 under the RCP8.5 scenario; Goyet et al., 2016). Given that specific laboratory conditions (i.e., 24°C/7.7 pH, 24/26°C) significantly alter the development of P. lividus from various populations, local OW&A conditions are likely to have a considerable impact on the distributional range of this species in the Mediterranean Sea.

4 | DISCUSSION

Ongoing global changes are modifying the fisheries distribution and the productivity of many aquaculture practices (Froehlich et al., 2018; Maulu et al., 2021; Wallhead et al., 2018). Understanding the way by which warming and acidification may affect the life cycle of marine organisms is essential to assess the future of marine ecosystems and the services they provide. Nevertheless, other environmental changes must also be taken into account in order to provide a more complete overview of coming changes, like hypoxia, freshwater inputs and primary production turnover (Castilla-Gavilán et al., 2018; Hu et al., 2020; Shen et al., 2019).

Within a specific range, OW enhances the development of various sea urchins' life stages, with inhibitory responses only after the tolerance threshold is exceeded. Rising temperatures, for example, improve body size and gonad index of settled forms (Byrne and Hernàndez, 2020; Siikavoupio et al., 2012; Sole et al., 2020; Table 1). However, excessive warming alters basic physiological processes, impairing juvenile development and finally increasing mortality in several populations (Santos et al., 2020; Yeruham et al., 2019; Zhao et al., 2018b; Table 1). Additionally, temperature strongly influences larval settlement, which regulates population spread (Okamoto et al., 2019). Fast-growing

embryos and larvae reduce spread-specific capacity in the environment, limiting dispersal and reducing connectivity among populations (Duarte, 2007; O'Connor et al., 2007).

Among the present studies, the OA threshold of 7.7 pH is frequently associated to several development issues in both planktonic and benthic stages of several species (Table 1). Such findings are consistent with the work of Bednarsek et al. (2021), who established a general tolerance threshold in echinoderms between 7.60 and 7.75, above which impaired physiological responses appear. Water acidification has a significant impact on the body development of both larval and juvenile forms, altering their morphology and metabolism, with subsequent severe consequences on individual fitness (Gaitan-Espita et al., 2017; Li et al., 2020; Mačeta et al., 2022; Stumpp et al., 2011; Zhan et al., 2016; Table 1). Nonetheless, the OA threshold of sea urchins is habitat dependent, indicating that acclimatisation and adaptation processes can shape the individual's sensitivity to lower pH at local scale (Gaitan-Espita et al., 2017; Kapsenberg et al., 2017). Furthermore, OA vulnerability appears to be strongly influenced by carryover effects related to the living environment of parents (Chin et al., 2021; Mačeta et al., 2022; Moulin et al., 2011; Zhao et al., 2018b).

Considered together, OW&A operate in either synergistically or antagonistically ways at different life stages of echinoids. In some cases, warming mitigate the effect of acidification on larvae and juveniles, but they also act synergistically generating damaging outcomes (Byrne & Hernàndez, 2020; Garcia et al., 2018; Manrìquez et al., 2017; Wong & Hofmann, 2020). Warming, in particular, mitigates the negative effects of acidification when temperatures remain within the tolerance species range (Garcia et al., 2015; Garcia et al., 2018; Wong and Hofmann, 2018). Conversely, when warming exceeds a specific threshold, the negative effects of both stressors cumulate, resulting in far-reaching consequences (Manrìquez et al., 2017; Manrìquez et al., 2019). Because both factors act concurrently in the marine environment, future research must examine the impact of concurrent factors.

In this review, we considered different populations to assess their adaptation potential to changing environmental conditions. Such ability results from genetic adaptation to living in habitats where organisms routinely experience temperature and/or acidification variations. In particular, populations exposed to a broad range of environmental conditions are good candidates to provide insights about transgenerational plasticity (Byrne et al., 2020). In general, areas naturally subjected to altered physical–chemical conditions (e.g., upwelling zones, CO2 vents, intertidal plan) demonstrate the possibility of phenotypic adjustment and/or beneficial genetic selection, revealing complex plasticity–adaptation interactions (Byrne et al., 2020; Collard et al., 2016; Kapsenberg et al., 2017; Moulin et al., 2011). As reported, sea urchins from populations enduring extreme environmental conditions appear more resilient to the tested laboratory conditions. Byrne et al. (2020) report that parental conditioning over few generations has limited benefits on offspring's stress resilience in the face of global change consequences. Nonetheless, over longer periods (i.e., with sufficient time to adapt), population's genetic diversity may constitute a foundation for selecting features most adapted to new altered

conditions, potentially increasing the resilience of some populations facing OW&A.

From a management perspective, several methodologies have been provided to minimise the effects of OW&A. According to the adaptive plasticity concept, selective breeding is a technique used in aquaculture to optimise production, overcome reduction in growth performance and thus can be very useful to recover from diseases and other stressors (Clements & Chopin, 2017; Reid et al., 2019). Nevertheless, in the presence of multiple stressors, species at the limit of their tolerance range should have reduced survival and fitness (Froehlich et al., 2018). In aquaculture, the IMTA is defined as a sustainable and economically rewarding system as well as more resilient to global change (Maulu et al., 2021). For instance, farmed seaweed and macrophytes should constitute valuable cultures to provide localised OA mitigation by producing oxygen, sequestering CO_2 and increasing pH (Clements & Chopin, 2017). Furthermore, local food availability is also a major factor in determining the magnitude of stressors as a great food supply can dampen the negative impacts of water warming and/or acidification on particular species (Melzer et al., 2011; Feehan et al., 2018). It should be pointed out that species exhibiting sensitive life stages might be farmed in appropriate land-based basins under monitored conditions and subsequently moved onto outdoor farming. This strategy could make it possible to protect organisms from exceptional stress events (i.e., marine heatwaves or upwelling events; Reid et al., 2019). As an example, S. purpuratus is sensitive to high temperatures (above 16°C) that may often be reached during increasingly frequent Warm Blob events along the Northeast Pacific Ocean and the establishment of a similar farming strategy could rescue a large part of the production.

In conclusion, the direct consequences of OW&A result in substantial changes in all life stages of various echinoid populations, from eggs to adults. The reported findings help in defining the highly variable bearing capacity of populations in order to develop valid predictive models about fishery trends. As reported by several observations, the distribution limits of many sea urchins' populations are changing, with important consequences for ecological and economic systems. Assessments that identify alternative ways to shift fishery emphasis from more vulnerable to resilient species will increasingly play a crucial role in maintaining productivity in local industries. Understanding and evaluating the effects of stressors on the organisms' life cycle is crucial to identify possible adaptive deficiencies of populations facing future environmental changes. Starting from practical observations such as the accessibility, growth rate, abundance of produced meat or marketable qualities and correlating them with the capacity to withstand OW&A, would make it possible to achieve innovative production models to stabilise the industry and thus satisfy the growing demand for foodstuffs by human populations.

5 | PERSPECTIVES

In this review, we illustrate the crucial need to conduct studies examining the effects of OW&A on different life stages of several species

of sea urchin in order to obtain an overall picture of their future distribution and availability in different geographical areas. However, it is still challenging to find life cycles that are fully and exhaustively studied (Table 1). Especially, authors reported a significant lack of knowledge about the impacts of OW&A on the fertilisation process in several species (especially L. albus, M. franciscanus and S. intermedius). Early planktonic life stages (i.e., embryos and larvae) are better studied, although large gaps exist (see L. albus and S. intermedius). Generally, there is still a major lack of studies reporting the simultaneous action of OW&A on sea urchins, leaving the potential cumulative or dampening effects largely unknown. In addition, we note a lack of data on populations found in areas predicted to be most affected by global changes, such as the S. intermedius population on Hokkaido Island, the easternmost populations of P. lividus in the Mediterranean Sea and S. droebachiensis in the northern seas (Table 1).

Researchers interested in the effects of global changes on various marine organisms must adapt their experimental models to the expected environmental alterations within the geographical area typically occupied by the considered population, taking into great account the local adaptation potential of the selected individuals. The capacity to withstand OW&A consequences is strongly associated with genetic features, transgenerational plasticity and the life experience of progenitor. Several studies show that transgenerational adaptation is possible over the long-term period, though some authors argue that this feature shows ambiguous effects (see Byrne et al., 2020). Such uncertainties highlight the importance of studying the effects of OW&A over multiple generations, allowing for more robust interpretations of population vulnerability to environmental changes.

Due to logistical constraints, many studies use short stressor exposure at rates much faster than projected global changes. The duration of exposure to stressors is critical in experimental designs because organisms need time to acclimate to newly imposed conditions (see Collard et al., 2016; Stumpp et al., 2012). In fact, the final results of many OW&A-related studies vary greatly depending on the duration of the experiment (see Dupont et al., 2013). Many of the studies reported here focus on the individual's acclimation potential to altered environmental conditions while overlooking the species' adaptive potential over long period of exposure to future OW&A. It is then critical for future research to address long-term effects of stressors in order to gain a better understanding and make more accurate predictions of how OW&A will affect underwater life and marine ecosystems.

AUTHOR CONTRIBUTION

Thomas Uboldi: Conceptualisation, investigation, methodology, writing – original draft; **Rejean Tremblay**: Supervision, validation, writing – review and editing; Frederic Olivier: Supervision, validation, writing – review and editing; **Laurent Chauvaud**: Supervision, validation, writing – review and editing

CONFLICT OF INTEREST STATEMENT

The authors whose names are listed immediately above certify that they have no affiliations with or involvement in any organisation or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership or other equity interest; and expert testimony or patent-licensing arrangements) or nonfinancial interest (such as personal or professional relationships, affiliations, knowledge or beliefs) in the subject matter or materials discussed in this manuscript.

FUNDING INFORMATION

This research did not receive any specific grant from funding agencies in the public, commercial or not-for-profit sectors.

DATA AVAILABILITY STATEMENT

The authors declare that the data supporting the findings of this study are available within the article.

ETHICS STATEMENT

This material is the authors' own original work, which has not been previously published elsewhere.

ORCID

Thomas Uboldi https://orcid.org/0000-0001-9946-5796

PEER REVIEW

The peer review history for this article is available at: https://publons.com/publon/10.1002/aff2.107

Bibliography

Asnaghi, V., Chiantore, M., Mangialajo, L., Gazeau, F., Francour, P., Alliouane, S. et al. (2013) Cascading effects of ocean acidification in a rocky subtidal community. *PLoS ONE*, 8, e61978. https://doi.org/10.1371/journal.pone.0061978

Azad, A.K., Pearce, C.M. & McKinley, R.S. (2011) Effects of diet and temperature on ingestion, absorption, assimilation, gonad yield, and gonad quality of the purple sea urchin (*Strongylocentrotus purpuratus*). *Aquaculture*, 317, 187–196. https://doi.org/10.1016/j.aquaculture.2011.03.019

Baggini, C., Issaris, Y., Salomidi, M. & Hall-Spencer, J. (2015) Herbivore diversity improves benthic community resilience to ocean acidification. *Journal of Experimental Marine Biology and Ecology*, 469, 98–104. https://doi.org/10.1016/j.jembe.2015.04.019

Bednaršek, N., Calosi, P., Feely, R.A., Ambrose, R., Byrne, M., Chan, K.Y.K., et al. (2021) Synthesis of thresholds of ocean acidification impacts on echinoderms. *Frontiers in Marine Science*, 8, 602601. https://doi.org/10.3389/fmars.2021.602601

Bif, M.B., Siqueira, L. & Hansell, D.A. (2019) Warm events induce loss of resilience in organic carbon production in the northeast Pacific Ocean. *Global Biogeochemical Cycles*, 33, 1174–1186. https://doi.org/10.1029/2019GB006327

Bögner, D., Bickmeyer, U. & Köhler, A. (2014) CO_2-induced fertilization impairment in *Strongylocentrotus droebachiensis* collected in the Arctic. *Helgoland Marine Research*, 68, 341–356. https://doi.org/10.1007/s10152-014-0394-3

Brady, R.X., Lovenduski, N.S., Yeager, S.G., Long, M.C. & Lindsay, K. (2020) Skillful multiyear predictions of ocean acidification in the California Current System. *Nature Communications*, 11, 1–9. https://doi.org/10.1038/s41467-020-15722-x

Bray, L., Pancucci-Papadopoulou, M.A. & Hall-Spencer, J.M. (2014) Sea urchin response to rising pCO2 shows ocean acidification may fundamentally alter the chemistry of marine skeletons. *Mediterranean Marine Science*, 510–519. https://doi.org/10.12681/mms.579

Broitman, BR, Lagos, NA, Opitz, T, Figueroa, D, Maldonado, K, Ricote, N et al. (2021) Phenotypic plasticity is not a cline: thermal physiology of an intertidal barnacle over 20 of latitude. *Journal of Animal Ecology*, 90:1961–1972. https://doi.org/10.1111/1365-2656.13514

Byrne, M. (2011) Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Oceanogr Mar Biol: An Annual Review*, pp. 1–42.

Byrne, M., Foo, S.A., Ross, P.M. & Putnam, H.M. (2020) Limitations of cross- and multigenerational plasticity for marine invertebrates faced with global climate change. *Glob. Chan. Bio.*, 26, 80–102. https://doi.org/10.1111/gcb.14882

Byrne, M & Hernández, JC (2020) Sea urchins in a high CO_2 world: impacts of climate warming and ocean acidification across life history stages. In: *Dev. in Aquac. and Fish. Sci.*, Elsevier, p 281–297. https://doi.org/10.1016/B978-0-12-819570-3.00016-0

Byrne, M., Lamare, M., Winter, D., Dworjanyn, S.A. & Uthicke, S. (2013) The stunting effect of a high CO_2 ocean on calcification and development in sea urchin larvae, a synthesis from the tropics to the poles. *Philosophical Transactions of the Royal Society B*, 368, 20120439. https://doi.org/10.1098/rstb.2012.0439

Byrne, M., Smith, A.M., West, S., Collard, M., Dubois, P., Graba-landry, A. et al. (2014) Warming influences Mg^{2+} content, while warming and acidification influence calcification and test strength of a sea urchin. *Environmental Science & Technology*, 48, 12620–12627. https://doi.org/10.1021/es5017526

Byrne, M., Soars, N., Selvakumaraswamy, P., Dworjanyn, S.A. & Davis, A.R. (2010) Sea urchin fertilization in a warm, acidified and high pCO2 ocean across a range of sperm densities. *Marine Environment Research*, 69, 234–239. https://doi.org/10.1016/j.marenvres.2009.10.014

Cai, W., Santoso, A., Collins, M., Dewitte, B., Karamperidou, C., Kug, J.-S. et al. (2021) Changing El Niño–Southern Oscillation in a warming climate. *Nature Reviews Earth & Environment*, 2, 628–644. https://doi.org/10.1038/s43017-021-00199-z

Calosi, P., Rastrick, S.P.S., Graziano, M., Thomas, S.C., Baggini, C., Carter, H.A. et al. (2013) Distribution of sea urchins living near shallow water CO_2 vents is dependent upon species acid–base and ion-regulatory abilities. *Marine Pollution Bulletin*, 73, 470–484. https://doi.org/10.1016/j.marpolbul.2012.11.040

Castilla-Gavilán, M., Buzin, F., Cognie, B., Dumay, J., Turpin, V. & Decottignies, P. (2018) Optimising microalgae diets in sea urchin *Paracentrotus lividus* larviculture to promote aquaculture diversification. *Aquaculture*, 490, 251–259. https://doi.org/10.1016/j.aquaculture.2018.02.003

Chan, K.Y.K., García, E. & Dupont, S. (2015) Acidification reduced growth rate but not swimming speed of larval sea urchins. *Scientific Reports*, 5. https://doi.org/10.1038/srep09764

Chen, W. -Y. & Lin, H. -C. (2018) Probabilistic risk assessment of the effect of acidified seawater on development stages of sea urchin (*Strongylocentrotus droebachiensis*). *Environmental Science and Pollution Research*, 25, 12947–12956. https://doi.org/10.1007/s11356-018-1577-2

Chi, X., Shi, D., Ma, Z., Hu, F., Sun, J., Huang, X. et al. (2021) Carryover effects of long-term high water temperatures on fitness-related traits of the offspring of the sea urchin *Strongylocentrotus intermedius*. *Marine Environmental Research*, 169, 105371. https://doi.org/10.1016/j.marenvres.2021.105371

Clemente, S., Lorenzo-Morales, J., Mendoza, J., López, C., Sangil, C., Alves, F. et al. (2014) Sea urchin *Diadema africanum* mass mortality in the subtropical eastern Atlantic: role of waterborne bacteria in a warming ocean. *Marine Ecology Progress Series*, 506, 1–14. https://doi.org/10.3354/meps10829

Clements, J.C. & Chopin, T. (2017) Ocean acidification and marine aquaculture in North America: potential impacts and mitigation strategies. *Reviews in Aquaculture*, 9, 326–341. https://doi.org/10.1111/raq.12140

Cohen-Rengifo, M., Garcia, E., Hernandez, C. A., Hernandez, J. C. & Clemente, S. (2013) Global warming and ocean acidification affect fertilization and early development of the sea urchin *Paracentrotus lividus*. *Cahiers de Biologie Marine*, 54, 667–675.

Collard, M., Rastrick, S.P., Calosi, P., Demolder, Y., Dille, J., Findlay, H.S. et al. (2016) The impact of ocean acidification and warming on the skeletal mechanical properties of the sea urchin *Paracentrotus lividus* from laboratory and field observations. *ICES Journal of Marine Science*, 73, 727–738. https://doi.org/10.1093/icesjms/fsv018

Darmaraki, S., Somot, S., Sevault, F., Nabat, P., Cabos Narvaez, W.D., Cavicchia, L., et al. (2019) Future evolution of marine heatwaves in the Mediterranean Sea. *Climate Dynamics*, 53, 1371–1392. https://doi.org/10.1007/s00382-019-04661-z

Détrée, C., Navarro, J.M., Font, A. & Gonzalez, M., (2020) Species vulnerability under climate change: study of two sea urchins at their distribution margin. *Science of the Total Environment*, 728, 138850. https://doi.org/10.1016/j.scitotenv.2020.138850

Donham, E.M., Strope, L.T., Hamilton, S.L. & Kroeker, K.J. (2022) Coupled changes in pH, temperature, and dissolved oxygen impact the physiology and ecology of herbivorous kelp forest grazers. *Global Change Biology*, 28, 3023–3039. https://doi.org/10.1111/gcb.16125

Dorey, N., Butera, E., Espinel-Velasco, N. & Dupont, S. (2022) Direct and latent effects of ocean acidification on the transition of a sea urchin from planktonic larva to benthic juvenile. *Scientific Reports*, 12, 1–10. https://doi.org/10.1038/s41598-022-09537-7

Dorey, N., Maboloc, E. & Chan, K.Y.K. (2018) Development of the sea urchin *Heliocidaris crassispina* from Hong Kong is robust to ocean acidification and copper contamination. *Aquat. Tox.*, 205, 1–10. https://doi.org/10.1016/j.aquatox.2018.09.006

Duarte, C. (2007) Marine ecology warms up to theory. *Trends in Ecology & Evolution*, 22, 331–333. https://doi.org/10.1016/j.tree.2007.04.001

Dupont, S., Dorey, N., Stumpp, M., Melzner, F. & Thorndyke, M. (2013) Long-term and trans-life-cycle effects of exposure to ocean acidification in the green sea urchin *Strongylocentrotus droebachiensis*. *Marine Biology*, 160, 1835–1843. https://doi.org/10.1007/s00227-012-1921-x

Dupont, S. & Thorndyke, M.C. (2009) Impact of CO_2-driven ocean acidification on invertebrates early life-history—what we know, what we need to know and what we can do. *Biogeosciences Discussions*, 6, 3109–3131. https://doi.org/10.5194/bgd-6-3109-2009

Dworjanyn, S.A. & Byrne, M. (2018) Impacts of ocean acidification on sea urchin growth across the juvenile to mature adult life-stage transition is mitigated by warming. *Proceedings of the Royal Society B*, 285, 20172684. https://doi.org/10.1098/rspb.2017.2684

Ebert, T.A. (2001) Growth and survival of post-settlement sea urchins. *Developments in Aquaculture and Fisheries Science*, 32, 79–102. https://doi.org/10.1016/s0167-9309(01)80007-7

Evans, T.G., Padilla-Gamiño, J.L., Kelly, M.W., Pespeni, M.H., Chan, F., Menge, B.A. et al. (2015) Ocean acidification research in the 'post-genomic'era: Roadmaps from the purple sea urchin *Strongylocentrotus purpuratus*. *Comparative Biochemistry and Physiology*, 185, 33–42. https://doi.org/10.1016/j.cbpa.2015.03.007

Falvey, M. & Garreaud, R.D. (2009) Regional cooling in a warming world: recent temperature trends in the southeast Pacific and along the west coast of subtropical South America (1979–2006). *Journal of Geophysical Research: Atmospheres*, 114. https://doi.org/10.1029/2008JD010519

FAO (2016) The State of World Fisheries and Aquaculture (SOFIA)(FAO, 2016).

Feehan, C.J., Ludwig, Z., Yu, S. & Adams, D.K. (2018) Synergistic negative effects of thermal stress and altered food resources on echinoid larvae. *Scientific Reports*, 8, 1–7. https://doi.org/10.1038/s41598-018-30572-w

Feng, W., Nakabayashi, N., Inomata, E., Aoki, M.N. & Agatsuma, Y. (2021). Impacts of water temperature on the physiology and behaviours of the sea urchins *Heliocidaris crassispina* and *Mesocentrotus nudus* that reflect their range extension and disappearance in the Oga Peninsula, northern Honshu, *Japan. Can. J. of Fisheries and Aquatic Sciences*, 78, 580–588. https://doi.org/10.1139/cjfas-2020-0327

Feng, W., Nakabayashi, N., Narita, K., Inomata, E., Aoki, M.N. & Agatsuma, Y. (2019) Reproduction and population structure of the sea urchin *Heliocidaris crassispina* in its newly extended range: the Oga Peninsula in the Sea of Japan, northeastern Japan. *PLoS ONE*, 14, e0209858. https://doi.org/10.1371/journal.pone.0209858

Freiwald, J., Wisniewski, C.J. & Abbott, D. (2016) Northward range extension of the crowned sea urchin (*Centrostephanus coronatus*) to Monterey Bay, *California. Calif. Fish and Game*, 102, 37–40.

Froehlich, H.E., Gentry, R.R. & Halpern, B.S. (2018) Global change in marine aquaculture production potential under climate change. *Nature Ecology & Evolution* ,2, 1745–1750. https://doi.org/10.1038/s41559-018-0669-1

Fujii, M., Takao, S., Yamaka, T., Akamatsu, T., Fujita, Y., Wakita, M. et al. (2021) Continuous monitoring and future projection of ocean warming, acidification, and deoxygenation on the subarctic coast of Hokkaido. *Japan. Fro. Marine Science*, 8, 590020. https://doi.org/10.3389/fmars.2021.590020

Gaitán-Espitia, J.D., Villanueva, P.A., Lopez, J., Torres, R., Navarro, J.M. & Bacigalupe, L.D. (2017) Spatio-temporal environmental variation mediates geographical differences in phenotypic responses to ocean acidification. *Biol. Let.*, 13, 20160865. https://doi.org/10.1098/rsbl.2016.0865

García, E., Clemente, S. & Hernández, J.C. (2015) Ocean warming ameliorates the negative effects of ocean acidification on *Paracentrotus lividus* larval development and settlement. *Marine Environment Research*, 110, 61–68. https://doi.org/10.1016/j.marenvres.2015.07.010

García, E., Hernández, J.C. & Clemente, S. (2018) Robustness of larval development of intertidal sea urchin species to simulated ocean warming and acidification. *Marine Environment Research*, 139, 35–45. https://doi.org/10.1016/j.marenvres.2018.04.011

García-Reyes, M. & Largier, J. (2010) Observations of increased wind-driven coastal upwelling off central California. *J. Geophys. Res.Oceans*, 115. https://doi.org/10.1029/2009JC005576

Girard, D., Clemente, S., Toledo-Guedes, K., Brito, A. & Hernández, J.C. (2012) A mass mortality of subtropical intertidal populations of the sea urchin *Paracentrotus lividus*: analysis of potential links with environmental conditions. *Marine Ecology*, 33(3), 377–385. https://doi.org/10.1111/j.1439-0485.2011.00491.x

Goyet, C., Hassoun, A., Gemayel, E., Touratier, F., Abboud-Abi Saab, M. & Guglielmi, V. (2016) Thermodynamic forecasts of the Mediterranean sea acidification. *Mediterranean Marine Science*, 17, 508–518. https://doi.org/10.12681/mms.1487

Grosso, L., Rakaj, A., Fianchini, A., Morroni, L., Cataudella, S. & Scardi, M. (2021) Integrated Multi-Trophic Aquaculture (IMTA) system

combining the sea urchin *Paracentrotus lividus*, as primary species, and the sea cucumber *Holothuria tubulosa* as extractive species. *Aquaculture*, 534, 736268. https://doi.org/10.1016/j.aquaculture.2020.736268

Gruber, N., Hauri, C., Lachkar, Z., Loher, D., Frölicher, T.L. & Plattner, G.-K. (2012) Rapid progression of ocean acidification in the *California Current System*. *Sciences*, 337, 220–223. https://doi.org/10.1126/science.1216773

Hale, R., Calosi, P., McNeill, L., Mieszkowska, N. & Widdicombe, S. (2011) Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. *Oikos*, 120, 661–674. https://doi.org/10.1111/j.1600-0706.2010.19469.x

Harianto, J., Nguyen, H. D., Holmes, S. P. & Byrne, M. (2018) The effect of warming on mortality, metabolic rate, heat-shock protein response and gonad growth in thermally acclimated sea urchins (*Heliocidaris erythrogramma*). *Marine Biology* 165(6), 96. https://doi.org/10.1007/s00227-018-3353-8

Hart, M.W. & Scheibling, R.E. (1988) Heat waves, baby booms, and the destruction of kelp beds by sea urchins. *Marine Biology*, 99, 167–176. https://doi.org/10.1007/BF00391978

Hermans, J., Borremans, C., Willenz, P., André, L. & Dubois, P. (2010) Temperature, salinity and growth rate dependences of Mg/Ca and Sr/Ca ratios of the skeleton of the sea urchin *Paracentrotus lividus* (Lamarck): an experimental approach. *Marine Biology*, 157, 1293–1300. https://doi.org/10.1007/s00227-010-1409-5

Hernández, M., Bückle, F., Guisado, C., Barón, B. & Estavillo, N. (2004) Critical thermal maximum and osmotic pressure of the red sea urchin *Strongylocentrotus franciscanus* acclimated at different temperatures. *Journal of Thermal Biology*, 29, 231–236. https://doi.org/10.1016/j.jtherbio.2004.03.003

Hofmann, G.E., Evans, T.G., Kelly, M.W., Padilla-Gamiño, J.L., Blanchette, C.A., Washburn, L. et al. (2014) Exploring local adaptation and the ocean acidification seascape—studies in the California Current Large Marine Ecosystem. *Biogeosciences*, 11, 1053–1064. https://doi.org/10.5194/bg-11-1053-2014

Hu, F., Luo, J., Yang, M., Sun, J., Leng, X., Liu, M. et al. (2020) Effects of macroalgae *Gracilaria lemaneiformis* and *Saccharina japonica* on growth and gonadal development of the sea urchin *Strongylocentrotus intermedius*: new insights into the aquaculture management in southern China. *Aquaculture Reports*, 17, 100399. https://doi.org/10.1016/j.aqrep.2020.100399

IPCC, (2021). In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S. et al. (Eds.), Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

James, P., Noble, C., Hannon, C., Stefansson, G., Thórarinsdóttir, G., Sloane, R. et al. (2016). Sea urchin fisheries, management and policy review (Activity A4. 2.1 of the URCHIN project).

Kapsenberg, L., Okamoto, D.K., Dutton, J.M. & Hofmann, G.E. (2017) Sensitivity of sea urchin fertilization to pH varies across a natural pH mosaic. *Ecology and Evolution*, 7, 1737–1750. https://doi.org/10.1002/ece3.2776

Kawana, S.K., Catton, C.A., Hofmeister, J.K., Juhasz, C.I., Taniguchi, I.K., Stein, D.M. et al. (2019) Warm water shifts abalone recruitment and sea urchin diversity in Southern California: implications for climate-ready abalone restoration planning. *Journal of Shellfish Research*, 38, 475–484. https://doi.org/10.2983/035.038.0231

Khosravi, N., Wang, Q., Koldunov, N., Hinrichs, C., Semmler, T., Danilov, S. et al. (2022) The Arctic Ocean in CMIP6 models: biases and projected changes in temperature and salinity. *Ear. Fut.*, 10, e2021EF002282. https://doi.org/10.1029/2021EF002282

Lauzon-Guay, J.-S. & Scheibling, R.E. (2007) Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (*Strongylocentrotus droebachiensis*) in relation to wave action and sea temperature.

Marine Biology, 151, 2109–2118. https://doi.org/10.1007/s00227-007-0668-2

Lawrence, JM, Zhao, C & Chang, Y-Q (2019) Large-scale production of sea urchin (*Strongylocentrotus intermedius*) seed in a hatchery in China. *Aquaculture International*, 27, 1–7. https://doi.org/10.1007/s10499-018-0319-2

Lee, H. -G., Stumpp, M., Yan, J. -J., Tseng, Y. -C., Heinzel, S. & Hu, M.Y. -A. (2019) Tipping points of gastric pH regulation and energetic in the sea urchin larva exposed to CO_2-induced seawater acidification. *Comparative Biochemistry & Physiology A*, 234, 87–97. https://doi.org/10.1016/j.cbpa.2019.04.018

Li, C., Yang, D. & Zhai, W. (2022) Effects of warming, eutrophication and climate variability on acidification of the seasonally stratified North Yellow Sea over the past 40 years. *Science of the Total Environment*, 815, 152935. https://doi.org/10.1016/j.scitotenv.2022.152935

Li, Y., Yin, W., Zhan, Y., Jia, Y., Cui, D., Zhang, W. et al. (2020) Comparative metabolome analysis provides new insights into increased larval mortality under seawater acidification in the sea urchin *Strongylocentrotus intermedius*. *Science of the Total Environment*, 747, 141206. https://doi.org/10.1016/j.scitotenv.2020.141206

Lima, F.P. & Wethey, D.S. (2012) Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nature Communications*, 3, 1–13. https://doi.org/10.1038/ncomms1713

Manríquez, P.H., González, C.P., Brokordt, K., Pereira, L., Torres, R., Lattuca, M.E. et al. (2019) Ocean warming and acidification pose synergistic limits to the thermal niche of an economically important echinoderm. *Science of The Total Environment*, 693, 133469. https://doi.org/10.1016/j.scitotenv.2019.07.275

Manríquez, P.H., Torres, R., Matson, P.G., Lee, M.R., Jara, M.E., Seguel, M.E. et al. (2017) Effects of ocean warming and acidification on the early benthic ontogeny of an ecologically and economically important echinoderm. *Marine Ecology Progress Series*, 563, 169–184. https://doi.org/10.3354/meps11973

Marčeta, T., Locatello, L., Alban, S., Hassan, M.S.A., Azmi, N.-N.N.M., Finos, L. et al. (2022) Transgenerational effects and phenotypic plasticity in sperm and larvae of the sea urchin *Paracentrotus lividus* under ocean acidification. *Aquatic Toxicology*, 106208. https://doi.org/10.1016/j.aquatox.2022.106208

Martin, S., Richier, S., Pedrotti, M.-L., Dupont, S., Castejon, C., Gerakis, Y. et al. (2011) Early development and molecular plasticity in the Mediterranean sea urchin *Paracentrotus lividus* exposed to CO_2-driven acidification. *The Journal of Experimental Biology*, 214, 1357–1368. https://doi.org/10.1242/jeb.051169

Martino, C., Byrne, M., Roccheri, M.C., Chiarelli, R., (2021) Interactive effects of increased temperature and gadolinium pollution in *Paracentrotus lividus* sea urchin embryos: a climate change perspective. *Aquat. Tox.*, 232, 105750. https://doi.org/10.1016/j.aquatox.2021.105750

Matranga, V., Pinsino, A., Celi, M., Natoli, A., Bonaventura, R., Schröder, H.C. et al. (2005) Monitoring chemical and physical stress using sea urchin immune cells, in: Matranga, Valeria (Ed.), *Echinodermata*. Springer-Verlag, Berlin/Heidelberg, pp. 85–110. https://doi.org/10.1007/3-540-27683-1_5

Maulu, S., Hasimuna, O.J., Haambiya, L.H., Monde, C., Musuka, C.G., Makorwa, T.H. et al. (2021) Climate change effects on aquaculture production: sustainability implications, mitigation, and adaptations. *Frontiers in Sustainable Food Systems*, 5, 609097. https://doi.org/10.3389/fsufs.2021.609097

McBride, S.C., Pinnix, W.D., Lawrence, J.M., Lawrence, A.L. & Mulligan, T.M. (1997). The effect of temperature on production of gonads by the sea urchin *Strongylocentrotus franciscanus* fed natural and prepared diets. *Journal of the World Aquaculture Society*, 28, 357–365. https://doi.org/10.1111/j.1749-7345.1997.tb00282.x

Melzner, F., Stange, P., Trübenbach, K., Thomsen, J., Casties, I., Panknin, U. et al. (2011) Food supply and seawater pCO_2 impact calcification and

internal shell dissolution in the blue mussel *Mytilus edulis. PLoS ONE*, 6, e24223. https://doi.org/10.1371/journal.pone.0024223

Miller, B.A. & Emlet, R.B. (1999) Development of newly metamorphosed juvenile sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*): morphology, the effects of temperature and larval food ration, and a method for determining age. *Journal of Experimental Marine Biology and Ecology*, 235, 67–90. https://doi.org/10.1016/S0022-0981(98)00164-6

Minuti, J.J. & Russell, B.D. (2020) Functionally redundant herbivores: urchin and gastropod grazers respond differently to ocean warming and rising CO2. *Mar. Ecol. Prog. Ser.*, 656, 239–251. https://doi.org/10.3354/meps13416

Molinet, C, Balboa, CA, Moreno, CA, Diaz, M, Gebauer, P, Niklitschek, EJ & Barahona, N (2013) Variability in the growth patterns of *Loxechinus albus* along a bathymetric gradient associated with a fishing ground. *Bulletin of Marine Science*, 89:699–716. https://doi.org/10.5343/bms.2012.1063

Moreno, R.A., Sepúlveda, R.D., Badano, E.I., Thatje, S., Rozbaczylo, N. & Carrasco, F.D. (2008) Subtidal macrozoobenthos communities from northern Chile during and post El Nino 1997–1998. *Helgoland Marine Research*, 62, 45–55. https://doi.org/10.1007/s10152-007-0095-2

Moulin, L., Catarino, A.I., Claessens, T. & Dubois, P. (2011) Effects of seawater acidification on early development of the intertidal sea urchin *Paracentrotus lividus* (Lamarck 1816). *Marine Pollution Bulletin*, 62, 48–54. https://doi.org/10.1016/j.marpolbul.2010.09.012

Nyhagen, F.O., Christie, H. & Norderhaug, K.M. (2018) Will altered climate affect a discrete population of the sea urchin *Strongylocentrotus droebachiensis? Journal of Sea Research*, 132, 24–34. https://doi.org/10.1016/j.seares.2017.12.001

Occhipinti-Ambrogi, A. (2007) Global change and marine communities: alien species and climate change. *Marine Pollution Bulletin*, 55, 342–352. https://doi.org/10.1016/j.marpolbul.2006.11.014

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. et al. (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences*, 104, 1266–1271. https://doi.org/10.1073/pnas.0603422104

O'Donnell, M.J., Hammond, L.M. & Hofmann, G.E., (2009) Predicted impact of ocean acidification on a marine invertebrate: elevated CO_2 alters response to thermal stress in sea urchin larvae. *Marine Biology*, 156, 439–446. https://doi.org/10.1007/s00227-008-1097-6

O'Donnell, MJ, Todgham, AE, Sewell, MA, Hammond, LM, Ruggiero, K, Fangue, NA et al. (2010) Ocean acidification alters skeletogenesis and gene expression in larval sea urchins. *Marine Ecology Progress Series*, 398:157–171. https://doi.org/10.3354/meps08346

Ohgaki, S.-I., Kato, T., Kobayashi, N., Tanase, H., Kumagai, N.H., Ishida, S. et al. (2019) Effects of temperature and red tides on sea urchin abundance and species richness over 45 years in southern. *Japan. Ecol. Ind.*, 96, 684–693. https://doi.org/10.1016/j.ecolind.2018.03.040

Okamoto, D.K., Schroeter, S. & Reed, D.C. (2018) Effects of ocean climate on spatiotemporal variation in sea urchin settlement and recruitment. *Ecology*, https://doi.org/10.1101/387282

Padilla-Gamiño, J.L., Kelly, M.W., Evans, T.G. & Hofmann, G.E. (2013) Temperature and CO_2 additively regulate physiology, morphology and genomic responses of larval sea urchins, *Strongylocentrotus purpuratus. Proceedings of the Royal Society B*, 280, 20130155. https://doi.org/10.1098/rspb.2013.0155

Pearce, C.M., Williams, S.W., Yuan, F., Castell, J.D. & Robinson, S.M. (2005) Effect of temperature on somatic growth and survivorship of early post-settled green sea urchins, *Strongylocentrotus droebachiensis* (Müller). *Aquaculture Research*, 36, 600–609. https://doi.org/10.1111/j.1365-2109.2005.01264.x

Pearse, J.S. (2006) Ecological role of purple sea urchins. *Science*, 314, 940–941. https://doi.org/10.1126/science.1131888

Ramírez-Gómez, F. & García-Arrarás, J. E. (2010) Echinoderm immunity. *Invertebrate Survival Journal*, 7(2), 211–220.

Reid, G.K., Gurney-Smith, H.J., Marcogliese, D.J., Knowler, D., Benfey, T., Garber, A.F. et al. (2019) Climate change and aquaculture: considering biological response and resources. *Aquaculture Environment Interactions*, 11, 569–602. https://doi.org/10.3354/aei00332

Reuter, K.E., Lotterhos, K.E., Crim, R.N., Thompson, C.A. & Harley, C.D. (2011) Elevated pCO2 increases sperm limitation and risk of polyspermy in the red sea urchin *Strongylocentrotus franciscanus. Global Change Biology*, 17, 163–171. https://doi.org/10.1111/j.1365-2486.2010.02216.x

Rodríguez, A., Hernández, J.C., Brito, A. & Clemente, S. (2017) Effects of ocean acidification on juveniles sea urchins: predator-prey interactions. *Journal of Experimental Marine Biology and Ecology*, 493, 31–40. https://doi.org/10.1016/j.jembe.2017.04.005

Rogers-Bennett, L. (2007) *The ecology of* Strongylocentrotus franciscanus *and* Strongylocentrotus purpuratus, *in: Developments in Aquaculture and Fisheries Science.* Elsevier, pp. 393–425. https://doi.org/10.1016/B978-0-12-396491-5.00027-7

Rogers-Bennett, L. & Okamoto, D. (2020) Mesocentrotus franciscanus *and* Strongylocentrotus purpuratus, *in: Developments in Aquaculture and Fisheries Science.* Elsevier, pp. 593–608.

Ross, PM, Parker, L, O'Connor, WA & Bailey, EA (2011) The impact of ocean acidification on reproduction, early development and settlement of marine organisms. *Water*, 3:1005–1030. https://doi.org/10.3390/w3041005

Rossi, S. & Soares, M. de O. (2018) Effects of El Niño on the coastal ecosystems and their related services. Mercator (Fortaleza) 16. https://doi.org/10.4215/rm2017.e16030

Sanchez-Cabeza, J.-A., Herrera-Becerril, C.A., Carballo, J.L., Yáñez, B., Álvarez-Sánchez, L.F., Cardoso-Mohedano, J.-G. et al. (2022) Rapid surface water warming and impact of the recent (2013–2016) temperature anomaly in shallow coastal waters at the eastern entrance of the Gulf of California. *Prog. Oceano.*, 202, 102746. https://doi.org/10.1016/j.pocean.2022.102746

Santos, P.M., Albano, P., Raposo, A., Ferreira, S.M., Costa, J.L. & Pombo, A. (2020) The effect of temperature on somatic and gonadal development of the sea urchin *Paracentrotus lividus* (Lamarck, 1816). *Aquaculture*, 528, 735487. https://doi.org/10.1016/j.aquaculture.2020.735487

Sato, K.N., Powell, J., Rudie, D. & Levin, L.A. (2018) Evaluating the promise and pitfalls of a potential climate change–tolerant sea urchin fishery in southern California. *Ices Journal of Marine Science*, 75, 1029–1041. https://doi.org/10.1093/icesjms/fsx225

Shaltout, M. & Omstedt, A. (2014) Recent sea surface temperature trends and future scenarios for the Mediterranean Sea. *Oceanologia*, 56, 411–443. https://doi.org/10.5697/oc.56-3.411

Shen, Y., Huang, Z., Liu, G., Ke, C. & You, W. (2019) Hemolymph and transcriptome analysis to understand innate immune responses to hypoxia in Pacific abalone. *Comparative Biochemistry & Physiology D*, 30, 102–112. https://doi.org/10.1016/j.cbd.2019.02.001

Sheppard Brennand, H., Soars, N., Dworjanyn, S.A., Davis, A.R. & Byrne, M. (2010) Impact of Ocean warming and Ocean acidification on larval development and calcification in the sea urchin *Tripneustes gratilla. PLoS ONE*, 5, e11372. https://doi.org/10.1371/journal.pone.0011372

Shpigel, M., Shauli, L., Odintsov, V., Ben-Ezra, D., Neori, A. & Guttman, L. (2018) The sea urchin, *Paracentrotus lividus*, in an Integrated Multi-Trophic Aquaculture (IMTA) system with fish (*Sparus aurata*) and seaweed (*Ulva lactuca*): Nitrogen partitioning and proportional configurations. *Aquaculture*, 490, 260–269. https://doi.org/10.1016/j.aquaculture.2018.02.051

Siikavuopio, S.I., Christiansen, J.S. & Dale, T., (2006) Effects of temperature and season on gonad growth and feed intake in the green sea urchin (*Strongylocentrotus droebachiensis*). *Aquaculture*, 255, 389–394. https://doi.org/10.1016/j.aquaculture.2005.12.021

Siikavuopio, S.I., Mortensen, A. & Christiansen, J.S. (2008) Effects of body weight and temperature on feed intake, gonad growth and oxygen consumption in green sea urchin, *Strongylocentrotus droebachiensis. Aquaculture*, 281, 77–82. https://doi.org/10.1016/j.aquaculture.2008.05.033

Siikavuopio, S.I., James, P., Lysne, H., Sæther, B.S., Samuelsen, T.A. & Mortensen, A. (2012) Effects of size and temperature on growth and feed conversion of juvenile green sea urchin (*Strongylocentrotusdroebachiensis*).*Aquaculture*, 354–355, 27–30.https://doi.org/10.1016/j.aquaculture.2012.04.036

Stefánsson, G., Kristinsson, H., Ziemer, N., Hannon, C. & James, P. (2017) Markets for sea urchins: a review of global supply and markets. *Skỳrsla Matís*, 45.

Stumpp, M., Trübenbach, K., Brennecke, D., Hu, M.Y. & Melzner, F. (2012) Resource allocation and extracellular acid–base status in the sea urchin *Strongylocentrotus droebachiensis* in response to CO_2 induced seawater acidification. *Aquatic Toxicology*, 110, 194–207. https://doi.org/10.1016/j.aquatox.2011.12.020

Stumpp, M., Wren, J., Melzner, F., Thorndyke, M.C. & Dupont, S.T. (2011). CO_2 induced seawater acidification impacts sea urchin larval development I: Elevated metabolic rates decrease scope for growth and induce developmental delay. *Comparative Biochemistry and Physiology, Part A: Molecular & Integrative Physiology*, 160, 331–340. https://doi.org/10.1016/j.cbpa.2011.06.022

Sung, C.-G., Kim, T.W., Park, Y.-G., Kang, S.-G., Inaba, K., Shiba, K. et al. (2014) Species and gamete-specific fertilization success of two sea urchins under near future levels of pCO_2. *Journal of Marine Systems* 137, 67–73. https://doi.org/10.1016/j.jmarsys.2014.04.013

Sweet, M., Bulling, M. & Williamson, J. (2016) New disease outbreak affects two dominant sea urchin species associated with Australian temperate reefs. *Marine Ecology Progress Series*, 551, 171–183. https://doi.org/10.3354/meps11750

Tegner, M.J. & Dayton, P.K. (1981) Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Marine Ecology Progress Series*, 5, 255–268.

Tomanek, L. & Somero, G.N. (2000) Time Course and Magnitude of Synthesis of Heat-Shock Proteins in Congeneric Marine Snails (Genus *Tegula*) from Different Tidal Heights. *Physiological and Biochemical Zoology*, 73, 249–256. https://doi.org/10.1086/316740

Ulbricht, R.J. & Pritchard, A.W. (1972) Effect of the temperature on the metabolic rate of sea urchins. *Biological Bulletin*, 142, 178–185. https://doi.org/10.2307/1540254

Uthicke, S., Liddy, M., Nguyen, H.D. & Byrne, M., (2014). Interactive effects of near-future temperature increase and ocean acidification on physiology and gonad development in adult Pacific sea urchin, *Echinometra sp.*, A. *Coral Reefs*, 33, 831–845. https://doi.org/10.1007/s00338-014-1165-y

Varela, R., Lima, F.P., Seabra, R., Meneghesso, C. & Gómez-Gesteira, M. (2018) Coastal warming and wind-driven upwelling: a global analysis. *Science of the Total Environment*, 639, 1501–1511. https://doi.org/10.1016/j.scitotenv.2018.05.273

Vergara-Amado, J., Silva, A.X., Manzi, C., Nespolo, R.F. & Cárdenas, L. (2017) Differential expression of stress candidate genes for thermal tolerance in the sea urchin *Loxechinus albus*. *Journal of Theoretical Biology*, 68, 104–109. https://doi.org/10.1016/j.jtherbio.2017.03.009

Wallhead, P., Chen, W., Falkenberg, L., Norling, M., Bellerby, R., Dupont, S. et al. (2018) Urchin harvesting and kelp regrowth in northern Norway under ocean acidification and warming. *Ann*, 2, 79–90.

Whitehead, A (2012) Comparative genomics in ecological physiology: toward a more nuanced understanding of acclimation and adaptation. *The Journal of Experimental Biology*, 215, 884–891. https://doi.org/10.1242/jeb.058735

Wong, J.M. & Hofmann, G.E. (2020) The effects of temperature and pCO_2 on the size, thermal tolerance and metabolic rate of the red sea urchin (*Mesocentrotus franciscanus*) during early development. *Marine Biology*, 167, 1–15. https://doi.org/10.1007/s00227-019-3633-y

Yeruham, E., Abelson, A., Rilov, G., Ezra, D.B. & Shpigel, M. (2019) Energy budget of cultured *Paracentrotus lividus* under different temperatures. *Aquac.*, 501, 7–13. https://doi.org/10.1016/j.aquaculture.2018.11.006

Yeruham, E., Rilov, G., Shpigel, M. & Abelson, A., (2015) Collapse of the echinoid *Paracentrotus lividus* populations in the Eastern Mediterranean—result of climate change? *Scientific Reports*, 5, 1–6. https://doi.org/10.1038/srep13479

Zhan, Y., Cui, D., Xing, D., Zhang, J., Zhang, W., Li, Y. et al. (2020) CO_2-driven ocean acidification repressed the growth of adult sea urchin *Strongylocentrotus intermedius* by impairing intestine function. *Marine Pollution Bulletin*, 153, 110944. https://doi.org/10.1016/j.marpolbul.2020.110944

Zhan, Y., Hu, W., Zhang, W., Liu, M., Duan, L., Huang, X. et al. (2016) The impact of CO_2-driven ocean acidification on early development and calcification in the sea urchin *Strongylocentrotus intermedius*. *Marine Pollution Bulletin*, 112, 291–302. https://doi.org/10.1016/j.marpolbul.2016.08.003

Zhang, L., Zhang, L., Shi, D., Wei, J., Chang, Y., & Zhao, C. (2017) Effects of long-term elevated temperature on covering, sheltering and righting behaviours of the sea urchin *Strongylocentrotus intermedius*. *PeerJ*, 5, e3122. https://doi.org/10.7717/peerj.3122

Zhang, T., Li, X., Cao, R., Zhang, Q., Qu, Y., Wang, Q. et al. (2022) Interactive effects of ocean acidification, ocean warming, and diurnal temperature cycling on antioxidant responses and energy budgets in two sea urchins *Strongylocentrotus intermedius* and *Tripneustes gratilla* from different latitudes. *Science of the Total Environment*, 824, 153780. https://doi.org/10.1016/j.scitotenv.2022.153780

Zhao, C., Feng, W., Wei, J., Zhang, L., Sun, P. & Chang, Y. (2016). Effects of temperature and feeding regime on food consumption, growth, gonad production and quality of the sea urchin *Strongylocentrotus intermedius*. *ournal of the Marine Biological Association of the United Kingdom*, 96, 185–195. https://doi.org/10.1017/S0025315415001617

Zhao, C., Zhang, L., Qi, S., Shi, D., Yin, D. & Chang, Y. (2018a) Multilevel effects of long-term elevated temperature on fitness related traits of the sea urchin *Strongylocentrotus intermedius*. *Bulletin of Marine Science*, 94, 1483–1497. https://doi.org/10.5343/bms.2017.1180

Zhao, C., Zhang, L., Shi, D., Ding, J., Yin, D., Sun, J. et al. (2018b) Transgenerational effects of ocean warming on the sea urchin *Strongylocentrotus intermedius*. *Ecotoxicology and Environmental Safety*, 151, 212–219. https://doi.org/10.1016/j.ecoenv.2018.01.014