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A framework for experimental scenarios of global change in marine systems using coral reefs as a case study

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Understanding the consequences of rising CO_2 and warming on marine ecosystems is a pressing issue in ecology. Manipulative experiments that assess responses of biota to future ocean warming and acidification conditions form a necessary basis for expectations on how marine taxa may respond. Although designing experiments in the context of local variability is most appropriate, local temperature and CO_2 characteristics are often unknown as such measures necessitate significant resources, and even less is known about local future scenarios. To help address these issues, we summarize current uncertainties in CO_2 emission trajectories and climate sensitivity, examine region-specific changes in the ocean, and present a straightforward global framework to guide experimental designs. We advocate for the inclusion of multiple plausible future scenarios of predicted levels of ocean warming and acidification in forthcoming experimental research. Growing a robust experimental base is crucial to understanding the prospect form and function of marine ecosystems in the Anthropocene.

1. Introduction

Rising atmospheric CO_2 will continue to alter ecosystems worldwide through concomitant global warming and ocean acidification (OA) [1–3]. Although advances have been made in understanding the consequences of these anthropogenic drivers (e.g. [4–6]), our ability to anticipate the future of ecosystems requires quantifying responses to a palette of plausible future

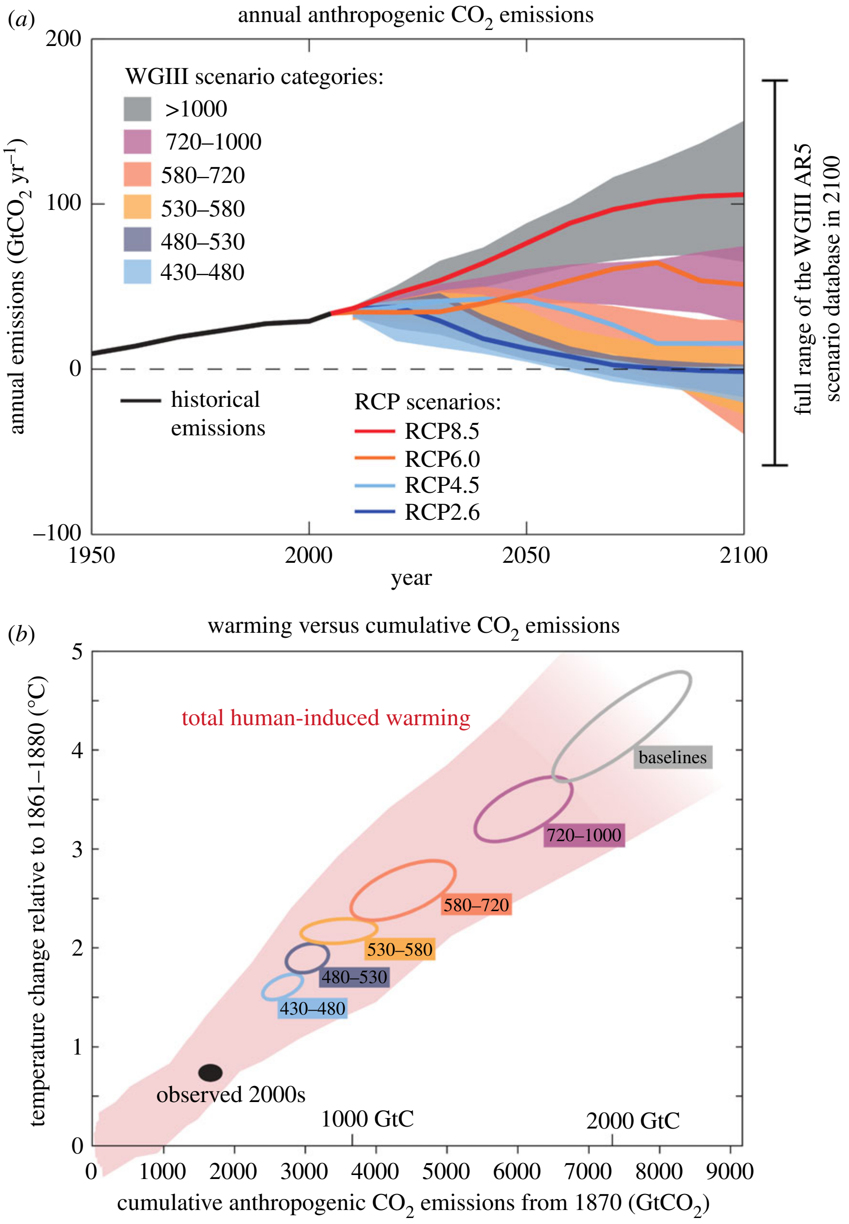

Figure 1. (*a*) The projected greenhouse gas emissions through to the year 2100 based on the four representative concentration pathway scenarios (RCPs) (*b*) and the average temperature and atmospheric CO_2 concentrations (ppm). The coloured plume shows the spread of past and future projections from a hierarchy of climate carbon cycle models driven by historical emissions and the four RCPs to 2100. Ellipses shows global warming in 2100 versus cumulative CO_2 emissions from 1870 to 2100 from respective emission scenarios. The width of the ellipses in terms of temperature is caused by the impact of different scenarios for non-CO_2 climate drivers. The filled black ellipse shows observed emissions to 2005 and observed temperatures from 2000 to 2009 with associated uncertainties. Source: Ref: [7], fig. SPM.04 in Climate Change 2014: Synthesis Report.

climate scenarios. The selection of plausible scenarios for experimental research is complicated by spatial and temporal variation, uncertainties in future CO_2 emission trajectories and associated climate sensitivity (figure 1). Such uncertainties pose a substantial challenge for researchers who must inevitably simplify expected CO_2 concentrations and temperature in their experimental designs.

The consideration of local, baseline variation when determining ambient and future experimental levels is optimal [8–10]. However, local characteristics are often unknown probably because of the significant resources needed to measure them, particularly CO_2 and researchers should be aware of databases that collate relevant datasets (e.g. The Surface Ocean CO_2 Atlas and the Global CO_2 Time-Series and Moorings Project). The limited availability of local data and the need for a framework on how to choose experimental levels is highlighted by a review of temperature and CO_2 experiments along the west coast of the USA, which found that 80% and 13% of the studies gave no rationale for temperature and CO_2 levels, respectively [8]. In addition, 45% of OA studies used mean surface global Intergovernmental Panel on Climate Change (IPCC) values for CO_2 levels, while 31% of experimental CO_2 levels were based on a combination of region models, local field data and IPCC projections [8]. Arguably, the need to understand the response of communities to environmental change is great enough to necessitate experiments even if local environmental characteristics are unknown. Although the IPCC assessments and the European Project on Ocean Acidification (EPOCA) report provide comprehensive information and future projections [7,11,12], we lack a parsimonious framework to guide scientists in the selection of experimental levels of projected CO_2 and warming. Here, we summarize current uncertainties in CO_2 emissions trajectories and provide a parsimonious framework that includes a comprehensive set of plausible CO_2 and warming scenarios, with the aim to aid in the design of climate change experiments when local characteristics and future projections are lacking.

2. Plausible future scenarios and associated uncertainties

The IPCC assessments provide estimates and associated uncertainties of future CO_2 concentrations and temperatures including representative concentration pathway scenarios (RCPs; figure 1). RCPs include an ambitious mitigation scenario (RCP2.6), two scenarios (RCP4.5 and 6.0) representing moderate reductions in CO_2 emissions [13] and a 'business-as-usual' scenario based on the absence of future efforts to reduce emissions (RCP8.5). CO_2 emissions and observed global warming, combined with projected trajectories in all RCPs towards the year 2100, depict a strong relationship between global cumulative CO_2 emissions and warming for both the global mean and for ocean surface temperature (figures 1*b* and 2*a*).

The most optimistic mitigation scenario (RCP2.6) relies on a rapid reduction in CO_2 emissions to reach net-zero greenhouse gas emissions (GHGs) towards the year 2080, in accordance with the Paris Agreement [7]. RCP2.6 restricts increases in atmospheric CO_2 concentrations to between 144 and 194 ppm and +1.6°C for the years 2081–2100 relative to pre-industrial values ([9], fig. 2.5b). Yet, recent assessments still estimate a median warming of +2.6 to +3°C, implying that a substantial (and unlikely) reduction in emissions is required to restrict warming to below +2°C [15]. For this reason, RCP4.5 and 6.0 (RCP6.0 equating to an increase of 351 ppm CO_2 and +2.8°C for the years 2081–2100 relative to pre-industrial values) are probable and warrant inclusion when selecting experimental treatments ([7], fig. 2.5b). Although efforts will hopefully be taken to reduce CO_2 emissions, the experimental evaluation of outcomes under the baseline scenario RCP8.5, corresponding to an increase of 614 ppm CO_2 and +4°C for the years 2081–2100 relative to pre-industrial values ([7], fig. 2.5b), is consistent with emission trajectories. Recent advances regarding uncertainties in climate sensitivity and concentrations of other GHGs suggest that ranges of CO_2 at +2°C may be underestimated by some commonly used models (e.g. CMIP5 ensemble), and that the 5 and 95 percentiles of current models for global increases in CO_2 concentrations at +2°C above pre-industrial levels are 143 and 820 ppm, respectively [16]. Given the uncertainty of atmospheric CO_2 trajectories (figure 1), we suggest there is a clear need to explore the ecological consequences of all RCPs.

A potential complication for marine scientists is that the majority of the IPCC data provides global surface projections, but the ocean is warming slower than land [17] (figure 2*a*). Within the IPCC reports, projections of CO_2 content and warming for the global ocean are limited relative to those that apply to the atmosphere. However, we extracted the mean temperature projections for the four RCPs towards the end of this century based on the mean of the three main ocean basins ([7], table SM30–4; figure 1*a*). Future oceanic CO_2 values are needed given that marine values often deviate from atmospheric CO_2 values [18] (figure 2*a*). The IPCC's regional projections exclude polar areas, which is notable given that the Arctic is warming two to three times faster than the global average [19,20]. In this study (and from now on), we focus on the marine-only projections, unless otherwise noted.

3. Framework for designing research on future warming and elevated CO_2

We present a framework for designing experiments to assess the responses of marine biota to future climate scenarios that encompasses a range of scenarios considered in the IPCC projections (figures 1 and 2*a*). As a case study, we use the database of experimental warming and OA experiments for coral reef ecosystems provided by Hughes *et al.* [14] to compare the temperature and pCO_2 manipulations reported in the literature to the range of possible scenarios (figure 2*c*,*d*). In this case, approximately one-fourth of warming levels employed (24%; figure 2*b*) fell within scenarios (less than or equal to 2.79°C, RCP8.5). We based this assessment on levels of ocean warming expected from recent temperatures (i.e. ambient,

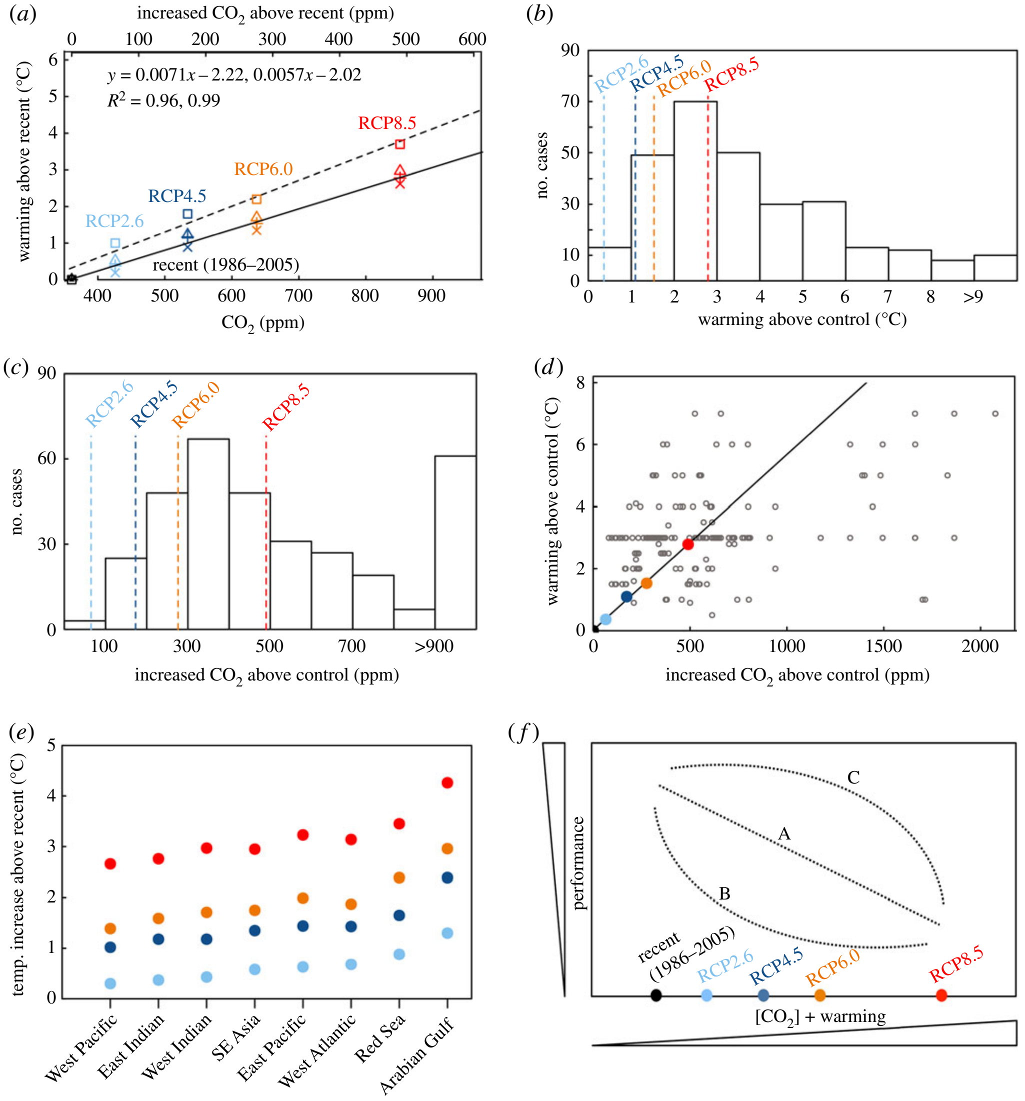

Figure 2. Climate change and experiments. (*a*) The linear relationship between projected global atmospheric CO_2 concentrations (squares and dashed line) and surface temperatures of the world (solid line) and oceans (Atlantic, triangles; Pacific, crosses; Indian, x marks). Data for panel (*a*) was extracted from fig. 2.5b and table SM30-4 of SPM, IPCC report [7]. Symbols indicate projected values for the end of the twenty-first century under each RCP. The frequency of (*b*) temperature and (*c*) CO_2 levels used to experimentally simulate warming and acidification in coral reef research. Data for panels (*b,c*) were obtained from the electronic supplementary material, tables S1 and S2 of [12] and data we added (RCP overlay assumes control of recent CO_2, 361 ppm; electronic supplementary material, S4). (*d*) Relationship between levels of warming and elevated CO_2 within dual-stressor treatments of coral reef research [14], and the linear relationship between projected oceanic CO_2 concentrations and increases in ocean temperature from (*a*). (*e*) Region-specific temperature increases expected for eight major coral reef provinces for the years 2010–2099 under RCPs ([7], table SM30-4, Ch. 30SM). (*f*) Theoretical performance of marine organisms to an experimental gradient of dual climate change stressors (CO_2 concentrations and warming) using a continuous scale, where A represents a linear decrease in performance, while B and C represent two of many potential nonlinear responses. The diagram in (*f*) represents a negative effect of stressors, but both null and positive effects are also possible. Colours in all panels represent values projected (surface ocean mean for *b*–*d*) under RCP2.6 (light blue), RCP4.5 (dark blue), RCP6.0 (orange) and RCP8.5 (red). Data is provided in the electronic supplementary material, S1–S4.

current-day conditions) as most studies in this dataset were conducted post year 2000. However, Hughes *et al.* [14] assessed whether warming levels in these studies aligned with those expected from pre-industrial temperatures levels, highlighting the need to distinguish between increases from current conditions versus pre-industrial levels in experimental studies. To assess the difference between experimental and control pCO_2, we revisited references provided by Hughes *et al.* as their data only included levels for future treatments (control pCO_2 is included in the electronic supplementary material, S4). Approximately 57% of the studies used elevated pCO_2 concentrations that were within RCP scenarios (less than or equal to +490 ppm, RCP8.5; figure 2*c*). This suggests that the majority of studies are assessing impacts within expected scenarios, although there remain many studies (43%) that may be overestimating the consequences of OA. For other marine biomes, it is probable that experimental designs may also require prompt assessment, and future reviews that quantify experimental treatments are warranted.

Projected increases in CO_2 and temperature are correlated at broad-scales (figures 1*b* and 2*a*). However, the majority of coral reef studies from Hughes *et al.* [14] (62%) that aimed to simulate future ocean warming and OA manipulated these drivers independently (figure 2*d*). Of the remaining studies that assessed the drivers concomitantly (38%), most levels of warming and elevated pCO_2 within dual-stressor treatments deviate from the linear relationship between CO_2 concentrations and warming (figure 2*d*). Although this may reflect variability associated with local characteristics, existing reviews indicate the majority of studies do not base experimental levels on local conditions [8]. Ecologists may consider shifting their experimental designs to a gradient approach that explores a range of CO_2 and warming conditions given that responses are possibly nonlinear [8,12,18,21–24] (figure 2*f*). Nonlinear responses could also result in null effects or positive effects (not shown in figure 2*f*). Theoretical predictions have been made to estimate the nature of biotic responses to the dual stressors along a continuous gradient [25,26] and although full factorial experiments remain critical [27,28], experimental data of biota responses over a continuous scale of climate change scenarios are needed.

We recognize our proposed framework probably oversimplifies the CO_2 and temperature regimes that vary locally, but accurate characterizations of local and regional variability are currently rare, especially for pCO_2 concentrations [29]. As we move forward to characterize and understand drives of high-frequency temperature and CO_2 regimes in coastal systems, this framework could be used to complement baseline observations. This is especially vital for future research focusing on coastal marine habitats that already experience temperatures or pCO_2 levels considerably higher than large-scale means or future projections. Large local variation can result from *in situ* biological processes [30–33], watershed characteristics [34–36] and upwelling [37].

4. Regional-specific climate change

Global projections of OA and warming may not represent specific systems and choosing levels for experimental research warrants consideration of projections specific to the geographical location being studied [38]. For instance, global average temperature estimates can be greater than future temperature increases in the ocean as well as in specific ocean provinces, and experiments should account for region-specific heterogeneity [14] which is summarized for eight major coral reef provinces (figure 2*e*). Fine-scale projections of future temperatures for each RCP are also available as global layers (approx. 10 km grid of globe, http://www.bio-oracle.org/) [39]. Measures and projections of local CO_2 regimes are scarce because pCO_2 levels vary considerably from atmosphere levels because of community metabolism [40], local geology [36] or upwelling [37], and researchers often need find an alternative method to determine experimental levels. *In lieu* of such information, our framework could be used to obtain a proxy of ΔCO_2 based on the linear relationship with temperature (figure 2*a*). For example, in the case of coral reef provinces, the possible range of end-of-century warming and ΔCO_2 that would need to be explored spans from 1.5°C to 4.5°C (relative to pre-industrial) and from 144 to 614 ppm, respectively (figure 2*d*). The IPCC provides comprehensive temperature projections for the near- (years 2010–2039) and long-term (years 2010–2099) scenarios for most marine regions ([7], table SM30–4, Ch. 30SM).

5. Comparison to published experimental suggestions

The EPOCA [11,12] suggested several levels of CO_2 for the design of experiments testing OA. They suggest 280 ppm (pre-industrial), 385 ppm (present day), 750 ppm (moderate prediction) and then include 1000 ppm (high prediction) and more increments in between these values if possible [12]. We make similar suggestions based on different RCPs (global mean), which includes 360, 430, 530, 640 and 850 ppm, corresponding to recent (1986–2005), and RCPs 2.6, 4.5, 6.0 and 8.5. We provide suggestions on how to manipulate concomitant temperature and CO_2, which is not provided by EPOCA but highly relevant under current and future climate change conditions [9,10].

Few reviews have assessed whether experimental treatments are tailored to plausible future climate conditions. Exceptions include a review of empirical studies that simulated global warming and OA on coral reef organisms [14] and on species in upwelling coastal systems along the USA west coast [8]. Hughes *et al.*'s [14] recommendations for forthcoming experiments of warming and OA focused on the global surface mean (both land and oceans) that relied on a rapid transition to net-zero GHGs [41] and restraining global warming to less than +2°C (approx. 410–420 ppm atmospheric CO_2) [14]. These calculations were based on equilibrium climate sensitivity [41], which is generally intended as benchmarks for comparing the magnitude of climate response projected by climate models [42]. We advocate for the preferential use of RCPs, as adopted by the IPCC [7], for estimating future CO_2 concentrations and warming. IPCC scenarios indicate that a +2°C (1.4 above current 1986–2005 levels) increase in global mean temperature (relative to pre-industrial) corresponds with a mean increase in atmospheric CO_2 concentration of +234 ppm to approximately 520 ppm (figure 2*a*), some 100 ppm greater than suggestion by Hughes *et al.* [14]. If focusing on marines systems, a +1.4°C increase above current levels corresponds with an atmospheric concentration of approximately 705 ppm (figure 2*a*). Reum *et al.* [8] provide two insightful frameworks for determining levels of experiments that manipulate temperature and CO_2. The first used three temperature levels based on local measures and two CO_2 levels based on IPCC future ocean surface CO_2 (390 and 788 ppm). The second uses local measures of both temperature and CO_2 with future CO_2 levels based on present-day local measures and future dissolved inorganic carbon estimates. Their framework is very useful when local characteristics are available. However, some researchers will need to determine levels for experiments manipulating temperature and CO_2 when knowledge of local characteristics is lacking. Our framework provides a starting point and location of pertinent information.

6. Baselines in climate change experiments

A reoccurring issue, which seems to be overlooked by many climate change researchers, is whether experimental manipulations are based on increases from pre-industrial or present conditions. For instance, the degree of warming projected in the RCPs are typically values relative to the years 1850–1900, and given that the globe (on average) has already warmed by approximately 0.88°C, +2.4°C warming projected in RCP4.5 would equate to a global increase of approximately 1.52°C from current conditions. What might come across as an obvious and simple concept, may be unnoticed in the manipulation of experimental treatment levels for warming where researchers apply levels of warming projected in RCPs to current conditions, inadvertently treating ambient conditions as those of the pre-industrial era.

7. Conclusion

Given that time series of local temperature and CO_2 concentration are often lacking and the substantial uncertainties in future projections and climate sensitivity, we propose that a slate of likely climate change scenarios need to be explored in experiments to provide a 'covering all bases' approach to understand future marine ecosystems. Although we primarily focused on the ocean, much of the discussion and framework could also apply to terrestrial and freshwater ecosystems. Conducting experiments that replicate local, baseline variation alongside future scenarios necessitates complicated logistical efforts and significant resource investments, especially when dealing with CO_2. We hope recommendations provided here enhance the accuracy of future studies and initiate discussion among researchers to improve the exploration of the future performance of biota in the Anthropocene.

Data accessibility. Data for this article are in the electronic supplementary material.
Authors' contributions. N.R.G., S.G.K., A.A. and C.M.D. conceived the study. N.R.G., S.G.K. and A.A. collated data and N.R.G. created the figure. N.R.G. and S.G.K. wrote the initial draft of the manuscript, while all authors contributed to editing of the manuscript. All authors gave final approval for publication.
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