Climate Change Ecology 4 (2023) 100059

Contents lists available at ScienceDirect

Climate Change Ecology

journal homepage: www.journals.elsevier.com/climate-change-ecology

Review

Systematic review and meta-analysis of ocean acidification effects in Halimeda: Implications for algal carbonate production

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ARTICLE INFO

Keywords:
Calcareous green algae
Calcification
Climate change

ABSTRACT

Ocean acidification (OA) has been identified as one of the major climate-change related threats, mainly due to its significant impacts on marine calcifiers. Among those are the calcareous green algae of the genus *Halimeda* that are known to be major carbonate producers in shallow tropical and subtropical seas. Hence, any negative OA impacts on these organisms may translate into significant declines in regional and global carbonate production. In this study, we compiled the available information regarding *Halimeda* spp. responses to OA (experimental, in situ), with special focus on the calcification responses, one of the most studied response parameters in this group. Furthermore, among the compiled studies ($n = 31$), we selected those reporting quantitative data of OA effects on algal net calcification in an attempt to identify potential general patterns of species- and/or regional-specific OA responses and hence, impacts on carbonate production. While obtaining general patterns was largely hampered by the often scarce number of studies on individual species and/or regions, the currently available information indicates species-specific susceptibility to OA, seemingly unrelated to evolutionary lineages (and associated differences in morphology), that is often accompanied by differences in a species' response across different regions. Thus, for projections of future declines in *Halimeda*-associated carbonate production, we used available regional reports of species-specific carbonate production in conjunction with experimental OA responses for the respective species and regions. Based on the available information, declines can be expected worldwide, though some regions harbouring more sensitive species might be more impacted than others.

1. Introduction

Calcareous green algae of the genus *Halimeda* have high $CaCO_3$ production and turnover rates, forming calcified thalli that can contain >90% $CaCO_3$ [1,2]. They are considered major contributors to carbonate and sediment production in tropical and subtropical regions [3–9], with some tropical sand beaches found to be composed of up to 90% of *Halimeda* carbonate fragments [10]. Their carbonate production can locally reach very high rates that, depending on species productivity and abundance, ranges between 0.8 to 4200 g $CaCO_3$ m^{-2} $year^{-1}$ in the Caribbean and Wider Caribbean region and ~6 to 3650 g $CaCO_3$ m^{-2} $year^{-1}$ in the Pacific, with the highest values reported for the Indo-Pacific (up to 17,663 g $CaCO_3$ m^{-2} $year^{-1}$) (Fig. 1; Table A.1). Furthermore, *Halimeda* meadows can build-up extensive bioherms [11] that have been estimated to globally accumulate approximately 0.15–0.4 Gt $CaCO_3$ $year^{-1}$ [12,13].

Considering the importance of *Halimeda* spp. for carbonate production and accumulation and potentially the global carbon budget [11], understanding how these algae are affected by environmental changes, particularly those associated with global climate change, is critical for future projections of *Halimeda* species abundances, primary productivity and associated carbonate and sediment production. In this context, ocean acidifaction (OA) has been acknowledged as one of the main climate-change related factors that negatively impacts calcifying organisms [14,15]. In the case of *Halimeda*, to more accurately project the future of habitats where these calcareous green algae play essential ecological roles, OA effects have been tested experimentally in laboratories around the world. These studies led to varying conclusions, from negative to neutral OA responses, though in situ observations of *Halimeda* spp. at the tropical CO_2 vents in Papua New-Guinea suggests that

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https://doi.org/10.1016/j.ecochg.2022.100059
Received 8 February 2022; Received in revised form 13 April 2022; Accepted 14 June 2022

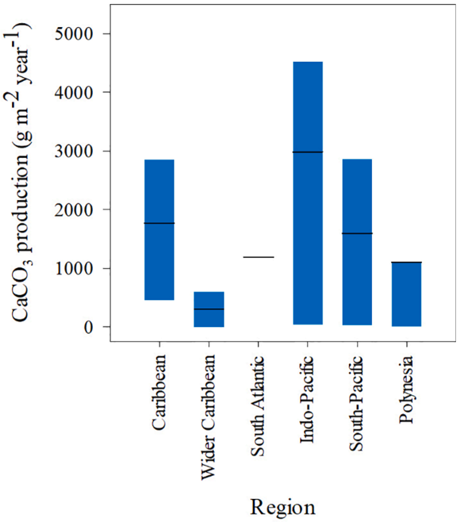

Fig. 1. Carbonate production rates of *Halimeda* spp. in different oceanic regions (for details see Table A.1).

several species in this group are able to withstand low-pH conditions [16]. The latter study showed no significant differences in net calcification in *H. digitata* and *H. opuntia* at the seep, compared to a control site, and carbon isotope signatures indicated decreased carbon limitation for photosynthesis through increased uptake of CO_2 over HCO_3^-.

Currently, a systematic revision of these results for a better understanding of the drivers of the variability in response to OA, such as phylogeny, geography or co-occurring environmental conditions, is still missing. An earlier review on the topic showed that photosynthesis in *Halimeda* species is mainly unresponsive to OA, while species' calcification exhibited a wide range of responses [17]. This might be associated to species-specific sensitivity to OA, as also supported by multi-species studies [18–21]. Though differences due to a large variability in treatments (i.e., pCO_2 levels) and the different secondary incubation conditions during the experiments (e.g. light intensity, flow, temperature) may also be partially responsible for the differing responses [17].

In this review, our aim was to gather the currently available knowledge of *Halimeda* responses to OA through (1) a qualitative review of the published information regarding the effects of OA in different species and regions, (2) meta-analyses of the effects of OA on species and regional calcification, and (3) projected declines under RCP8.5 CO_2 emission scenario, considering *Halimeda* community composition and regional carbonate production rates.

2. Materials and methods

2.1. Literature search and selection of studies

A systematic literature search was carried out according to the method described by Siddaway et al. [22] and the Preferred Reporting Items for Systematic Reviews and MetaAnalyses (PRISMA) checklist and flow diagram [23]. Firstly, a qualitative literature review was performed to summarize existing knowledge regarding the observed and predicted impacts of ocean acidification (OA) on calcareous macroalgae of the genus *Halimeda*. A search string consisting of “Halimeda”, combined with “ocean acidification” or “climate change” was used to search for relevant literature in Web of Science, complemented by a search in Google Scholar. From these results, non peer-reviewed articles, reviews, duplicates, and those written in languages other than English were excluded. A total of 31 studies were identified and included in the qualitative review (Table A.2), as they met the eligibility criteria based on the screening of the title and abstract.

2.2. Meta-analysis

The systematic review of OA studies on *Halimeda* spp. showed that calcification was the most commonly recorded parameter and the RCP8.5 “business-as-usual” scenario for 2100 the most used experimental OA simulation. Thus, a meta-analysis was performed to explore patterns of OA effects on *Halimeda* spp. net carbonate production. For this analysis, from the previously identified pool of OA studies in *Halimeda* spp. ($n = 31$), studies were selected that (1) reported quantitative data on the effects of OA on *Halimeda* calcification ($n = 25$), (2) reported net calcification rates (either as buoyant weight, growth rate or integrating light and dark calcification rates; $n = 19$), with exlcusion of negative values, and (3) used an OA-treatment corresponding to the RCP8.5 scenario (ΔpH=0.3–0.4; $n = 16$) to avoid introducing variability due to differences in OA-treatments (see Table A.2). In cases where the data were not deposited freely online, calcification data were extracted from figures within publications, using the measuring tool in Adobe Acrobat.

Means of calcification rates, standard errors or deviations and sample sizes were extracted from the studies and the relative effect size was calculated as the ln-transformed response ratio to OA, using the formula LnRR = ln(xT) −ln(xC), where xT and xC are the mean values for the biological responses in the CO_2 experimental treatment and the respective control. This response ratio (LnRR) has been proven to be a robust metric for small sample sizes and to have the ability to detect true effects [24,25]. The LnRRs were weighted by the inverse of the pooled standard deviation of both treatments to incorporate a measure of the robustness of the response ratio of each study. Meta-analyses were conducted to test for (a) species-specific OA responses (including species where ≥2 reports were available) and (b) general regional-specific OA responses (regions with ≥2 reports available). Statistically significant effect sizes were identified from 95% bias-corrected bootstrapped confidence intervals (generated from 9999 iterations), which did not encompass zero. The omnibus (QM) statistic was used to test for the differences in response ratios in the different treatments. A significant QM implies that there are differences in mean effect sizes among groups; thus, a non-significant QM does not preclude individual groups showing significant effect sizes (i.e., individual confidence intervals do not overlap zero). All meta-analyses were conducted in MetaWin Version 2.0 [26].

3. Results and discussion

3.1. General overview

First experimental studies investigating the OA responses of *Halimeda* spp. were published in 2009 and since then experienced an increasing trend over the following decade, reaching a current total of 31 studies. Of these, ~50% focused on the sole effect of OA, while others investigated potential interactions with temperature, light intensity and/or nutrient concentration (Fig. 2a). In these studies, the OA responses of 18 *Halimeda* species were assessed, of which *H. opuntia* is by far the most studied, followed by *H. macroloba* and *H. incrassata* (Fig. 2b). Geographically, *Halimeda* spp. responses to OA have been mainly studied on species from Florida, the Caribbean and the Great Barrier Reef (Fig. 3).

Overall, the studies are almost exclusively based on short- to medium-term experiments, ranging from determining the immediate response to OA conditions [27–29] to exposing the algae to reduced seawater pH from a few days to several weeks. Most frequently, the experiments lasted between one and four weeks (Fig. 4a), with the longest experimental OA exposure lasting for 60 days [30,31]. The majority of the studies focused on the comparison of a control condition to a treatment simulating future OA conditions projected for 2100 (pH decrease of 0.3–0.4 units; Fig. 4b), while in others the algae were exposed to a range of different pH or pCO_2 conditions [19,20,31-36]. In

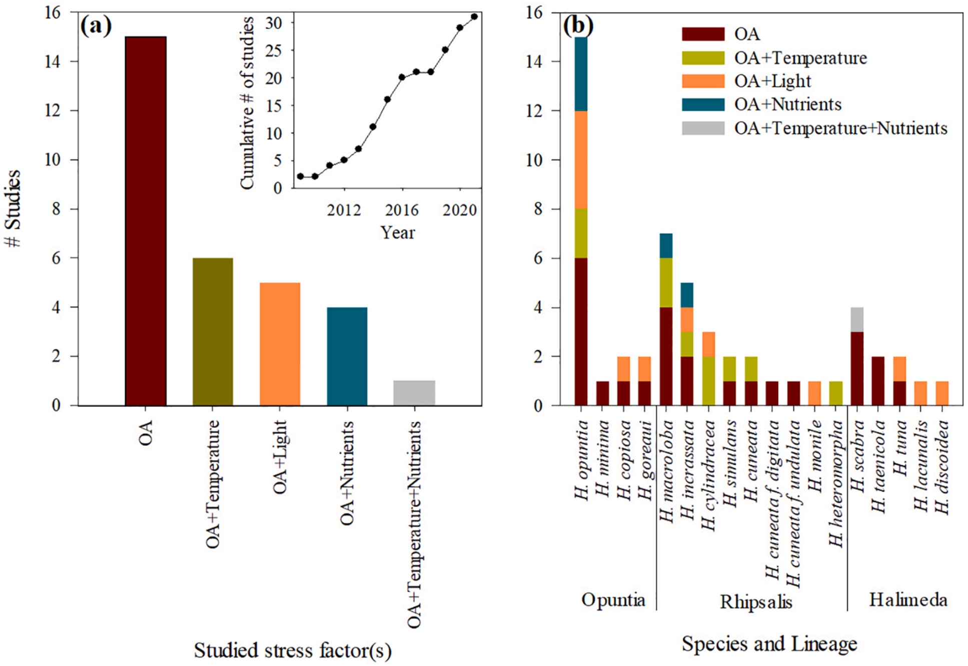

Fig. 2. Summary of OA-related studies in *Halimeda* spp. (a) and the trend of the cumulative number of studies during 2009–2021 (inlet graph). (b) Type and number of studies in different *Halimeda* lineages and species.

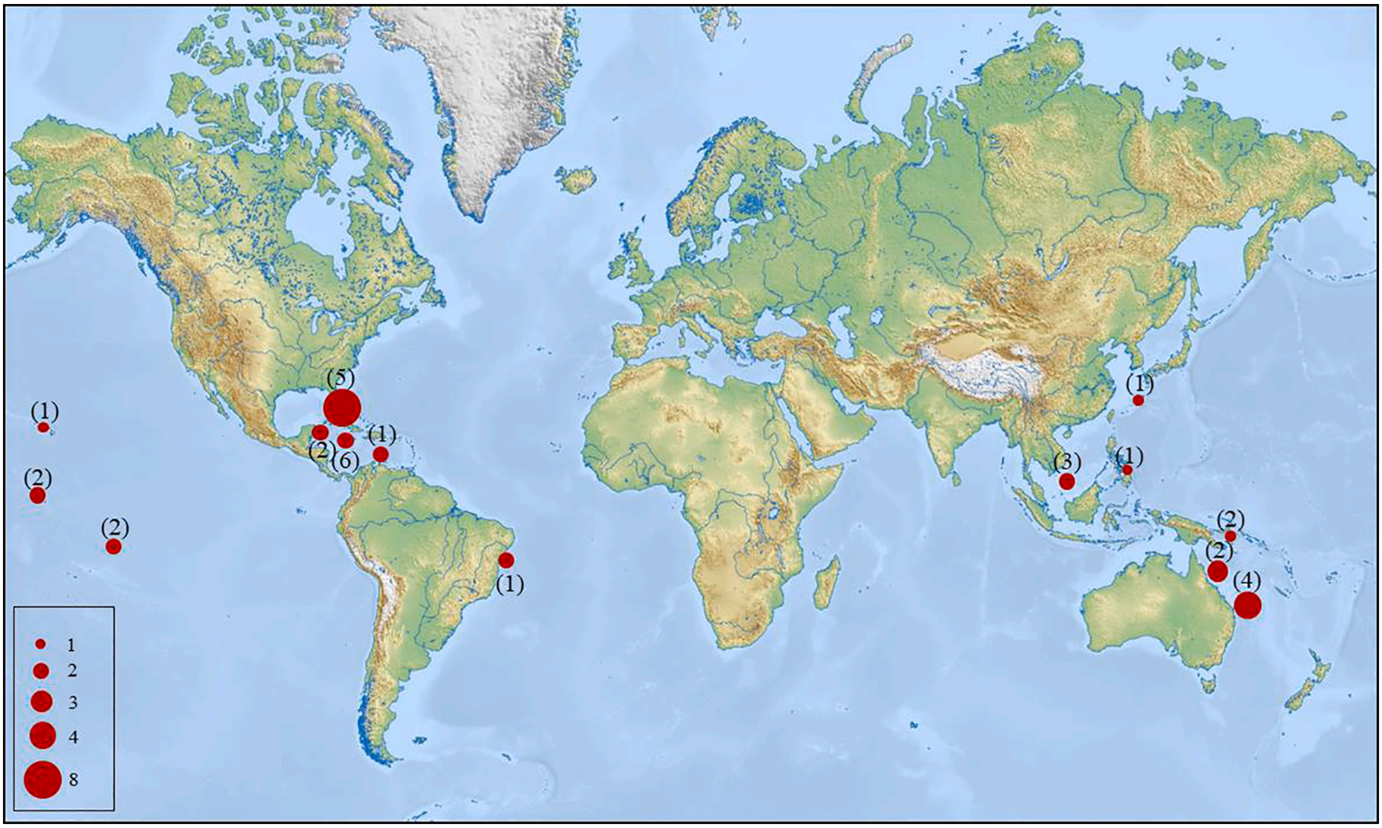

Fig. 3. Geographical distribution of the collection sites of *Halimeda* species on which OA studies have been performed (n = 31 studies). Number of studies per location is indicated by different circle sizes and numbers in parentheses indicate the number of studied species per location. The map was downloaded from Mapswire (https://mapswire.com/).

contrast to experimental works, in situ studies are almost non-existent, with the exception of a work on *H. cuneata f. digitata* and *H. opuntia* at the volcanic CO_2 seeps in Papua New Guinea [16].

3.2. Responses of Halimeda spp. to OA

Assessments of *Halimeda* spp. responses to different OA treatments

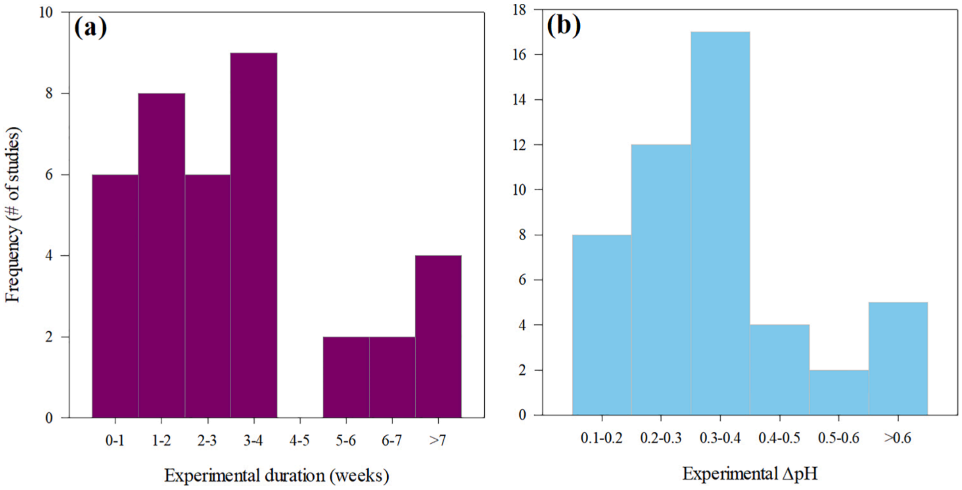

Fig. 4. Frequency of (a) the duration and (b) the magnitude of OA (expressed as ΔpH) in experimental studies on *Halimeda* species.

have been made mainly by measuring the algal physiological and/or biochemical responses and the subsequent changes in net carbonate production. One of the most used parameters to evaluate potential OA effects is the response in calcification, but also the effects on thallus carbonate content, crystal microstructure and algal metabolic responses (photosynthesis, respiration) were often assessed (Fig. 5). In addition, some studies evaluated OA effects on algal tissue carbon and nitrogen contents, antioxidant capacity, enzyme activity (carbonic anhydrase, nitrogen reductase), as well as compounds associated to algal defenses against competitors and herbivores.

3.2.1. *Calcification*

Net calcification responses to OA in *Halimeda* spp. are determined either through measurements of instantaneous calcification rates (total-alkalinity anomaly technique) or by assessing changes in algal growth/biomass (by buoyant weight). The results suggest species-specific differences, as in over 40% of the studied species no significant effects have been detected, while in others both neutral and negative responses have been found (Fig. 6a). In contrast, only negative OA effects on net calcification have been reported for four species, though in those species so far only one or two experimental studies have been carried out.

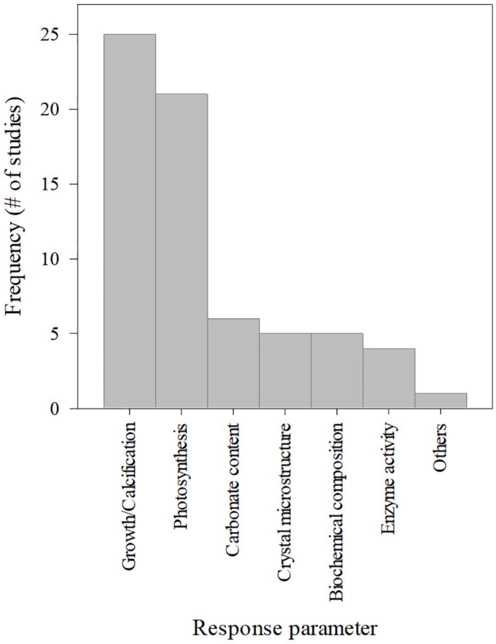

Fig. 5. Frequency of measured response parameters in experimental OA studies on *Halimeda* spp..

This species-specificity in OA responses is also highlighted through studies that used measurements of instantaneous calcification rates, which allow a better mechanistic understanding by distinguishing effects on algal light and/or dark calcification. In some species (*H. opuntia, H. scabra, H. copiosa, H. lacunalis*) no effect of OA on light calcification has been reported, while at the same time dark calcification was negatively affected, resulting in $CaCO_3$ dissolution [17,28,29,36-38]. In contrast, others (*H. incrassata, H. cuneata, H. cylindracea, H. goreaui*) experienced a significant decrease in light calcification, while dark calcification in *H. goreaui* did not exhibit any negative effects [29,36,39,40]. Yet, in *H. macroloba* neither the light nor dark calcification rates were significantly altered by the effects of OA [37]. Similar findings of species-specific differences have been reported in situ from the volcanic CO_2 seeps in Papua New Guinea [16]. While dark calcification in *H. opuntia* was negatively affected in plants grown close to the CO_2 seeps, it was unaffected in *H. cuneata f. digitata*. On the other hand, and in contrast to experimental OA studies, in both species light calcification was enhanced due to the low pH conditions. In *H. opuntia*, this increase compensated for the lower dark calcification rates and resulted in similar daily net calcification of plants growing at the seeps and an un-impacted control site several hundred meters away.

Synthesizing reported OA responses to predict a species' resistance/susceptibility and infer about potential species-specific differences is a difficult undertaking due to differences in experimental treatments (pCO_2 levels, experimental duration; Fig. 4) and additional incubation conditions (light intensity, water flow, nutrient concentrations, etc.…). Here, one of the factors that may contribute to reported differences in the direction and magnitude of OA responses is the experimental light level. Often, its ecological relevance to the locations at which the algae were collected is overlooked. For example, OA effects in *H. macroloba* found in different studies from French Polynesia and the Great Barrier Reef vary between neutral and negative calcification responses [19,32,33,37,41]. When comparing these responses with the experimental light levels used in the studies, all of them performed on algae collected at shallow depths (0.3–3.5 m), it shows that the neutral responses were recorded in experiments using higher light intensities that were closer to the natural levels at the collection depth (650–700 µmol m^{-2} s^{-1}) [19,33]. In contrast, the negative OA responses found in *H. macroloba* derived from OA mesocosm studies using irradiances substantially lower than those in the algae's natural shallow-water environment (150–300 µmol m^{-2} s^{-1}) [32,37,41].

Nevertheless, studies evaluating the OA responses in more than one

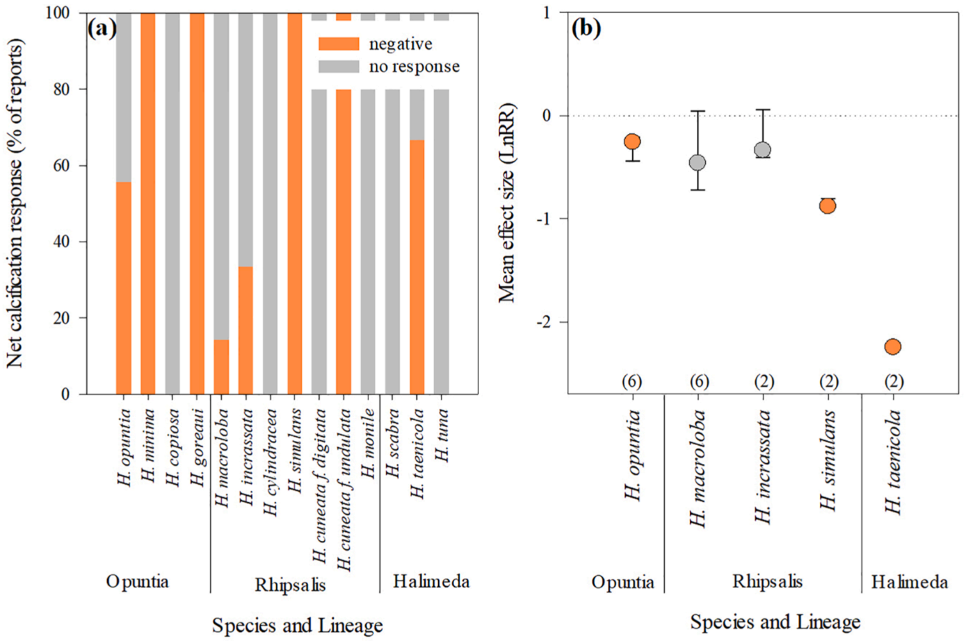

Fig. 6. (a) General overview of the type of growth/calcification (light or net calcification) responses to OA in different *Halimeda* species and (b) mean effect size of reported species-specific net calcification responses to OA. Orange circles indicate significant negative effects and gray circles indicate effect sizes not significantly different from zero (numbers in parenthesis indicate the number of studies - only species with two or more reports were analyzed).

species, either simultaneously or using the same experimental design to assess the responses of different species, provide ample evidence that species show differences either in the type of response (neutral or negative) or the magnitude of negative OA effects [18-20,29,32,36,37,41-43]. The species-specific susceptibility to OA has been related to morphological and/or physiological differences among species [18-21,37]. This seems reasonable, considering that in *Halimeda* spp., $CaCO_3$ precipitation is the result of photosynthesis and the anatomy of the algal thallus, though there is evidence that these algae exert only a limited biological control over calcification [30,44].

Calcium carbonate precipitation in *Halimeda* spp. occurs outside the cells in a semi-isolated compartment, the intercellular space (ICS), separated from the external medium by a layer of tightly appressed tube-like filaments, called utricles (intercellular calcification) [45]. The primary utricle (PU) morphology is related to the length of diffusion pathways that influences ion uptake (i.e., Ca^{2+}, HCO_3^-, CO_3^{2-}) and H^+ fluxes and consequently, affects calcification and inorganic $CaCO_3$ content of the algal thallus [46]. As PU morphology of *Halimeda* species is consistent within the different evolutionary lineages (Opuntia, Rhipsalis, Halimeda) [47,48], several authors reasoned that this might explain the mixed OA responses of *Halimeda* species [18,43]. For example, species of the Opuntia lineage (e.g., *H. opuntia*), with slender PUs and consequently shorter diffusion pathways and higher $CaCO_3$ content, have shown a higher susceptibility to OA in multi-species studies [18,20,21]. Yet, the assumption of a relationship between lineage and OA susceptibility does not hold when comparing OA responses in species from different lineages (Fig. 6). This might be due to the above mentioned problems of comparing data sets collected through different experimental designs and/or differences in species' physiology. The latter could play an important role, considering the strong relationship between metabolism and calcification in these calcareous green algae.

The first related studies in this genus were performed in the seventies, reporting a light stimulation of calcification [49] and its relationship to photosynthesis [50]. Later, it was proposed by Borowitzka and Larkum [45] that the photosynthetic CO_2 uptake from the intercellular space may lead to a localized pH increase, therefore raising the $[CO_3^{2-}]$ in the intercellular medium and favoring $CaCO_3$ precipitation. Hence, both processes correlate positively [45], with photosynthesis assumed to promote calcification, while calcification might increase the concentration of CO_2 available for photosynthesis ($2HCO_3^- + Ca^{2+} \rightarrow CaCO_3 + H_2O + CO_2$). Also, internal carbon-recycling has been demonstrated to play an important role for photosynthesis and calcification in *Halimeda* spp., with up to 25–50% of the carbon used for calcification originating from respiratory CO_2 [45,51].

In addition to the formation of primary needles induced by *Halimeda*'s photosynthetic activity, their partial dissolution, recrystallization and breakdown into micro-anhedral crystals (MACs) have been documented. This process leads to the cementation of the living segments and has been associated to nighttime respiration, a process that results in a decrease in pH and consequently, the carbonate saturation within the ICS [52,53]. The presence or absence of MACs has been associated to differences in PU morphology among species, as it is consistent within, but not between the three evolutionary lineages (Halimeda, Opuntia, Rhipsalis) [46]. Species with smaller PUs (Opuntia lineage) and hence, shorter diffusion pathways for ions (e.g., Ca^{2+}, CO_3^{2-}) to the primary inter-utricular space, usually exhibit a substantial formation of MACs on top of the aragonite needles that is minimal or absent in species with larger PUs [46]. Thus, OA-induced changes in calcification (needle formation and/or cementation), either as a direct abiotic effect due to lower seawater pH or indirectly due to OA effects on algal metabolism, will potentially have an impact on the ecological fitness of *Halimeda* spp., affecting growth rates, thallus carbonate content and consequently thallus rigidity.

When examining the OA effects on *Halimeda* spp. calcification from a regional perspective, it becomes apparent that most regions where species' OA responses have been studied might experience declines in calcareous macroalgal carbonate production (Fig. 7a, b). Yet, the magnitude will likely differ, depending on local *Halimeda* spp. abundance and species composition. For example, the reported OA responses on *Halimeda* spp. calcification from Polynesia were highly variable (Fig. 7b). This was mostly due to the large negative OA impacts found for *H. taenicola* at the Palmyra Atoll [18,42], while OA effects in other species in this region (*H. macroloba, H. minima*) were much smaller [19,33]. No negative OA effects on *Halimeda* spp. have been reported so far in Japan and Papua New Guinea (Melanesia), though this might be related to only one study in the former region [33] and the fact that the

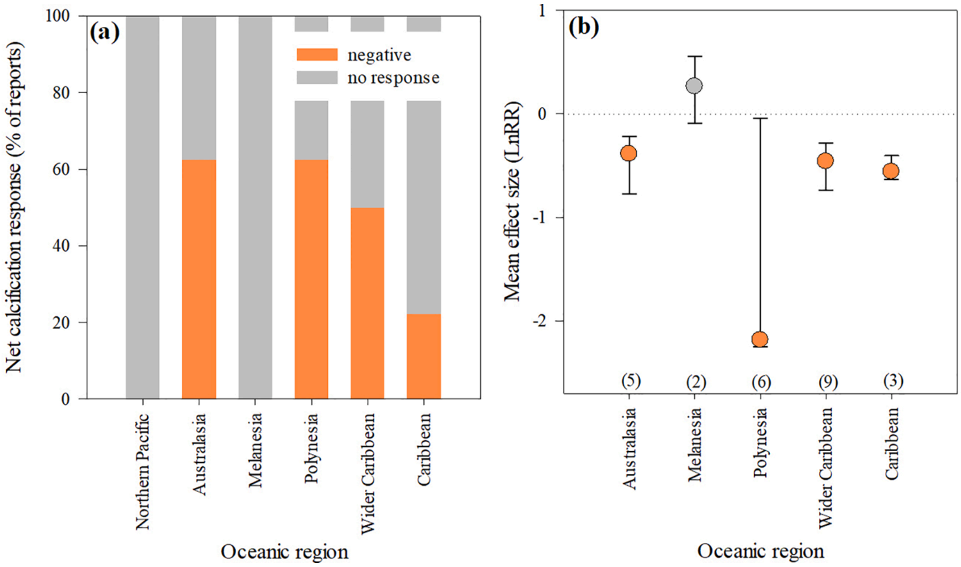

Fig. 7. (a) General overview of the type of net calcification responses to OA in different oceanic regions and (b) mean effect size of OA impacts on regional carbonate production of *Halimeda* spp.. Orange circles indicate significant negative effects and gray circles indicate effect sizes not significantly different from zero (numbers in parenthesis indicate the number of studies- only regions with two or more reports were analyzed).

only data available for Melanesia derive from an in situ study at volcanic CO_2 seeps [16].

Species-specific OA responses and hence, *Halimeda* spp. community composition might play a key role in defining the regional impact on *Halimeda*-derived carbonate production. However, it cannot be excluded that regional environmental variability and related local acclimatization of the algae also play an important part. This is for example supported by in situ observations at volcanic CO_2 seeps, reporting the presence of *Halimeda* spp. at tropical low-pH vents [16], while they were absent at temperate vents [54].

Generally, comparing species' experimental OA responses from different locations and associating them to differences in regional environmental variables (e.g., seawater carbonate chemistry) is difficult. So far, only one study attempted to reduce the problems by conducting identical OA experiments on *H. macroloba* at multiple locations in the Pacific (Moorea, Hawaii, Okinawa) [33] and assess the potential importance of regional acclimatization for OA responses. The results showed that this species was consistently insensitive to OA conditions (700–1000 ppm), independent of the geographical location, though another calcareous alga, the coralline alga *Porolithon onkodes*, exhibited location-specific OA effects. This suggests that *H. macroloba* might be generally resistant to OA, as also supported by findings of other studies [19,37]. However, there exist contrary reports for this species from Australasia (GBR) suggesting negative [32,41] or neutral OA responses [37]. Similarly, the reported type of OA response for *H. opuntia* varies among regions and also for the same region. While this species showed consistently no negative OA impacts on calcification in the Caribbean [17,43,55], all studies in the Wider Caribbean and Polynesia reported negative OA responses [18,20,21,42]. In contrast, a study on *H. opuntia* at the Great Barrier Reef reported its resistance towards OA [38], which agrees with the in situ response found at the Papua New-Guinea volcanic vents [16], while another study (also at the GBR) reported negative OA effects on net calcification [37].

3.2.2. *Thallus carbonate content*

The above mentioned differential responses of light and dark calcification in *H. cuneata f. digitata* and *H. opuntia* from the volcanic CO_2 seeps in Papua New Guinea were also reflected in their thallus carbonate content. While it was higher in the former species when grown close to the CO_2 seeps (+22%), it was significantly decreased in *H. opuntia* (−8%) [16]. This was in accordance with the increased light calcification and nighttime $CaCO_3$ dissolution exhibited by *H. cuneata f. digitata* and *H. opuntia*, respectively.

On the other hand, in most laboratory experiments no response of thallus $CaCO_3$ content to OA has been found, even though some of the studied species exhibited a significant decrease in calcification rates due to lower pH [18,20,21]. Yet, the opposite response pattern has also been found in some studies, where no negative OA effects on *Halimeda* calcification were detected, but the algal thallus $CaCO_3$ was significantly decreased [17,20]. In this regard, Campbell et al. [20] suggested that the reason for this often found mismatch between the OA responses of calcification vs. thallus $CaCO_3$ content might be related to different strategies among *Halimeda* spp., i.e. increased vs. reduced segment production with lower vs. unaltered $CaCO_3$ content, respectively. OA-induced declines in the thallus carbonate content might have indirect effects on *Halimeda* spp., as it has been shown to increase the alga's palatability with respect to specific herbivores (e.g., sea urchins) [20].

Additionally, OA has also been shown to affect the formation of MACs and hence, the cementation of living *Halimeda* segments. A substantial loss of MACs (35–173% thinner calcified rims of central utricles) was observed in *H. opuntia* and related to increased nighttime $CaCO_3$ dissolution [52], which is consistent with the species' dark calcification response to OA in laboratory experiments and in situ [16,37,38].

3.2.3. *Crystal microstructure*

The skeletal $CaCO_3$ microstructure found in the aragonite-precipitating *Halimeda* spp. (i.e., primary needles, micro-anhedral carbonate, secondary needles) is the result of complex interactions between environmental parameters (e.g., seawater carbon chemistry, light availability, temperature) and algal physiological processes (i.e., photosynthesis and respiration) [53]. Thus, another approach to identifying potential OA impacts on *Halimeda* spp. calcification has been undertaken through the study of the skeletal $CaCO_3$ microstructure by Scanning Electron Microscopy, specifically the density and morphology of the crystals formed during the calcification process. Their formation is influenced by the strong diurnal variation in seawater pH and $CaCO_3$ saturation (Ω) that occurs naturally within the inter-utricular space as a result of the algal cell metabolism [56,57]. It can vary among species due to their differences in PU morphology [46], potentially leading to species-specific responses to OA. In several species, OA did not cause an alteration in crystal width and density [34,43,58], while other studies reported an increase in the number of crystals and/or thinner crystals under low-pH conditions [32,52,58]. However, the low number of studies on this subject and the variable responses do not allow identifying potential species-specific OA responses regarding skeletal microstructure. Also, the varying OA responses of *H. opuntia* with regards to crystal density and morphology [43,52,58] point towards differential responses due to experimental conditions, rather than due to species specificity in the calcification process and OA susceptibility.

3.3. Interactive effects of OA with other environmental factors

Predicting the ecological consequences of OA is challenging, as its interactions with other environmental stressors, related to climate change or caused by other human activities, can be both positive and negative [59–61]. In the last decade, the field of multiple-stressor research has rapidly expanded [62]. Nevertheless, the existing evidence for *Halimeda* spp. is still very scarce ($n = 16$ studies), focused mostly on potentially interactive effects of OA with factors such as light, temperature, nutrients and water flow (Fig. 2).

3.3.1. Interactive effects of OA with light

Experimental evidence suggests that many *Halimeda* species are able to maintain calcification rates when exposed to OA under varying light conditions, but for some species, light limitation during exposure to OA may amplify any negative impacts. Several studies reported no significant interactive effect of light availability and OA on the calcification response in *Halimeda* spp. [34,38,43], which is consistent with findings in coralline algae [63–65]. Yet, another study reported that low light amplified the negative impacts of OA in *H. cylindracea* and *H. lacunalis* [36]. In this context, Vogel et al. [38] suggested that this may occur when the irradiance lies below the threshold until which photosynthesis can maintain the pH at the calcification site and hence, act as a buffer against reduced pH of the bulk seawater due to OA. A similar assumption was made in coralline algae, where lower light conditions decreased calcification rates, which led to net dissolution under OA exposure, even though in this case no interaction between the two factors was found [65]. This explanation seems reasonable, considering the evidence provided by microsensor studies in *Halimeda* spp., showing that the pH increase at the algal surface associated with photosynthetic activity depends on light intensity [57]. Further evidence in coralline algae demonstrated the direct link between metabolic activity and the build-up of a pH gradient [27,66], which was suggested to provide a buffer against negative OA effects on coralline algal calcification [27,67].

3.3.2. Interactive effects of OA with temperature

Ocean acidification responses of *Halimeda* spp. also differed widely among species/studies when combined with elevated temperature. Some species exhibited a mitigating effect of elevated temperature on the negative OA effect on calcification [21]. Other studies reported a strong synergistic effect of these parameters, with dramatic reductions in photosynthesis and calcification at temperatures ≥ 32 °C, combined with pH ≤ 7.7 [32,41]. Though, in these studies the combination of a more realistic future scenario (pH 7.9, 32 °C) did not result in reduced calcification rates. Again other studies found no interactive effects of elevated temperature and OA on algal calcification rates [40,41]. These differential responses to OA in combination with elevated temperatures agree with those found in coralline algae, where it has been reported that warming either amplified the sensitivity to OA [68,69], had no effect [70] or could potentially mitigate the negative effects of OA on net calcification [71].

While the diverse responses in *Halimeda* spp. can potentially be the result of differences in species' susceptibilities, some evidence suggests that they may also be related to differences in the duration of the experiments [35] and/or thermal tolerance range of the organisms in relation to the temperatures increases used in the studies [21,72]. Regarding the latter, a key consideration that is often overlooked in temperature studies is the regional temperature acclimation (i.e., local maximum summer temperature) [73]. For example, in a seasonal study on the effects of OA and elevated temperature in *H. heteromorpha*, winter calcification rates were found to increase under the combined treatment (OA, +3.5 °C) [72]. In contrast, in the summer experiment the same treatment caused a decrease in calcification rates, which was most likely related to the fact that the elevated temperature scenario in summer represented a temperature above the local maximum summer value. In the same context, studies in which OA conditions were combined with an elevated temperature representing the regional summer maximum reported a mitigating effect on the negative OA effects in several species of the Wider Caribbean [21] and *H. incrassata* from the Caribbean (Schubert, unpubl. data). In the latter case this effect was found to be modulated by light, showing a decrease of the ameliorating effect of elevated temperature with decreasing light availability.

3.3.3. Interactive effects of OA with nutrients and dissolved organic carbon

Studies by Hofmann et al. [55,74] reported no significant effects of inorganic nutrient addition and OA on calcification rates in *H. opuntia*. In contrast, dissolved organic carbon (DOC) had varying effects on calcification in *Halimeda* species from different regions, either alone or when combined with OA [37,39]. Exposure to elevated DOC and OA did not induce an effect in *H. macroloba* from the GBR, but exerted an additive effect on dark calcification rates in *H. opuntia* [37]. In the latter, both treatments (OA, DOC) individually induced a reduction in dark calcification, an effect that was added in the combined treatment and resulted in a significant decrease in daily net calcification in this species. In contrast, in the Caribbean *H. incrassata*, both elevated DOC and OA individually reduced light calcification rates, but when combined exerted an antagonistic effect that mediated the individual negative effects [39]. The opposite findings regarding the effects of DOC may be contributed to differences or shifts in the algal-associated bacterial communities, but more studies on seaweed holobionts are necessary to better understand how shifts in bacterial composition or activity affect the algal host.

3.3.4. Interactive effects of OA with water flow

To date, only one study investigated the effects of variations in water flow on the OA response in a *Halimeda* species, finding no significant effect of these two factors on net calcification rates [75]. Though, studies in coralline algae suggest that water flow can modulate algal responses to OA [65,76,77]. Low water flow has been found to ameliorate the negative impact of OA on coralline algal calcification [76] or to amplify the effects, inducing net dissolution [65]. In contrast, fast flow generally enhanced net calcification rates of coral reef communities (corals and crustose coralline algae) and interacted with OA, inducing increased nighttime calcification under higher flow conditions [77].

Despite the lack of experimental data regarding the effect of water flow on the OA response in *Halimeda* spp., indirect evidence suggests that natural slow flow habitats, such as seagrass meadows, can act as refugia from OA for these organisms [40,78-81]. In these habitats, the combination of metabolic and structural features (e.g., shoot density, biomass, leaf area index) of the seagrass bed can buffer OA due to photosynthetically-induced increases in seawater pH and reduction of water flow, respectively [40,78,80,81]. This effect has been demonstrated in the tropical *H. cuneata*, which expressed a two-fold increase in calcification rates under OA conditions in the presence of seagrass, when compared to the alga alone [40], consistent with the reported enhanced in situ calcification rates of *H. renschii* within a seagrass meadow [78].

3.4. Implications for future net carbonate production

When upscaling the experimental evidence provided by OA mesocosm studies performed on different *Halimeda* species and in different regions, by using available regional reports of species-specific carbonate production (Table A.3), projections show that future declines in

Halimeda-associated carbonate production can be expected worldwide (Fig. 8). Nevertheless, the differences in species sensitivity of calcification to OA and apparent region-specific variability suggest that its occurrence and magnitude will be determined by community composition and/or region.

Two common species in the Caribbean and Wider Caribbean are *H. opuntia* and *H. incrassata*, species that exhibited consistently negative experimental OA effects on their calcification in these regions [20,21] and thus, projected declines in *Halimeda*-derived $CaCO_3$ production of ~30% will most likely occur in the near future throughout this region (Fig. 8). Similarly, but in greater magnitude, declines in carbonate production (based on data for *H. opuntia, H. taenicola* and *H. minima*) can also be expected in the Australasian and Polynesian region (Fig. 8). At the Great Barrier Reef, expected future *Halimeda*-derived carbonate production will be ~28% lower than current rates, while experimental evidence suggests that OA-related net carbonate dissolution may occur in the Polynesian region, due to the found decalcification response of *H. opuntia* from the Palmyra Atoll under OA conditions simulating the RCP8.5 scenario [18,42]. Based on the available carbonate production reports for this region, this would translate in a loss ranging from 0.1 to 4.7 kg $CaCO_3$ m^{-2} $year^{-1}$ (Fig. 8).

4. Conclusions and future considerations

Our approach provides a first estimate of OA impacts on future *Halimeda* net carbonate production, though it must be pointed out that the performed regional-scale projections do not consider potential interactions with other environmental (e.g., increased temperature, eutrophication) and biological factors (e.g., impacts on species interactions) or potential adaptation to OA that may influence the magnitude and/or direction of the OA response. In this context, verifying the so far existing experimental evidence of OA effects on

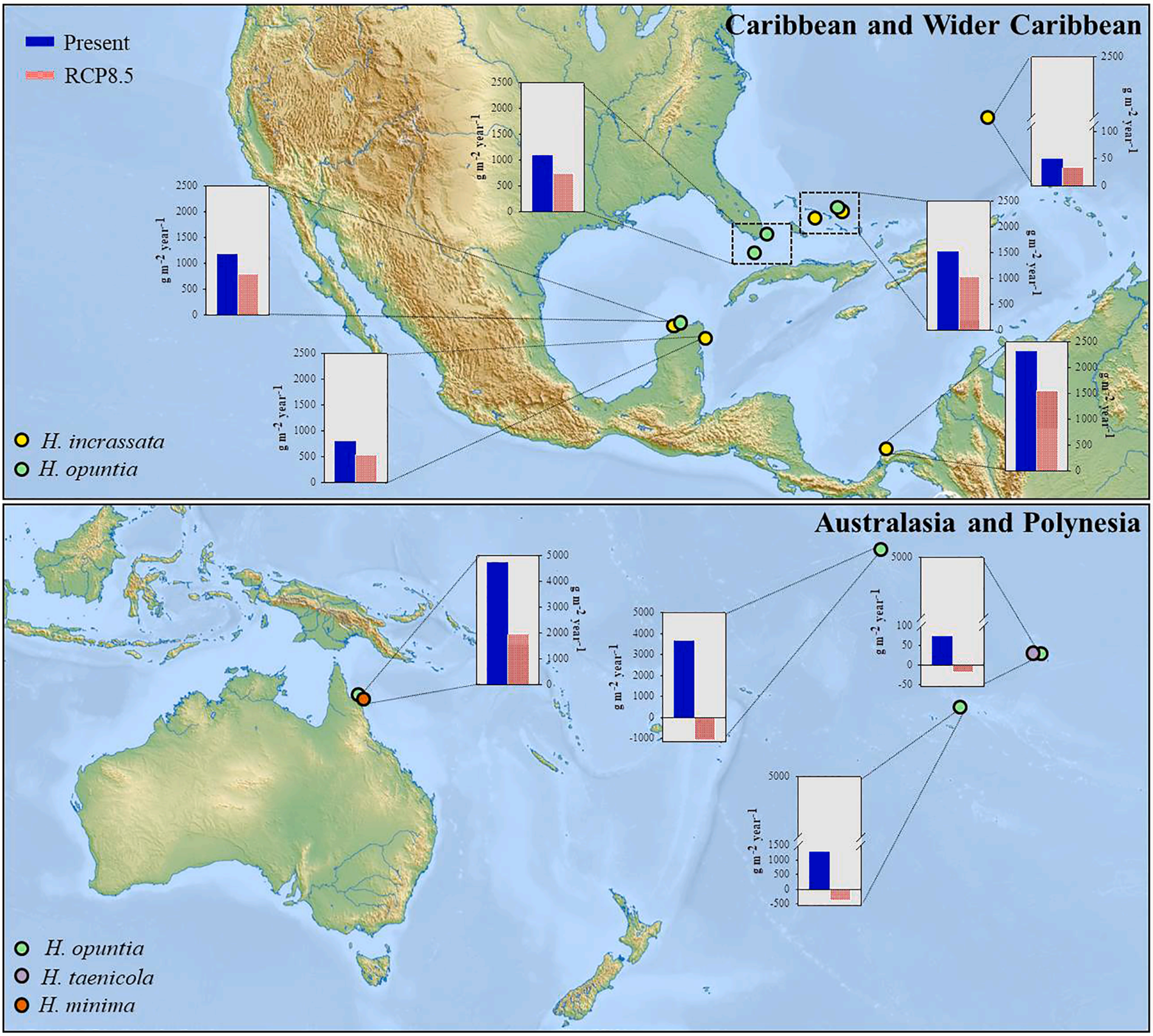

Fig. 8. Carbonate production (g m^{-2} $year^{-1}$) reported for different locations and species in the Caribbean and Wider Caribbean (upper panel) and in Australasia and Polynesia (lower panel), and the potential future changes (RCP8.5 by 2100), based on experimental species- and region-specific OA effects on net carbonate production (for details see Table A.3). The maps were downloaded from Mapswire (https://mapswire.com/).

Halimeda spp. by in situ observations is challenging, as climate-change related changes in seawater pH are often small compared to the natural variability in many systems and may not have crossed physiological thresholds yet. Currently, the only evidence of OA effects under natural settings derives from studies carried out at submarine CO_2 vents, which in the case of *Halimeda* spp. suggest that some species can acclimate and tolerate low-pH environments. For example, the presence of several species has been reported from CO_2 seep sites in Papua New-Guinea [16] and has also been observed at low-pH springs in the Mexican Caribbean (*H. incrassata*; N. Schubert pers. obs.).

This review highlights the general need for more studies, as there currently exist large gaps not only in the OA responses of particular *Halimeda* species, but also for particular regions, which makes identifying potential patterns difficult. In this context, the low number of available studies also limits a more informative meta-analysis, which in the present study represents only a first approximation. In future analyses, when more data sets are available, covariates (e.g., location, duration of exposure, secondary experimental conditions) and random factors (i.e., Study ID to account for multiple responses from the same study) should to be considered. Furthermore, experimental approaches should be accompanied by collection of ecological data, as confident predictions of OA-related impacts are often hindered due to missing local/regional information regarding *Halimeda* community composition, standing stocks and carbonate production. Nevertheless, the so far available information suggests that declines in *Halimeda*-derived carbonate production can be expected worldwide, though some regions harbouring more sensitive species might be more impacted than others.

Declaration of Competing Interest

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

Acknowledgments

This study received Portuguese national funds from FCT - Foundation for Science and Technology through projects UIDB/04326/2020, UIDP/04326/2020 and LA/P/0101/2020.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2022.100059.

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