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Additive impacts of ocean acidification and ambient ultraviolet radiation threaten calcifying marine primary producers

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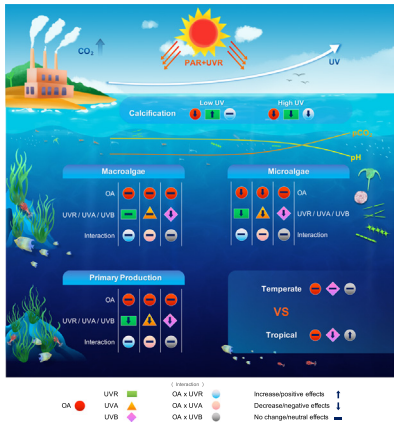
HIGHLIGHTS

- Ocean acidification (OA) acts additively with UVR on marine primary producers.
- UVR and OA showed additive inhibition of calcification at near in situ conditions.
- Small proportion of antagonism leads to neutral effects of OA combined with UVR.
- Magnitude of responses is strongly dependent on experimental duration.

GRAPHICAL ABSTRACT



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ABSTRACT

Ocean acidification (OA) represents a threat to marine organisms and ecosystems. However, OA rarely exists in isolation but occurs concomitantly with other stressors such as ultraviolet radiation (UVR), whose effects have been neglected in oceanographical observations. Here, we perform a quantitative meta-analysis based on 373 published experimental assessments from 26 studies to examine the combined effects of OA and UVR on marine primary producers. The results reveal predominantly additive stressor interactions (69–84% depending on the UV waveband), with synergistic and antagonistic interactions being rare but significantly different between micro- and macroalgae. In microalgae, variations in interaction type frequencies are related to cell volume, with antagonistic interactions accounting for a higher proportion in larger sized species. Despite additive interactions being most frequent, the small proportion of antagonistic interactions appears to have a stronger power, leading to neutral effects of OA in combination with UVR. High levels of UVR at near in situ conditions in combination with OA showed additive inhibition of calcification, but not when UVR was low. The results also reveal that the magnitude of responses is strongly dependent on experimental duration, with the negative effects of OA on calcification and pigmentation being buffered and amplified by increasing durations, respectively. Tropical primary producers were more vulnerable to OA or UVR alone compared to conspecifics from other climatic regions. Our analysis highlights that further multi-stressor long-term adaptation experiments with marine organisms of different cell volumes (especially microalgae) from different climatic regions are needed to fully disclose future impacts of OA and UVR.

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1. Introduction

The global ocean has been shielding our planet from abrupt climate changes by absorbing a third of anthropogenic CO_2 emissions and excess heat trapped in the atmosphere, leading to ocean acidification (OA, decreasing seawater pH) and warming (Caldeira and Wickett, 2003; IPCC, 2014). In addition, the increased use of chlorofluorocarbons (CFCs) as refrigerants and propellants led to an alarming depletion of stratospheric ozone starting in the 1970s (Molina and Rowland, 1974) and to a corresponding increase in ultraviolet-B (UV-B, 280–315 nm) radiation reaching the Earth's surface (Madronich et al., 1998). Stratospheric ozone depletion (inversely correlated with temperature in this atmospheric layer) was found to be accelerated by global warming (Neale et al., 2021), leading to increased incident surface UV-B (Williamson et al., 2014; Bais et al., 2019). In addition, the upper mixed layer (UML) in oceans becomes shallower due the enhanced stratification caused by ocean warming, hence the shoaling UML is supposed to expose organisms within this layer to high levels of UV-B (280–315 nm), UV-A (315–400 nm) and photosynthetically active radiation (PAR, 400–700 nm) due to a shortened irradiance pathlength (Boyd and Doney, 2002).

The development of adequate adaptation and mitigation strategies to deal with these ocean changes is critically important for human well-being and environmental sustainability (Barnes et al., 2019; IPCC, 2019). As such, the scientific community has directed considerable efforts toward examining the effects of global change-related drivers on marine biota (Hooper et al., 2012; Wernberg et al., 2012). The underlying mechanisms of both OA and UV radiation and their impacts on a wide variety of marine organisms have been extensively examined over the last twenty years. It was reported that OA showed negative yet variable effects on various marine organisms, with calcifying species being particularly prone to OA (Kroeker et al., 2013). Studies showed that UV-B exerted overall negative effects on marine biota such as protists, corals, crustaceans and fishes (Bancroft et al., 2007; Llabrés et al., 2013; Jin et al., 2017). Departing from the individual effects of OA or UV on marine biota, the interactions between OA or UV with other factors related to global change such as warming, ocean deoxygenation, increasing PAR and nutrient depletion/eutrophication have also been examined (Kroeker et al., 2013; Nagelkerken and Connell, 2015; Seifert et al., 2020; Jin et al., 2019; Sampaio et al., 2021; Steckbauer et al., 2020). Although the interactive effects of OA and UV on marine organisms (most of them being microalgae and macroalgae) have been investigated experimentally (e.g., Sobrino et al., 2008; Gao et al., 2009; Gao and Zheng, 2010; Jin et al., 2013), a quantitative meta-analysis of the interactions between these two global change-related factors on marine biota has not been documented yet. Previous experimental studies investigating the combined effects of OA and UV report context-dependent interactive (antagonistic or synergistic) or additive effects (Li et al., 2012; Jin et al., 2013), highlighting the need for further empirical investigations.

Here, we integrate published global change literature and help bridge the knowledge gap surrounding the combined effects of OA and UV on marine primary producers. We do so through a quantitative meta-analysis using the results of existing publications. Specifically, we firstly establish a comparative framework and analyse how distinct biological responses are impacted by OA, UV or both in combination. Secondly, we assess how expected responses to OA or UV or their combinations can vary across distinct taxonomical groups (microalgae and macroalgae) and the current abiotic conditions to which organisms are adapted and acclimatized (temperate or (sub-)tropical or polar). Thirdly, we tested how factors such as experiment duration and cell volume influence the effects across multiple response variables. Finally, we highlight new insights and discuss limitations in current studies. The findings presented here could help to estimate the full impacts of climate change on marine biota, which can support decision-making processes for human well-being and environmental sustainability.

2. Materials and methods

2.1. Literature search

We searched the published literature using ISI Web of Science (v.5.35) and Google Scholar for studies examining experimental responses of organisms to ocean acidification and ultraviolet radiation (UVR) in combination using the keywords: ocean acidification, high CO_2, elevated CO_2, ultraviolet radiation, UV-A radiation, UV-B radiation. These searches were conducted prior to 31 December 2020, updated on 1 March 2021, and yielded an initial pool of 425 published studies in total.

2.2. Study selection criteria

We assessed each publication for suitability and retained only those studies that examined the responses of organisms to ocean acidification and UVR in a full-factorial experiment, i.e., testing ocean acidification and UVR individually and in combination, and comparing responses to an ambient control treatment. This resulted in four treatments: control (C), ocean acidification (OA), ultraviolet (UVR), and a combination of ocean acidification and ultraviolet radiation (OA + UVR). Studies which did not meet this criterion were not considered for further analysis. The stressor manipulation level for OA was based on the representative concentration pathway (RCP) 8.5 emission scenario, the most widely used and well-established projection by IPCC for 2100 (IPCC, 2014). Under this scenario, the atmospheric CO_2 level increases from the current ~400 ppm to ~950 ppm by the end of this century, leading to a decrease in ocean surface pH of ~0.4 by 2100. Based on this analysis design, studies using higher values than predicted for the RCP 8.5 emission scenario were excluded from the analysis. In the context of ocean acidification research, the carbonate system should be manipulated properly according to the practice guide proposed by LaRoche et al., 2010. To be included in our study, the allowed maximal drift over the experiment was 10% for dissolved inorganic carbon (DIC) and 0.1 units for pH, respectively. Studies in which pH was manipulated using acid addition were excluded from the analysis.

Regarding UVR, the treatment without UVR or with the lowest level tested was considered the control as per the choice of the authors of the original studies, and each of the higher levels of UVR were taken individually as experimental treatments. For the papers (11 out of 26, Supplementary Table S1) distinguishing the effects of UV-A (315–400 nm) from that of UV-B (280–315 nm) (i.e., there were three treatments: PAR, PAR + UV-A, PAR + UV-A + UV-B), we treated PAR + UV-A (315–700 nm) as the control and PAR + UV-A + UV-B (280–700 nm) as the treatment to assess the effects of UV-B. Meanwhile, PAR (400–700 nm) was treated as the control, while PAR + UV-A was treated as the treatment to assess the effects of UV-A. These analyses were performed separately.

Studies that did not report, or where it was impossible to determine, the data variation (standard deviation, standard error, confidence intervals or variance) or sample size (absence or pseudo-replication) were not considered, according to the Preferred Reporting Items for Systematic Reviews and Meta-analyses guidelines (PRISMA) (Moher et al., 2009). We took into consideration the PRISMA checklist for meta-analysis and review papers/experiments to ensure the best practice in meta-analyses reporting.

2.3. Data collection

Datapoints, error estimates and sample sizes were extracted using published values or from relevant figures using GetData Graph Digitizer. For the meta-analysis, all extracted error estimates (variance, standard deviation, or standard errors) were transformed to standard error through appropriate mathematical formulas using sample sizes and means. To meet the statistical assumption of independence among

observations in the meta-analysis (Hedges et al., 1999), we either collected the data at the endpoint (e.g., photosynthetic rate) or derived them, using the time trend, a rate (e.g., growth) for data reported at multiple time intervals along the study. However, the data for all available time points within each study were extracted to construct a separate dataset to test the effects of experimental duration on biological responses. If an experiment reported the same biological response though different metrics at several times, only the most inclusive metric for that response variable was considered to avoid pseudo-replication (Kroeker et al., 2013). Where necessary, data were normalised to ensure consistency within each response.

The wide range of biological responses to stressors assessed in the literature were classified into categories as described by Jin et al., 2019 although with minor modifications, including: (1) growth; (2) survival (mortality was converted to survival by using 1 minus mortality where possible); (3) calcification; (4) photosynthesis (i.e., photosynthetic carbon fixation rate, photosynthetic oxygen evolution rate and parameters such as maximum photosystem II efficiency); (5) cellular/molecular, including enzyme activities such as nitrate reductase activity, and a range of properties such as rubisco and UV absorbing compounds; and (6) pigment, such as carotenoids and chlorophyll *a*, *b*, *c*. Beyond biological responses, we subdivided data into subsets according to: (1) taxonomical groups (microalgae, macroalgae and bacteria); and climate region where the organisms reside (temperate, tropical and polar).

2.4. Effect size calculation

We calculated individual, main, and interactive effect sizes for each test using Hedge's *d* (Hedges and Olkin, 1985) and followed the methods described by Gurevitch et al. (2000). Hedge's *d* was chosen over other available measures of effect size (e.g. natural logarithm of response ratio (lnRR)) because (1) it is consistent with the ANOVA model that was used in most of the publications, in which a significant interaction effect size indicates deviation from the null model of additive effects (Gurevitch et al., 2000); (2) it is unaffected by unequal sampling variances in the paired groups and includes a correction factor ($J(m)$, see below) for small sample sizes; and (3) it is currently the most commonly used metric for meta-analyses, thus facilitating comparisons with results reported in other studies.

Individual effects represent the response in the presence of a stressor alone relative to the control, while main effects compare the net effect of a stressor in the presence and absence of a second stressor. The individual effects of ocean acidification (d_{oa}) and UV radiation (d_{uv}) were calculated with respect to the control (d_c) by the following equation (Crain et al., 2008; Gurevitch and Hedges, 1993):

$$d_{oa} = \frac{Y_{oa} - Y_C}{s} J(m)$$

$$d_{uv} = \frac{Y_{uv} - Y_C}{s} J(m)$$

where Y_{oa}, Y_{uv} and Y_C are means of a variable in the treatment groups of OA, UV and the control, respectively; s and $J(m)$ are the pooled standard deviation and correction term for small samples, respectively, which were calculated using the equations below:

$$s = \sqrt{\frac{(n_C - 1)s_c^2 + (n_{oa} - 1)s_{oa}^2 + (n_{uv} - 1)s_{uv}^2 + (n_{oa+uv} - 1)s_{oa+uv}^2}{n_C + n_{oa} + n_{uv} + n_{oa+uv} - 4}}$$

$$J(m) = 1 - \frac{3}{4m - 1}$$

where n_C, n_{oa}, n_{uv} and n_{oa+uv} are the sample sizes, and s_C, s_{oa}, s_{uv} and s_{oa+uv} are the standard deviations in the control and experimental groups of OA, UV and their combination (OA + UV), respectively; m is the degree of freedom ($m = n_C + n_{oa} + n_{uv} + n_{oa+uv} - 4$). The main effects of OA (d_{OA}), UV (d_{UV}) and their interaction (d_{OA+UV}) were calculated as:

$$d_{OA} = \frac{(Y_{OA} + Y_{OA+UV}) - (Y_{UV} + Y_C)}{2s} J(m)$$

$$d_{UV} = \frac{(Y_{UV} + Y_{OA+UV}) - (Y_{OA} + Y_C)}{2s} J(m)$$

$$d_{OA+UV} = \frac{(Y_{OA+UV} - Y_{UV}) - (Y_{OA} - Y_C)}{2s} J(m)$$

For individual effects d_z (where z is *oa* or *uv*), the sampling variance is (Gurevitch et al., 2000):

$$v_z = \frac{n_z + n_c}{n_z n_c} + \frac{d_z^2}{2(n_z + n_c)}$$

and for a main effect d_Z (where Z is OA or UV), the sampling variance is (Gurevitch et al., 2000):

$$v_Z = \frac{1}{4}\left[\frac{1}{n_{OA}} + \frac{1}{n_{UV}} + \frac{1}{n_{OA+UV}} + \frac{1}{n_C} + \frac{d_Z^2}{2(n_{OA} + n_{UV} + n_{OA+UV} + n_C)}\right]$$

The interaction variance v_Z (where Z is OA + UV) is calculated as:

$$v_Z = \frac{1}{n_{OA}} + \frac{1}{n_{UV}} + \frac{1}{n_{OA+UV}} + \frac{1}{n_C} + \frac{d_Z^2}{2(n_{OA} + n_{UV} + n_{OA+UV} + n_C)}$$

Following Crain et al. (2008), we used individual effect sizes to classify the interactions of OA and UV into one of three types, i.e., additive, synergistic or antagonistic. If the 95% CI of the interaction term overlapped with zero, the interactive effect was considered to be additive. In cases where individual effects were either both negative or one positive and one negative, interaction effects < 0 were considered to be synergistic while effects > 0 were antagonistic. Interaction types were interpreted the opposite way when both stressors had a positive individual effect, i.e., interaction effects < 0 were antagonistic and >0 were synergistic (Piggott et al., 2015).

2.5. Statistical analyses

All analyses were performed with the statistical software R, using the function rma.mv (meta-analysis via multivariate/multilevel linear mixed-effects models) available in the *matafor* package (Viechtbauer, 2010). To begin with the analysis, mean interaction effect sizes and variances across studies were estimated from weighted meta-analyses at first using the function *escalc*. In each analysis, "Observation ID" was treated as a random effect to account for the random component of effect size variation among observations (Gurevitch and Hedges, 1993; see Supplementary Table S2 for equations and model details). In addition to using random effects meta-analyses to assess the global mean interaction effect sizes across all observations, we conducted a series of mixed effects meta-analyses where selected categorical moderators (e.g., taxon, response trait, climate region) were treated as fixed effects to assess mean interactions at each category level afterwards (see Table S2 for model terms). Then the inclusion of "−1" for the categorical moderator (e.g., taxon, response traits, climate regions) calculates estimates for each of the levels within said moderator, contrasted with a dummy variable zero (directly testing the null hypothesis), instead of using one of the moderator levels as a reference baseline. To guarantee a robust analysis, categories with sample sizes smaller than four ($n < 4$) were not included in the analysis. For these analyses, the heterogeneity within (Q_M) and between (Q_E) moderator levels (e.g., taxon, response trait, climate region) was compared using mixed models to assess the significance of each categorical moderator (Borenstein et al., 2011). Significant Q_T (total heterogeneity) indicates that the variance of effect

sizes among studies is higher than expected by sampling error and implies that there may be some underlying structure to the data. Q_M describes the amount of heterogeneity, which can be explained by the chosen categories (see Table S2 for model structure). If Q_M is significant, it means that the categorical moderator has a significant effect. Q_E describes the amount of heterogeneity, which is left unexplained after the model is considered. Therefore, a significant value of Q_E indicated that there was additional variance to be explained in the effect sizes.

Since methodological factors, such as experiment duration, may influence the effect size (Kroeker et al., 2013) or change the interaction type between stressors (Jin et al., 2019), we determined the experimental duration for each data point where possible. Subsequently, continuous random-effects meta-analyses were run to test the effects of this methodological factor on the effect sizes with duration of experiment as a continuous variable (Kroeker et al., 2013). Finally, frequencies of the three interaction types were calculated for different ranges of experimental durations. To facilitate the analysis, different ranges of experimental durations were classified into two categories: short-term, in which the durations of the experiments were shorter than or equal to 20 days (≤20 days), and long-term, where experiments were conducted for >20 days (>20 days). We also determined if the cell volume of microalgae species affects the response magnitude or the stressor interaction type. Thus, cell volume data were mined from the original studies were reported, and we derived those data of the same species from other published reports if they were not reported. We performed the analysis by following the same procedures as those of the methodological factor described above.

To assess the robustness of observed effects, we tested publication bias using Rosenthal's method of fail-safe numbers (Rosenthal, 1979). The Rosenthal's fail-safe number determines the number of effect sizes with no significant effect that are needed to change the significance (p value) reported by the model. We estimated a fail-safe number of 120,098, which far exceeds the minimum recommended number based on our sample size ($120{,}098 > 5(n) + 10$, where n is the number of the observations in the meta-analysis). In addition, using the trim and fill method (Duval and Tweedie, 2000), we tested how much impact a potential bias could have. The trim and fill analysis failed to identify any missing studies needed to restore symmetry (missing studies = 0). After completing these two tests, we concluded that there is no evidence of publication bias for the data set compiled.

3. Results

3.1. Database description

We found 26 articles reporting 373 assessments of organisms' responses to OA and UV radiation (Table S1). Data sources can be found in Supplementary Table S1. The majority of observations were from primary producers (microalgae: $n = 234$, macroalgae: $n = 131$), with only 8 observations testing responses of bacteria (Table S1). Nearly half (~50%) of the observations referred to the responses of organisms to UVR and OA, 24% of the observations describe responses to UV-A and OA, and the rest (26%) tested responses to UV-B and OA (Table S1). All studies were conducted experimentally; either in laboratories ($n = 201$) or in situ ($n = 172$). Most of the studies were carried out with species from temperate ($n = 80$) or tropical ($n = 70$) climate regions, with only one study investigating the responses of two Arctic kelps to OA and UV radiation (Gordillo et al., 2015) (Table S1, see Fig. 1 for study locations). Short-term experiments (≤20 days) dominated in all the assessments (81%). The remaining experiments were conducted in long-term (>20 days), with a maximum duration of 57 days whereby a calcifying microalga was studied (Xu and Gao, 2015). We performed a correlation analysis of the different biological responses, and we found that for the effects of UVR, the response trait calcification was negatively correlated with pigmentation (correlation = −0.9229) (Fig. S1). For the interactions, the

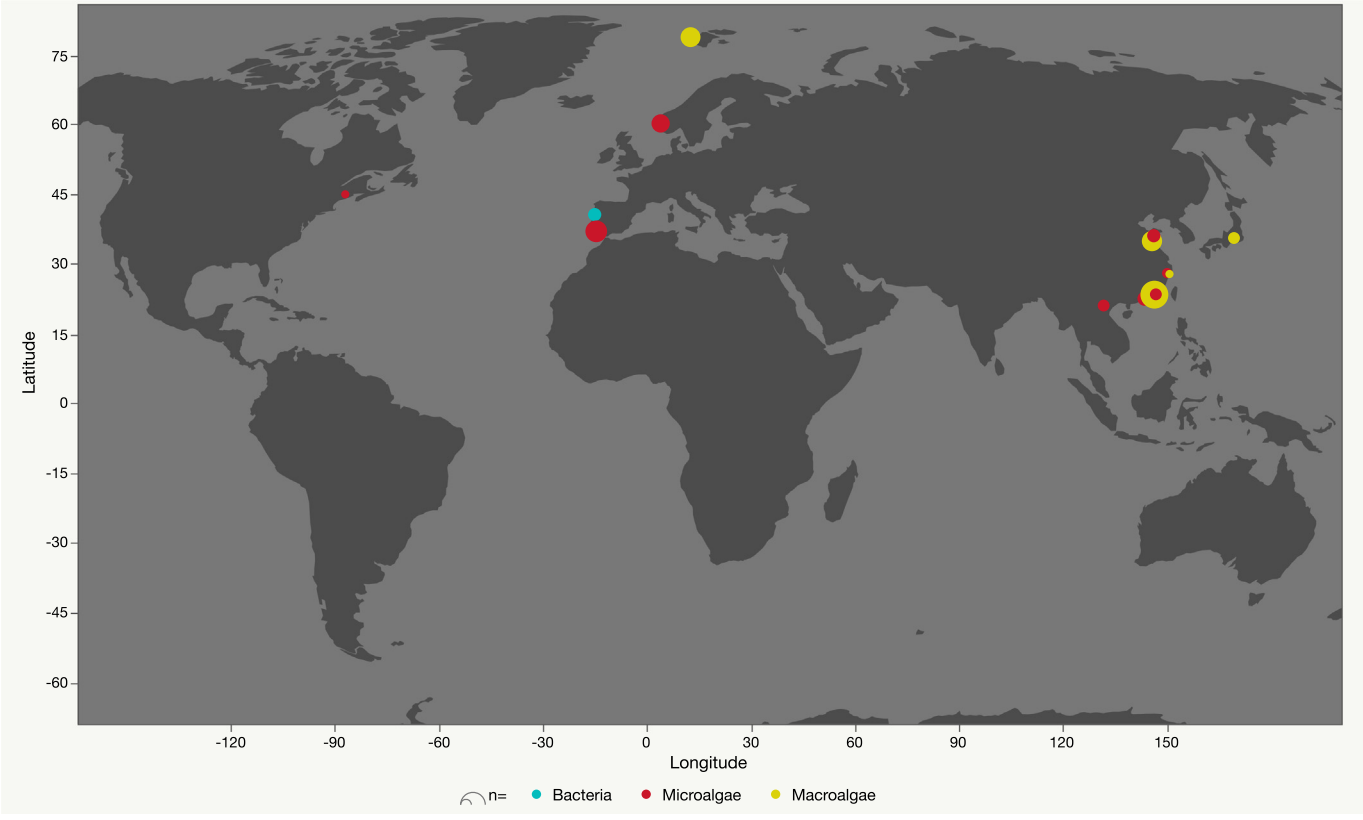

Fig. 1. Locations of field studies that investigated the combined effects of elevated ultraviolet radiation and ocean acidification on bacteria (blue), microalgae (red) and macroalgae (yellow). Symbol sizes indicate the number of observations.

response trait of calcification was negatively correlated with photosynthesis (correlation = −0.651) (Fig. S1).

3.2. Interactive effects of OA and UVR

Globally, our data showed a significant (i.e. the 95% CIs did not overlap with zero) negative effect of OA, d_{OA} (Hedge's $d = -1.306$, 95% CI = [−1.638, −0.973], $Z = -7.700$, $p < 0.001$) and also a negative effect of UVR, d_{UVR} (Hedge's $d = -0.719$, 95% CI = [−0.998, −0.440], $Z = -5.043$, $p < 0.001$) on the biological responses tested (Fig. 2). The 95% CI of the overall interaction term, d_{OA+UVR}, overlapped with zero (Hedge's $d = -0.149$, 95% CI = [−0.335, 0.037], $Z = -1.573$, $p = 0.116$), suggesting that there was no significant effect of OA in combination of UVR (Fig. 2). These results indicate that although most interactions were additive (74%), antagonism (17%) overwhelmed the additive interaction, resulting in limited responses when OA and UVR acted together (Fig. 1). Synergistic interactions were the smallest fraction (9%) (Fig. 2).

While OA and UVR showed significant negative effects on microalgae (OA: Hedge's $d = -0.570$, 95% CI = [−1.050, −0.091], $Z = -2.330$, $p = 0.020$; UVR: Hedge's $d = -0.611$, 95% CI = [−1.174, −0.047], $Z = -2.123$, $p = 0.034$), they did not exert any significant effect on macroalgae (Fig. 2). Despite the different responses of microalgae and macroalgae to OA and UVR, there were no significant differences between these two taxonomical groups (OA: $Q_M = 0.123$, $p = 0.726$; UVR: $Q_M = 0.439$, $p = 0.508$) (Fig. 2). When OA and UVR acted together, no significant effects were observed in either microalgae or macroalgae (Fig. 2). Given the significant negative effect of OA and UVR on microalgae, it appeared that the small fraction of antagonistic interactions (16%) overwhelmed the additive (79%), and therefore resulted in no effects of the combination of OA and UVR. The additive interaction term also dominated (65%), with smaller fractions of multiplicative interaction (synergistic: 17%; antagonistic: 17%) in macroalgae (Fig. 2). Although additive interactions were dominant in both taxonomical groups, overall, the interaction types differed significantly between the two groups ($\chi^2 = 9.086$, $p = 0.011$, df = 2, $n = 186$).

Apart from differences between taxonomical groups, we also hypothesized that organisms acclimated to different environmental conditions may show different responses to OA, UVR or both in combination. We detected significant negative effects of OA on organisms from the tropics (Hedge's $d = -1.099$, 95% CI = [−2.129, −0.070], $Z = -2.093$, $p = 0.036$), but not on those from temperate or polar regions (Fig. 2). Regarding the individual effect of UVR, our data showed a significant positive effect on the performance of organisms in polar regions (Hedge's $d = 1.895$, 95% CI = [0.593, 3.198], $Z = 2.852$, $p = 0.004$) (Fig. 2). The interactive effects of OA and UVR appeared to be neutral in all three climate regions (all $p > 0.05$) (Fig. 2). The additive interaction type dominated in all climate regions (polar: 50%; temperate: 71%; tropical: 67%), and there were no significant differences between the frequencies of interaction types among the three climate zones ($\chi^2 = 4.102$, $p = 0.392$, df = 4, $n = 113$).

To assess whether the various response traits are differentially affected by OA, UVR or their interaction, the wide range of biological responses were classified into various categories. Consistent with most of the previous experimental studies in the context of OA, our results showed that OA had predominantly negative effects, that is, an overall negative Hedge's d (Hedge's $d = -3.028$, 95% CI = [−4.542, −1.514], $Z = -3.919$, $p < 0.001$) (Fig. 2). OA also exerted negative effects on pigmentation (Hedge's $d = -1.858$, 95% CI = [−3.037, −0.679], $Z = -3.089$, $p = 0.002$) (Fig. 2). The other three response traits (cellular/molecular, growth, photosynthesis) appeared to more tolerant to OA, with no significant responses to OA (i.e., the 95% CIs overlapped with zero) (Fig. 2). As for UVR, photosynthesis was the most sensitive trait, significantly decreasing in response to elevated UVR (Hedge's $d = -1.109$, 95% CI = [−1.730, −0.488], $Z = -3.502$, $p = 0.0005$) (Fig. 2). For the interactions, no significant effects were observed in all the traits assessed (Fig. 2). Additive interactions prevailed across all response traits (calcification: 82%, cellular/molecular: 67%, photosynthesis: 75%; growth: 80%; pigment: 56%), and the frequency of interaction types did not differ significantly among the five response traits ($\chi^2 = 8.481$, $p = 0.388$, df = 8, $n = 186$). Thus, our results indicate that although OA or UVR had individual negative impacts on some specific performance traits (e.g., calcification, pigment), these effects appeared to be muted when OA and UVR act in combination.

3.3. Interactive effects of OA and UV-A

Similar to UVR, UV-A negatively affected the organisms' performance (Hedge's $d = -1.016$, 95% CI = [−1.355, −0.678], $Z = -5.885$, $p < 0.001$), while the effects of OA appeared to be neutral (Fig. 3). Interestingly, we detected a positive effect of the combination of OA and UV-A (Hedge's $d = 0.281$, 95% CI = [0.063, 0.500], $Z = 2.520$, $p = 0.012$), indicating an antagonistic interaction for the overall dataset, although its proportion was very small (9%) (Fig. 3). Most interactions were additive (87%), with the smallest proportion being synergistic (4%) (Fig. 3).

In microalgae, both OA and UV-A showed significant negative effects (OA: Hedge's $d = -0.967$, 95% CI = [−1.685, −0.248], $Z = -2.637$, $p = 0.008$; UV-A: Hedge's $d = -0.645$, 95% CI = [−1.185, −0.105], $Z = -2.339$, $p = 0.019$) (Fig. 3). However, no significant effects of their interaction were detected in microalgae (Fig. 3). Unlike microalgae, macroalgae were more tolerant to OA, UV-A and the combination thereof, showing no significant responses (Fig. 3). In spite of this, the frequency of interaction types did not differ significantly between these two taxonomic groups ($\chi^2 = 2.495$, $p = 0.287$, df = 2, $n = 90$), with predominantly additive interactions (microalgae: 85%; macroalgae: 90%) (Fig. 3).

When assessing the differences in responses to OA or UV-A or their interactions between organisms from temperate and tropical regions, we found a similar response pattern (OA: $Q_M = 2.370$, $p = 0.124$; UVR: $Q_M = 2.757$, $p = 0.100$; OA × UVR: $Q_M = 0.067$, $p = 0.796$) (Fig. 3). All interactions in temperature regions were additive, while in

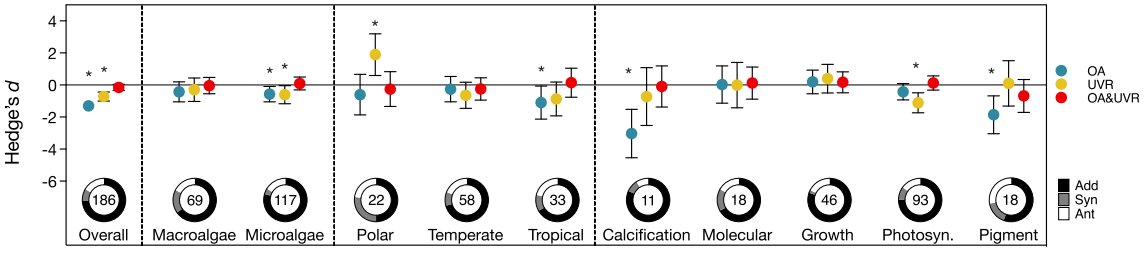

Fig. 2. Responses to the effects of ocean acidification (blue), ultraviolet radiation (UVR) (yellow) and their interaction (Hedge's *d*; red) observed for the overall dataset, different taxa, climatic regions, and organismal response levels. Error bars indicate 95% confidence intervals. For main effects of ocean acidification and UVR, confidence intervals overlapping zero indicate no effect; effects are positive when confidence interval (CI) > 0 and negative if <0. Significant effects are denoted by asterisks. Pie charts indicate the frequencies (%) of additive (black), synergistic (grey) and antagonistic (white) interaction types. Numbers inside pie charts indicate the number of observations.

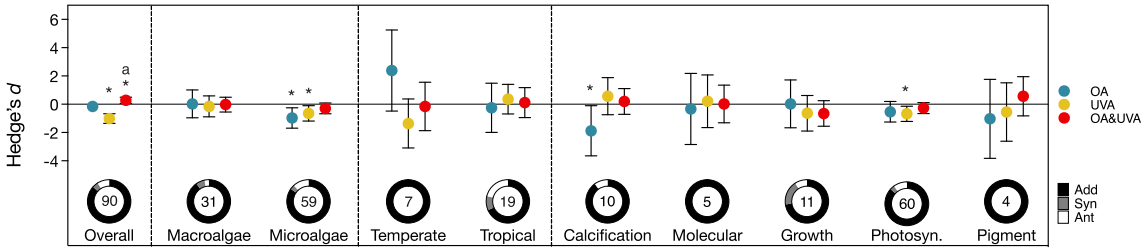

Fig. 3. Responses to the effects of ocean acidification (blue), ultraviolet-A radiation (UV-A) (yellow) and their interaction (Hedge's *d*; red) observed for the overall dataset, different taxa, climatic regions, and organismal response levels. For interactions, confidence intervals overlapping 0 indicate additive effects; those >0 or <0 indicate a significant interaction (antagonistic interactions are highlighted with the letter "a"). Descriptions of the error bars, pie charts, symbols and colour coding see Fig. 2.

tropical regions antagonistic (21%) and synergistic (11%) interactions showed considerable proportions (Fig. 3).

For the differences among responses traits, our assessments showed consistently negative responses of calcification to OA in experiments examining the interactive effects of OA and UV-A (Hedge's $d = -1.876$, 95% CI = [−3.646, −0.106], $Z = -2.078$, $p = 0.038$) (Fig. 3). Similar to UVR, no significant effects of UV-A or the combination of UV-A and OA were observed on calcification, indicating that the negative effects of OA on calcification were compensated by UV-A (Fig. 3). Other response traits such as growth and photosynthesis showed no obvious responses to OA (Fig. 3). As for the individual effect of UV-A, only photosynthesis showed a significant negative response (Hedge's $d = -0.673$, 95% CI = [−1.212, −0.134], $Z = -2.448$, $p = 0.014$), but the responses of photosynthesis and the other response traits to the combination of OA and UV-A tended to be neutral (Fig. 3). These results indicate that the negative effect of UV-A on photosynthesis was compensated by OA. While additive effects were most common across all biological traits (73%–100%), growth was frequently affected synergistically (18%) whereas effects on photosynthesis were often antagonistic (10%) (Fig. 3).

3.4. Interactive effects of OA and UV-B

For the interactive effects of OA and UV-B, we found that the individual effects of UV-B had a significantly negative response (Hedge's $d = -1.131$, 95% CI = [−1.543, −0.719], $Z = -5.379$, $p < 0.001$), but the individual effects of OA or its combination with UV-B were neutral (Fig. 4). Although additive interactions were the dominating interaction type (69%), antagonisms (21%) and synergisms (10%) were also frequent (Fig. 4).

The different responses among taxonomic groups showed similar response patterns compared to the overall dataset (all $p > 0.05$), with a significant negative response to elevated UV-B (microalgae: Hedge's $d = -1.055$, 95% CI = [−1.576, −0.533], $Z = -3.960$, $p < 0.001$; macroalgae: Hedge's $d = -1.643$, 95% CI = [−2.361, −0.926], $Z = -4.491$, $p < 0.001$) but not to OA solely or its combination with UV-B (Fig. 4). Only eight observations of bacteria were included in our analysis, none of which showed a significant response either to OA or UV-B individually or in combination (Fig. 4). The frequency of interaction types did not differ significantly among the three taxonomic groups ($\chi^2 = 5.154$, $p = 0.272$, df = 4, $n = 97$), with ~70% being additive, ~20% being antagonistic and ~10% being synergistic both in microalgae and macroalgae (Fig. 4).

Increased UV-B alone had a pronounced negative influence on organisms' performance (Hedge's $d = -2.136$, 95% CI = [−3.152, −1.121], $Z = -4.123$, $p < 0.001$), but this negative effect turned to be positive when it acted together with OA in tropical regions (Hedge's $d = 1.242$, 95% CI = [0.623, 1.980], $Z = 2.472$, $p = 0.013$) (Fig. 4). Given the insignificant effect of OA alone, these results indicate that UV-B acted antagonistically with OA. In supporting this, we observed a considerable proportion of antagonisms (39%) for the joint effects of OA and UV-B. However, neither the individual effect of OA and UV-B nor their interaction showed significant effects in temperate regions (Fig. 4). Similar to tropical regions, antagonistic (27%) and synergistic (20%) interactions accounted for considerable frequencies in temperate regions (Fig. 4). Overall, the frequency of interaction types did not differ significantly between two climate regions ($\chi^2 = 1.825$, $p = 0.402$, df = 2, $n = 33$).

The differences among response traits showed a similar pattern as observed for UV-A. Individual OA significantly decreased the calcification (Hedge's $d = -2.210$, 95% CI = [−3.661, −0.758], $Z = -2.984$, $p = 0.003$) and UV-B alone inhibited the photosynthesis (Hedge's $d = -1.336$, 95% CI = [−1.872, −0.799], $Z = -4.880$, $p < 0.001$), but the joint effects of these two drivers were neutral (Fig. 4). These results suggest that the negative effects of OA and UV-B on calcification or photosynthesis were compensated by UV-B or OA (Fig. 4). In line with this observation, antagonisms accounted for 20% in the response trait of photosynthesis (Fig. 4). The frequency of interaction types did not differ significantly across response traits ($\chi^2 = 12.251$, $p = 0.140$, df = 8, $n = 97$).

3.5. Effects of cell volumes on effect size

We also tested whether the cell volume (particularly of microalgae species) would affect the individual effect of OA/UV (the data of UV-A,

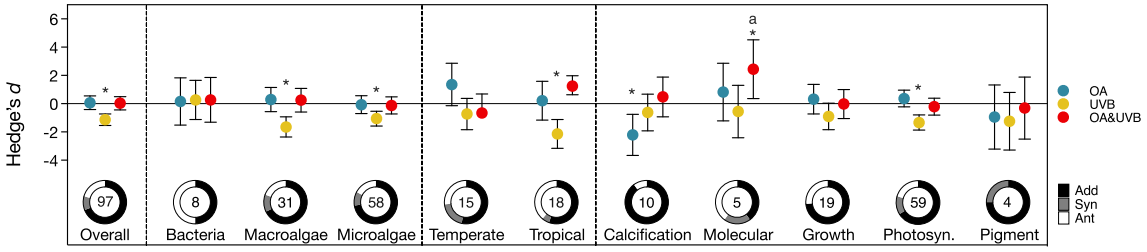

Fig. 4. Responses to the effects of ocean acidification (blue), ultraviolet-B radiation (UV-B) (yellow) and their interaction (Hedge's *d*; red) observed for the overall dataset, different taxa, climatic regions, and organismal response levels. For interactions, confidence intervals overlapping 0 indicate additive effects; those >0 or <0 indicate a significant interaction (antagonistic interactions are highlighted with the letter "a"). Descriptions of the error bars, pie charts, symbols and colour coding see Fig. 2.

UV-B and UVR were pooled together here) or their joint effect. We observed a positive correlation between the effect size of OA alone and cell volume (general linear regression, slope = 0.739, $p = 0.013$) (Fig. 5), indicating that larger cells were less impacted by OA or benefited more from OA conditions. The individual effect of UV or its joint effect with OA were not significantly affected by cell volume (UV: $p = 0.8956$; Interaction: $p = 0.1336$) (Fig. 5). The frequency of interaction types differed significantly among microalgae species of different cell volumes ($\chi^2 = 14.896$, $p = 0.005$, df = 4, $n = 193$) (Fig. 6). Antagonistic interactions accounted for a higher proportion in larger microalgae species (e.g., 45% in microalgae of which cell volume > 1000 μm^3) (Fig. 6).

3.6. Effects of experiment durations on effect size

To assess whether the methodological factor of experimental duration influences the effect size, their relations were tested using general linear models (Fig. 7). Our results showed that the responses of calcification to OA/UV (the data of UV-A, UV-B and UVR were pooled together here) were positively correlated with experimental duration, suggesting the decreased calcification in short-term experiments under OA/UV conditions might be restored after long-term exposure (general linear regression, OA: slope = 0.074, $p = 0.007$; UV: slope = 0.037, $p = 0.034$) (Fig. 7) (Table 1). In contrast, the concentration of pigmentation was negatively correlated with experimental duration under OA alone conditions, in which the responses become more negative with increased long-term exposure (general linear regression, slope = −0.230, $p = 0.001$) (Fig. 7) (Table 1). For the other response traits, significant effects of experiment duration on effect size were not detected (Fig. 5) (Table 1). We defined studies in which organisms were acclimated to the experimental conditions <20 days as short-term, and >20 days as long-term. Further analysis showed that the frequency of interaction types did not differ between these two timescales ($\chi^2 = 2.524$, $p = 0.283$, df = 2, $n = 443$) (Fig. 6).

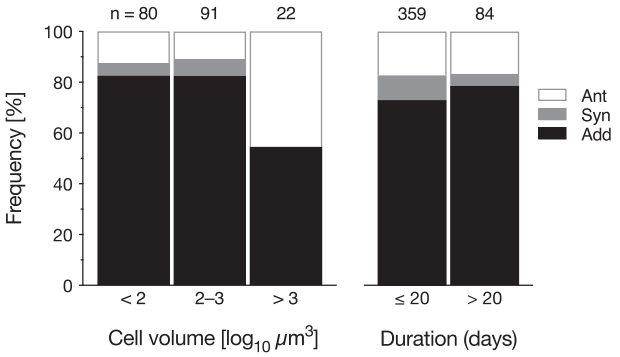

Fig. 6. Frequency (in %) of additive (black), synergistic (grey) and antagonistic (white) interactions depending on cell volume (in $\log_{10}$ μm^3; left panel) and experimental duration (in days; right panel). Values above bars denote the number of observations.

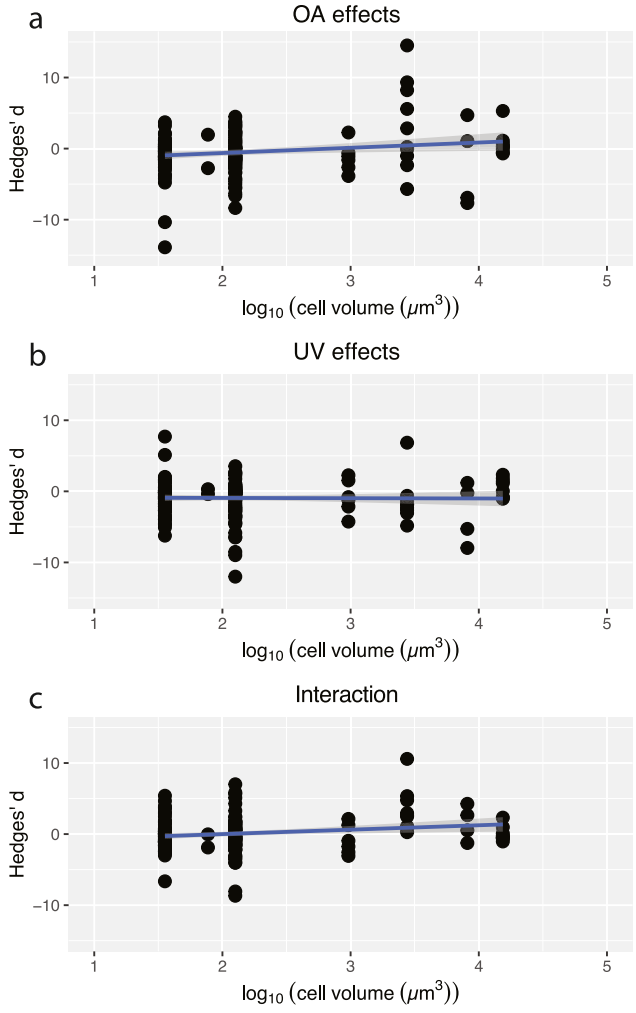

Fig. 5. The effect of cell volume (in $\log_{10}$ μm^3) on the effect size (Hedge's *d*) of ocean acidification (OA) (a), ultraviolet radiation (the data of UV-A, UV-B and UVR were pooled together) (b) and their interaction (c). The data were fitted with linear regressions.

4. Discussion

Overall, our results showed an overwhelming prevalence of additive effects of OA and increased UV radiation on marine primary producers, with synergistic and antagonistic interactions being rare but significantly different between taxonomic groups. The frequency of antagonistic effects increased with the cell volume of microalgae. The prevalence of additive interactions reported in the present study agrees with previous quantitative meta-analyses, in which most of the interaction types were additive across experimental studies (Darling and Côté, 2008; Przeslawski et al., 2015; Jin et al., 2019; Steckbauer et al., 2020), while overall synergisms or antagonisms were uncommon (Burkepile and Hay, 2006; Stephens et al., 2013; Jackson et al., 2016; Yue et al., 2017). Despite additive interactions being most frequent, the small proportion of antagonistic interaction appeared to have a stronger power, leading to neutral effects of OA in combination with UV, whereas the individual effects of each driver were negative. While some previous meta-analyses demonstrated that ocean acidification elicited more severe effects in combination with other stressors, such as warming (Harvey et al., 2013; Kroeker et al., 2013), our findings suggest that ocean acidification may compensate the negative effects of UVR on marine primary producers except algal calcifiers, whose responses to OA are UV intensity or dose-dependent.

It has been well recognized that OA negatively affects the calcification of marine algal calcifiers by an increased hydrogen ion (H^+) and reduced carbonate saturation state in many experimental studies (Riebesell et al., 2000; Gao et al., 2009; Gao and Zheng, 2010; Hofmann et al., 2013; Jin et al., 2017; McCoy et al., 2020) and quantitative meta-analyses studies (Kroeker et al., 2010, 2013; Nagelkerken and Connell, 2015). These results agree with the findings reported here. However, our meta-analysis found no obvious negative effects of UV or its combination with OA on calcification. Even in experiments exploring the interactions between OA and UV-A, UV-A alone could enhance calcification rates (i.e., a positive Hedge's *d* value), although the increases were not statistically significant. Such an effect was also observed in some experimental studies. For instance, a study with the coccolithophorid *Emiliania huxleyi* found that either UV-B (~0.2 W m^{-2}) or UV-A (~10 W m^{-2}) marginally stimulated calcification (Guan and Gao, 2010; Xu and Gao, 2015). Enhanced calcification by the same strain resulted in less photoinhibition caused by UVR, suggesting a

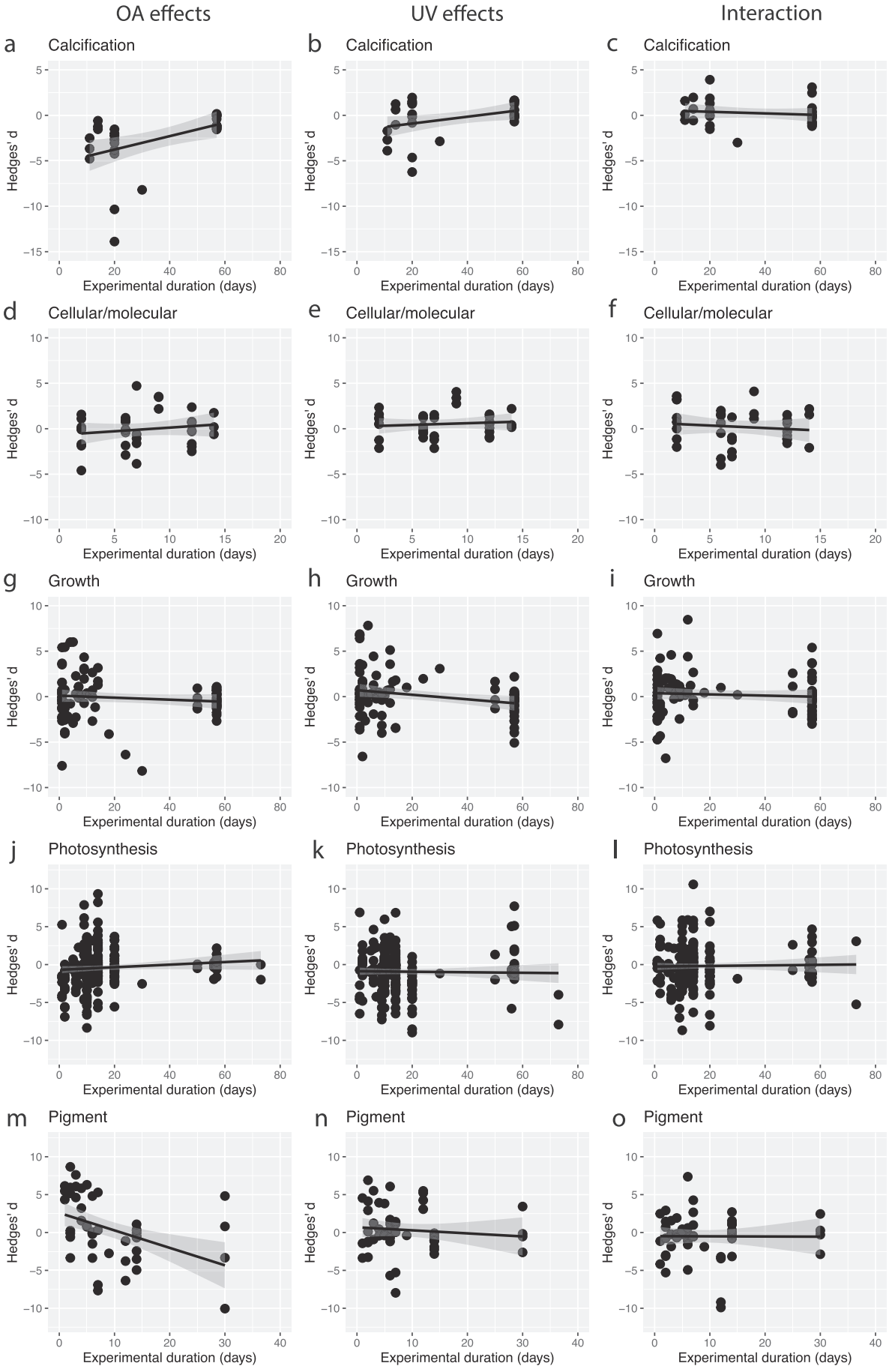
OA effects
UV effects
Interaction
a Calcification
b Calcification
c Calcification
d Cellular/molecular
e Cellular/molecular
f Cellular/molecular
g Growth
h Growth
i Growth
j Photosynthesis
k Photosynthesis
l Photosynthesis
m Pigment
n Pigment
o Pigment
Hedges' d
Experimental duration (days)

Table 1
The effect of experiment duration on the effect size (Hedge's *d*) from continuous random effect weighted meta-analysis.

	Response traits	df	Slope	F ratio	*P*-value
OA	Calcification	30	0.0737418	8.591	**0.007***
	Cellular·molecular	34	0.0803456	0.873	0.357
	Photosynthesis	229	0.0163391	2.014	0.157
	Growth	94	−0.0111596	1.285	0.260
	Pigment	51	−0.2304979	11.369	**0.001***
UV	Calcification	30	0.0374882	4.978	**0.034***
	Cellular·molecular	34	0.0369586	0.356	0.555
	Photosynthesis	229	−0.0041168	0.106	0.745
	Growth	94	−0.0232055	3.312	0.072
	Pigment	51	−0.0402106	0.507	0.480
OA × UV	Calcification	30	−0.008908	0.473	0.497
	Cellular·molecular	34	−0.055045	0.410	0.526
	Photosynthesis	229	−0.002959	0.052	0.820
	Growth	94	−0.006632	0.460	0.500
	Pigment	51	−0.002221	0.002	0.968

The numbers in bold and with asterisks represent significance at $p < 0.05$.

photoprotective role played by the coccolith (Gao et al., 2009; Xu and Gao, 2012). Furthermore, UV could induce the expression of defense genes in phytoplankton, activating antioxidant systems and photorepair processes (Häder et al., 2007). Calcification may serve as a defense strategy under UVR exposure since UV photoreceptors can trigger photoprotective processes (Ramos et al., 2012; Wu et al., 2012). In addition, UVR was shown to stimulate synthesis of periplasmic proteins (Wu and Gao, 2009) and up-regulate carbon concentration mechanisms (CCMs) in diatoms (Gao et al., 2021). These mechanisms are counteractive to the effects of OA, which down-regulates CCMs (Trimborn et al., 2009; Hopkinson et al., 2011; Gao et al., 2012; Liu et al., 2017). The enhanced periplasmic proteins may also play key roles in regulating the efflux and influx of protons to maintain the cells' homeostasis under OA conditions. Therefore, our study suggests that increased UV radiation may act antagonistically, thereby mitigating the deleterious effects of OA on calcification and photosynthetic processes, highlighting the importance of assessing the impacts of ocean acidification on primary producers under multiple stressor conditions.

Nevertheless, since most literatures that reported OA + UVR effects had been performed under low levels of artificial UV sources (e.g., Li et al., 2012), in situ UV levels and OA treatment may result in reduced calcification of coralline algae (Gao and Zheng, 2010) and may be responsible for the disappearance of coral reefs under ocean climate changes (Albright et al., 2018). Varied magnitudes of UVR are known to influence primary producers in different directions, i.e., stimulating effects under low- (Gao et al., 2007) but inhibiting under high exposures (Llabrés et al., 2013; Jin et al., 2017). For instance, the presence of UVR (UV-A, 19.5 W m^{-2}, UV-B 0.67 W m^{-2}) at incident solar UV levels significantly inhibited calcification of the coccolithophore *Emiliania huxleyi*, and the rates of calcification were further inhibited under OA conditions, indicating that OA exacerbated the negative effect of UVR (Gao et al., 2009). This synergistic interaction between OA and UVR was also observed in the calcifying macroalgae *Corallina sessilis*, at a UV-A level of ~20 W m^{-2} and a UV-B level of ~0.5 W m^{-2} (Gao and Zheng, 2010). The levels of UV-A and UV-B in the two studies were approximately two times higher than those used by Xu and Gao (2015), in which UV acted antagonistically with OA to stimulate the calcification of *E. huxleyi*. Therefore, we hypothesized that the antagonistic interaction between OA and UV on calcification may only occur at low or moderate levels of UVR, whereas the interaction may turn to be synergistic at high levels of UVR (Fig. 8). Since most of the experimental observations included in the present analysis did not report absolute values of UV radiation, we were unable to test such a hypothesis based on the nature of the whole dataset, however, this is worthy to be investigated in future studies. Thus, our findings emphasize the importance of investigating the concurrent impacts of OA and UVR on marine primary producers at a wide range of UVR levels, especially close to in-situ conditions.

In addition to the magnitude of drivers or stressors, the duration of experiments may also explain a significant amount of variability (Kroeker et al., 2013). For instance, it has been reported that experimental duration significantly affected the effect size of calcification in corals responding to ocean acidification (positive correlation) (Kroeker et al., 2013). Similarly, we detected that the magnitude of response of algal calcification to OA or UV alone were dependent on experimental duration (Fig. 5). The sensitivity of calcification to experimental duration was doubled in response to OA alone (slope: 0.074) compared with UV alone (slope: 0.037). The positive correlation suggests that the negative effects of OA on calcification may be mitigated by increasing experimental duration. Consistently, this contrasting response of calcification to short- and long-term OA conditioning was also observed in some previous experimental studies. For example, while the short-term OA exposure led to a decrease of calcification by ~30% in the cold-water coral *Lophelia pertusa*, it was capable to acclimate to long-term (6 months) OA exposure, resulting in slightly enhanced rates of calcification (Form and Riebesell, 2012). This response was also true for the planktonic calcifying species *Emiliania huxleyi*, in which the calcification was partly restored (up to 50%) after evolving to OA conditions for ~500 generations (~320 days) (Lohbeck et al., 2012). Mechanically, because of the short generation time, high population densities, and standing genetic variation of microalgae, they have a high potential to promote swift evolutionary responses to OA (Jin et al., 2013; Hutchins et al., 2015; Li et al., 2017), resulting in conversed responses of calcification to OA. Therefore, the findings obtained from the present study emphasize the general need for testing the biological responses of organisms in long-term experimental evolution research.

It is worth noting that any of the adaptations always come with costs, and such trade-offs have been reported in a large body of literature (e.g., Jin and Agustí, 2018; Aranguren-Gassis et al., 2019; Lindberg and Collins, 2020; Zhong et al., 2021). Therefore, we hypothesized that the negative responses of pigments to experimental duration in response to OA alone may be due to the trade-offs between calcification and pigmentation. The underlying mechanisms of trade-offs may lie in the myriad of metabolic and physiological pathways within the organisms. While more energy and resources were allocated to the adaptations of calcification to OA with increasing experimental duration, less may have been allocated to other metabolic processes, such as pigment synthesis. In line with this hypothesis, it has been reported that the increased calcification of the brittle star *Amphiura filiformis* under OA condition was accompanied with increased metabolic rates and a loss of arm muscle mass (Wood et al., 2008). Hence, we emphasize that multiple response traits should be assessed for parameterizing eco-physiological responses in the context of global change.

Our results showed that photosynthetic organisms from tropical regions were more sensitive to OA or UV radiation alone, showing larger negative effect sizes compared with those from other regions (Figs. 2 & 8). However, when the organisms were exposed to OA in combination with UV, their responses appeared to be positive (Fig. 2). It is common that populations of the same species from different climatic regions differ in their ability to withstand environmental stress (Gaston et al., 2009; Bozinovic et al., 2011; Calosi et al., 2017; Vargas et al., 2017). For example, the organisms from local populations exposed to higher CO_2 levels experienced a lower mean effect when compared to those exposed to lower CO_2 levels, suggesting those organisms are more resilient to future OA conditions (Vargas et al., 2017), though the

Fig. 7. The effect of experiment duration (days) on the effect size (Hedge's *d*) of ocean acidification (OA) (a, d, g, j, m), ultraviolet radiation (the data of UV-A, UV-B and UVR were pooled together) (b, e, h, k, n) and their interaction (c, f, i, l, o) in various response categories. a–c: calcification; d–f: cellular/molecular; g–i: growth; j–l: photosynthesis; m–o: pigment. The data were fitted with linear regressions.

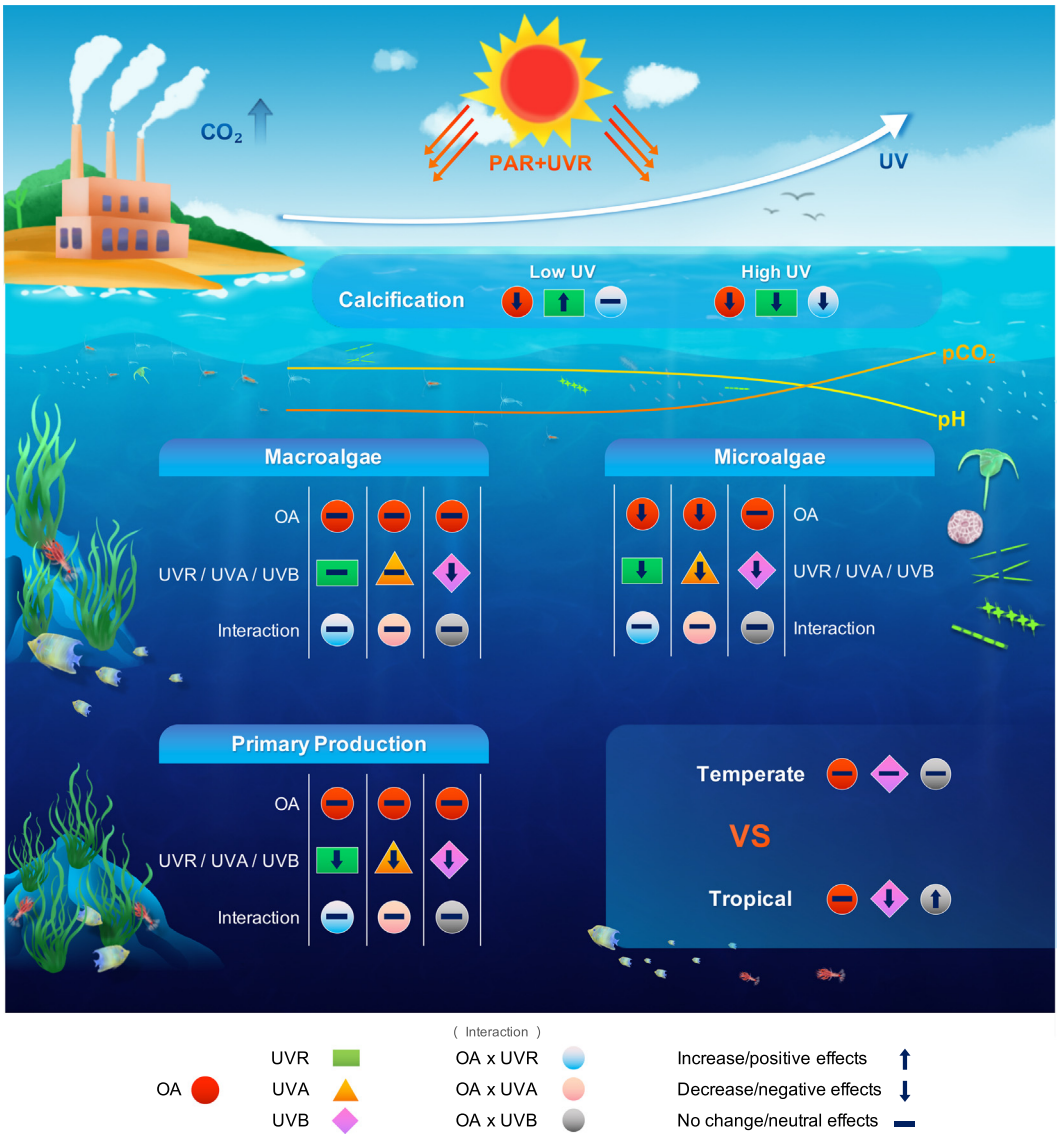

Fig. 8. Conceptual diagram illustrating the effects of ocean acidification (OA, red cycle), ultraviolet-A radiation (UV-A, yellow triangle)/ultraviolet-B radiation (UV-B, purple diamond), and their combination on marine primary producers based on the meta-analysis results as shown in the various figures of our study. The arrows indicate the direction of change.

abundance of benthic primary producers decreases toward the center of CO_2 vents (Agostini et al., 2018; Hall-Spencer and Harvey, 2019). This would also explain the findings obtained from the present study, in which the organisms from polar regions had lower effect size than those from tropical regions, as the acidification rate in polar regions is much more rapid than in temperate or tropical regions (Qi et al., 2017). In contrast, organisms in tropical regions, where UV levels are much higher than in temperate or polar regions, exhibited larger effect sizes.

Because of the nature of the meta-analysis dataset (i.e., we only included studies examining the interactions of OA and UV, while studies investigating the individual effects of each were excluded), our results showed no significant effects of individual OA or its combination with UVR on photosynthesis/growth of marine primary producers (Fig. 8). This is contrary to most previous studies, in which OA had positive effects by enhancing growth of coastal diatoms and macroalgae adapted to fluctuating diel pH, which potentially enhanced their contribution in carbon sequestration in coastal waters (Gao et al., 1993; Li et al., 2016; Zweng et al., 2018; Cornwall and Hurd, 2020). However, OA is supposed to decrease pelagic primary productivity, especially in oligotrophic waters (Gao et al., 2012; also see the review by Gao et al., 2019 and literature therein). These discrepancies suggest that the effects of OA on primary productivity might be buffered or amplified by other environmental factors, hence we propose that it is moreover critical to determine the responses of marine primary productivity to OA in the presence of multiple environmental change drivers in the context of global change.

Due to reduced emissions of chlorofluorocarbons (CFCs) in the last two decades, stratospheric ozone levels are expected to recover back to 1960s levels by the year 2100 (Barnes et al., 2019). However, since global warming is suggested to accelerate ozone depletion (Neale et al., 2021), increased UV-B irradiances at the earth's surface are being expected, especially in tropical regions until the end of this century (Bais et al., 2011; Williamson et al., 2014). In consequence, organisms from tropical regions are likely to be more influenced by UVR. Nevertheless, due to the counteractive effects of OA and UV on most primary producers as reflected in this meta-analysis, the combined effects of these two drivers may differ among different regions. In conclusion, our results highlight the importance of investigating biological responses of organisms to altered environmental conditions across geographic locations.

Our synthesis of published experimental information evaluated the interactions of OA and UV, and revealed that the frequency of interaction types was explained by cell volume, with a higher proportion of multiplicative interactions (45%) in large microalgae cells ($\log_{10}$ cell volume (μm^3) > 3) compared with those of smaller ones ($\log_{10}$ cell volume (μm^3) < 2) (18%). This finding indicates that the cumulative effects of OA and UV might be more difficult to predict for pelagic waters than for coastal regions because open ocean waters are dominated by small phytoplankton species. In most pelagic regions, nutrient availability is low, so that the capacity of phytoplankton to repair UV-induced damages using nutrients-requiring repair mechanisms is limited (see the review by Gao et al., 2019 and literatures therein). Therefore, more adverse impacts of OA + UV would be expected in these waters. While ocean warming is predicted to lead to a further expansion of picophytoplankton (Morán et al., 2010; Flombaum et al., 2013; Chen et al., 2014; Nagelkerken and Connell, 2015), picophytoplankton cells are more sensitive to UVR than microphytoplankton (Jin et al., 2017), and OA + UVR impacts in pelagic oceans are of higher uncertainty, considering warming can also stimulate the repair of UV-induced damages.

To summarize, our study has revealed that although most interactions between ocean acidification and UV are additive, but in some cases, the strong power of the antagonism allows ocean acidification to act antagonistically to alleviate the negative effect of UVR. However, the frequency of multiplicative interactions, increased with increasing cell volume, indicating that the cumulative effects of OA and UV will not be easily predictable in the context of climate change. The effect size, particularly of calcification, was found to be strongly dependent on experimental duration, highlighting the need to test organisms' long-term adaption capacity to changing environmental conditions. The trade-offs associated with the adaptations of specific response traits may reduce the performance of other traits because of physiological costs incurred by compensatory processes. The variability in responses of organisms from different climatic regions may further complicate predictions of how organisms will respond to ocean acidification and elevated UV radiation levels in the future.

CRediT authorship contribution statement

PJ and JX conceptualized the study. JW, JZ and PJ acquired the data. PJ, SO, JW and JZ performed the statistical analysis. PJ and SO generated the figures. PJ drafted the manuscript, and all authors discussed and edited the manuscript.

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.

Acknowledgements

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Data archiving statement

A list of the references from which the data were extracted can be found in Supplementary Information and all the data used in the meta-analysis are provided in Table S1.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.151782.

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