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REVIEW

A decade of climate change experiments on marine organisms: procedures, patterns and problems

THOMAS WERNBERG*†, DAN A. SMALE* and MADS S. THOMSEN*

UWA Oceans Institute and School of Plant Biology, University of Western Australia, 35 Stirling Highway, Crawley, 6009, WA Australia, †Australian Institute of Marine Science, 39 Fairway, Crawley, 6009 WA, Australia

Abstract

The first decade of the new millennium saw a flurry of experiments to establish a mechanistic understanding of how climate change might transform the global biota, including marine organisms. However, the biophysical properties of the marine environment impose challenges to experiments, which can weaken their inference space. To facilitate strengthening the experimental evidence for possible ecological consequences of climate change, we reviewed the physical, biological and procedural scope of 110 marine climate change experiments published between 2000 and 2009. We found that 65% of these experiments only tested a single climate change factor (warming or acidification), 54% targeted temperate organisms, 58% were restricted to a single species and 73% to benthic invertebrates. In addition, 49% of the reviewed experiments had issues with the experimental design, principally related to replication of the main test-factors (temperature or pH), and only 11% included field assessments of processes or associated patterns. Guiding future research by this inventory of current strengths and weaknesses will expand the overall inference space of marine climate change experiments. Specifically, increased effort is required in five areas: (i) the combined effects of concurrent climate and non-climate stressors; (ii) responses of a broader range of species, particularly from tropical and polar regions as well as primary producers, pelagic invertebrates, and fish; (iii) species interactions and responses of species assemblages, (iv) reducing pseudo-replication in controlled experiments; and (v) increasing realism in experiments through broad-scale observations and field experiments. Attention in these areas will improve the generality and accuracy of our understanding of climate change as a driver of biological change in marine ecosystems.

Keywords: ecological experiments, environmental change, global warming, ocean acidification, weighted evidence approach

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Introduction

Climate change is likely to have widespread and severe ecological and socio-economic implications (Harley *et al.*, 2006; Poloczanska *et al.*, 2007; Rosenzweig *et al.*, 2007; Hoegh-Guldberg & Bruno, 2010; Wernberg *et al.*, 2011a). Consequently, considerable policy and management attention is being directed towards curbing potential impacts and associated costs. Successful attribution, management and mitigation of environmental impacts are contingent on rigorous scientific evidence for the underlying drivers of change (Underwood, 1996; Sutherland *et al.*, 2004). Indeed, a lack of strong cause–effect relationships was (and may still be) at the core of scepticism of attributing ecological changes to climate change (Jensen, 2003). With the increasing need for a mechanistic understanding to underpin predictions of how the physical forcing of climate change might translate into impacts in the biological world, the new millennium saw a rapid, almost exponential, increase in the number of studies on the effects of climate change on organisms in both terrestrial and aquatic ecosystems (e.g. Harley *et al.*, 2006; Hoegh-Guldberg & Bruno, 2010; Brown *et al.*, 2011).

Providing >60% of the value of ecosystem services derived from nature (Costanza *et al.*, 1997), the marine biome is extremely important to humans. Although evidence and attribution is lacking far behind that from the terrestrial sphere (Richardson & Poloczanska, 2008; Rosenzweig *et al.*, 2008), there is scientific consensus that recent anthropogenic climate change has impacted marine ecosystems, and that impacts will intensify and become more widespread in the future (Harley *et al.*, 2006; Poloczanska *et al.*, 2007; Hawkins *et al.*, 2008; Hoegh-Guldberg & Bruno, 2010; Wernberg *et al.*, 2011a). The changes currently in progress will likely create physical and biological conditions not previously experienced in the evolutionary history of most organisms (e.g. Hoegh-Guldberg *et al.*, 2007; Kordas *et al.*, 2011).

Correspondence: Thomas Wernberg, tel. + 61 8 6369 4047, fax + 61 8 6488 1001, e-mail: thomas.wernberg@uwa.edu.au

These novel environments and ecological interactions imply that we cannot rely solely on modelling the past to predict the future: climate change experiments will continue to play a critical role in defining the understanding of how physical climate change is likely to drive biological changes (Benton *et al.*, 2007). It is therefore important that future experiments address knowledge gaps and provide the strongest possible inferences. However, the inaccessibility of the marine environment, in combination with its biophysical properties, presents great challenges to experimental scientists, and potentially imposes strong limitations on inferences that can be derived from their studies. Here, we review marine climate change experiments (hereafter MCCEs) from the first decade of the new millennium to identify what physical drivers have been tested, what kinds of species and environments have been targeted in these tests, and whether there have been any general issues relating to their experimental design. By taking stock of the breadth of experimental studies, and providing an inventory of their current strengths and limitations, we aimed to identify procedural efforts that would strengthen the mechanistic understanding of how climate change will affect marine organisms.

Methods

We searched the ISI databases (Web of Science, Current Contents), Google Scholar and reference lists for peer-reviewed papers published from 2000 to 2009, which made an explicit reference to climate change as part of the rationale for their study. Our search terms included combinations of 'marine', 'climate change', 'global warming', 'ocean acidification', 'temperature', 'carbon dioxide', 'experiment' and 'manipulation'. Additional papers were sourced by cross/back referencing. Limiting our review to the first decade of the millennium was a pragmatic decision to confine our searches. However, this time-period captures the onset of a substantial experimental climate change research effort and therefore also includes the vast majority of experimental climate change studies to date (Harley *et al.*, 2006; Hoegh-Guldberg & Bruno, 2010; Brown *et al.*, 2011; Fig. 1a). We focused on papers which reported manipulative field and laboratory experiments involving climate change variables (temperature, pCO_2/pH, or other factors argued by the authors to be climate change related, e.g. UV, sea level rise, storminess) and measured responses at the individual, population or community level. Studies on whole-organism physiological responses (e.g. metabolism, growth and calcification) were included, but biochemical responses at the organ, cell or subcellular level (e.g. acid-base chemistry, heat-shock proteins or gene expression) were not, primarily because of uncertainties with extrapolating biological responses beyond the individual organisms. We focused on experimental studies because these are necessary to establish mechanistic cause–effect relationships (Underwood, 1985, 1996; Sutherland, 2006; Benton *et al.*, 2007), and because procedural aspects of correlative time-series analyses have recently been reviewed (Brown *et al.*, 2011).

To assess the overall quality and interest in MCCEs we tested if these were published in journals with higher impact factors than marine studies in general. To do this, we compared the median 5-year impact factor (more consistent than annual impact factors) of journals publishing MCCEs to the median 5-year impact factor of journals listed under the '*Marine and Freshwater Biology*' subject area on the ISI Web of Science (n = 83, ISI Journal Citation Reports, 1 September 2010). Differences in medians were tested by a Mann–Whitney–Wilcoxon rank sum test.

All papers were classified according to broad categories describing which climate variables were manipulated (Fig. 2a), the climate affinity of the targeted biota (Fig. 2b), the type of organisms (zooplankton included only holoplanktonic species, whereas larval stages of benthic invertebrates and fishes were considered under these categories, respectively) (Fig. 2c), and the level of ecological organisation (Fig. 2d). Collectively, the classes under these four categories provide a coarse overview of potential biases in the experimental evidence for key ecological subjects. For each category, a χ^2-test tested if the frequency of studies was equal across all

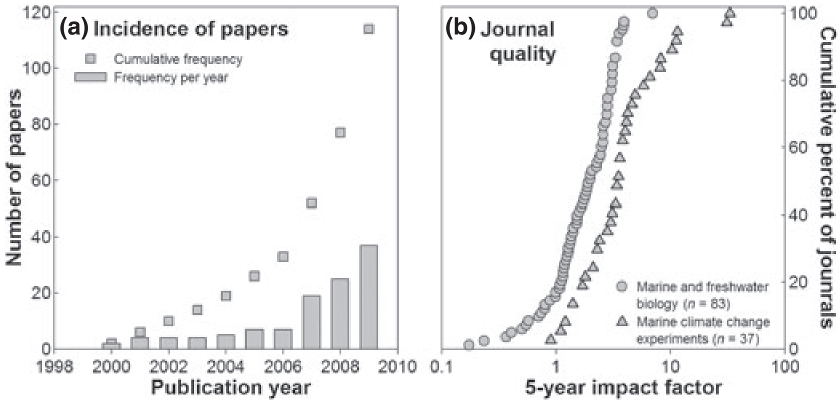

Fig. 1 (a) Frequency of Marine Climate Change Experiments each year, and (b) cumulative frequency of 5-year impact factors for journals in Marine and Freshwater Biology and journals publishing Marine Climate Change Experiments.

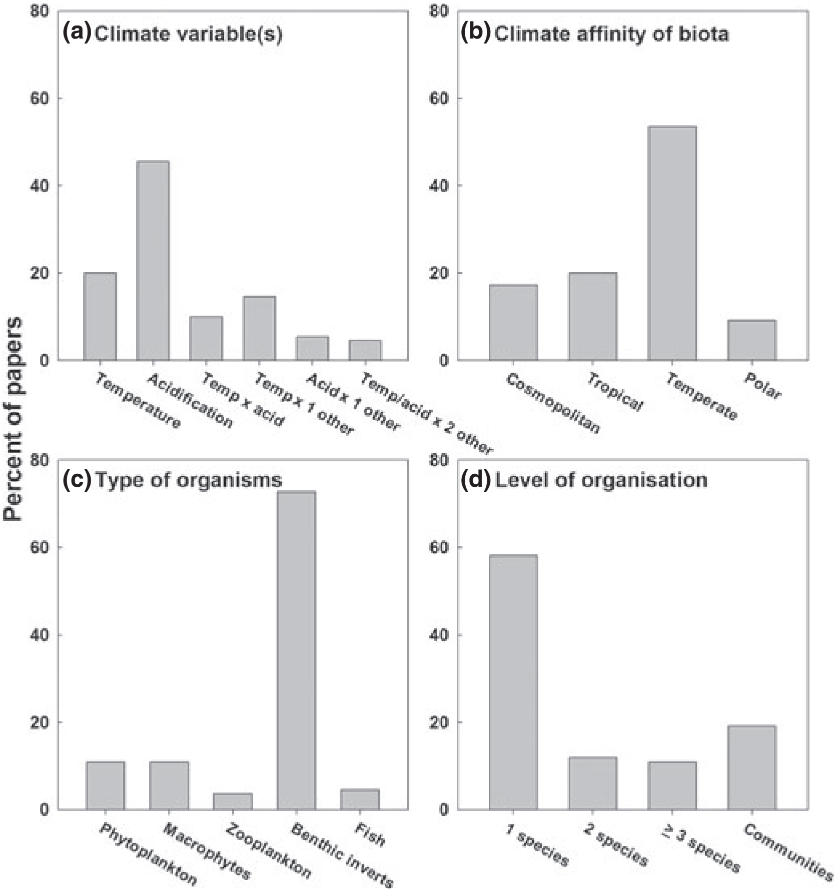

Fig. 2 Characteristics of experimental marine climate change studies (n = 110 papers). Classification of experimental studies according to (a) the climate variables tested; (b) the climate affinity of the study organisms; (c) the type of organisms (experiments including several types were counted more than once), and (d) the number of organisms included. All papers and their classifications are listed in Table S1. Acidification includes all pCO_2 experiments.

classes. In addition, it was noted whether the studies were laboratory-based or included field components, and if there were identifiable issues associated with the experimental procedures that potentially could weaken causal inferences (e.g. pseudo-replication, Hurlbert, 1984) (Table S1).

Results

Our searches returned 110 papers, and we believe that this is a near-complete list of all marine climate change experiments published during the period 2000–2009 (Table S1). The incidence of MCCEs increased consistently every year throughout the period from two papers (1.8%) in 2000 to 37 papers (32%) in 2009 (Fig. 1a). The 110 papers were published in 37 different journals (Table S1). The median 5-year impact factor of journals publishing MCCEs (IF5 = 3.50) was significantly higher than for journals in Marine and Freshwater Biology in general (IF5 = 1.99) ($W_{83,37}$ = 3036, P < 0.0001) (Fig. 1b).

Marine climate change experiments in the first decade of the millennium were dominated by single-factor manipulations of warming or acidification (collectively, 65% of all MCCEs), whereas experiments manipulating two (30%) or more (<5%) factors were significantly fewer (Fig. 2a, χ^2 = 79.8, P < 0.0001). Studies on temperate organisms (54%) were 3–6 times as prevalent as studies on polar, tropical or cosmopolitan organisms (Fig. 2b, χ^2 = 53.7, P < 0.0001). Animal studies accounted for 81% of all experiments, and were dominated by studies of benthic invertebrates, with zooplankton and fish being least studied (Fig. 2c, χ^2 = 189.4, P < 0.0001). Primary producers were considered in 22% of the studies, with an equal proportion of experiments on phytoplankton and macrophytes (Fig. 2c). Fifty-eight percent of the experimental studies quantified climate change effects on single species, with 19% of studies quantifying impacts at the community level (Fig. 2d, χ^2 = 67.1, P < 0.0001). The majority of MCCEs were tests of effects among categorical treatments (typically with 2–3 levels of a climate change driver). About half (49%) of the MCCEs had identifiable issues with their experimental procedures (Table S1), and of these studies, a lack of treatment replication or various kinds of pseudo-replication were most prevalent (91%), but there were also examples (9%) of extreme treatments with manipulations of temperature or pH far beyond projections for the coming century (Table S1). The majority of MCCEs were small-scale laboratory or enclosure-based experiments conducted under highly controlled conditions; only 11% of studies included a field assessment of processes or associated patterns (Table S1).

Discussion

Global climate change is one of the most pervasive human transformations of the Earth, and it represents one of the greatest threats to current ecological function and human socio-economic interests (Rosenzweig *et al.*, 2007). This relatively recent realisation led to a rapid increase in the production of papers concerned with marine climate change from an average of <15 per year in the preceding two decades, to >80 per year during the first decade of the new millennium (Hoegh-Guldberg & Bruno, 2010). Studies aiming to identify climate change as a driver of marine ecological change, either through observational analyses of time-series (Brown *et al.*, 2011) or experimental manipulations of climate change factors (this study), have increased similarly, although only accounting for 18% and 13% of all marine climate change papers, respectively. It is clear that MCCEs were published in higher impact journals compared with marine studies in general. The high incidence of identifiable limitations in experimental design suggests that this publication pattern has been driven by the topicality of the subject and broad scientific interest in establishing mechanistic relationships between climate change variables and biotic responses, rather than a 'higher-than-usual' quality of the experiments. A prominent feature for all MCCE classifications was a strong dominance of a few categories (Fig. 2a–c), demonstrating that the current mechanistic evidence for possible links between climate change and ecological changes is highly biased towards a limited subset of environmental and ecological conditions.

Physical and ecological scope

Acidification experiments (>60% of MCCEs) were more common than temperature experiments (~40%), and this is interesting because the evidence for physical change and ensuing biological consequences is much stronger for ocean warming than for ocean acidification (Harley *et al.*, 2006; Poloczanska *et al.*, 2007; Hawkins *et al.*, 2008; Rosenzweig *et al.*, 2008; Wootton *et al.*, 2008; Wernberg *et al.*, 2011a). The 'over-representation' of acidification experiments probably reflects the fact that ocean acidification is a novel, climate change-specific stressor, whereas temperature is a well-known driver of species distributions and interactions (Clarke & Gaston, 2006; Tittensor *et al.*, 2010), where there is a large body of mechanistic knowledge not explicitly linked to climate change. Acidification clearly affects marine organisms (e.g. Hall-Spencer *et al.*, 2008; Wootton *et al.*, 2008) and the scarcity of documentation for ongoing ocean acidification and associated biological impacts probably reflects a simple lack of data (Richardson & Poloczanska, 2008; Wernberg *et al.*, 2011a). Nevertheless, in contrast to the pervasive impacts of warming, impacts of acidification are idiosyncratic: virtually, all temperature experiments showed significant effects of warming, whereas many studies of acidification showed only subtle effects and 13 (18% of all ocean acidification experiments) found no effects at all (Table S1).

Single-factor experiments accounted for as many as 65% of all MCCEs. Yet, extensive meta-analyses of both marine (Crain *et al.*, 2008) and non-marine (Darling & Côté, 2008) experiments have shown that concurrent impacts of multiple stressors are predominantly non-additive and therefore cannot be understood or predicted in isolation from one another. In addition to the multiple physical manifestations of climate change, humans also have substantial non-climate impacts on their natural environment: introduced species, eutrophication, over-fishing and sedimentation caused by dredging, land run-off and marine infrastructure are also causing dramatic impacts and global transformation (Jackson *et al.*, 2001; Lotze *et al.*, 2006; Airoldi & Beck, 2007). Clearly, impacts of climate change are not isolated from these diverse stressors or their local environmental and biological context (Wernberg *et al.*, 2011a). The 38 MCCEs testing effects of more than one factor confirm the importance of multiple concurrent stressors as at least 82% found interactive effects.

Almost 60% of all MCCEs were studies of a single species. Single-species studies cannot consider ecological effects through changes to species interactions. Yet, all single-species populations are embedded in communities of multiple interacting species where ecological effects mediated by shifts in species interactions might be as strong as, or stronger than, autecological effects driven by species tolerances (Hawkins *et al.*, 2008; Kordas *et al.*, 2011).

The overall implication of the apparent biases in physical and ecological scope of MCCEs is that we have a poor understanding of how physical and biological changes combine in their direct and indirect effects. Consequently, there is a great need for studies targeting interactions between multiple stressors and multiple species, particularly under climate change specific scenarios. To address this knowledge-gap, future experiments must include more than one test-factor and change the focus from assessing the performance of individuals (metabolism, growth, reproduction etc.) to assessing effects on species interactions such as the strength of competition, predation or herbivory. This will necessitate multispecies experiments combining currently co-occurring species as well as species that might only co-occur in the future.

Organisms and environments

Most studies tested effects on temperate species, and this probably reflects that most marine laboratories are located on temperate shores in Europe, North America and Australasia. This geographical bias is unfortunate because tropical and polar organisms are likely to be under severe threat from climate change, having adapted to climatically extreme, but relatively stable environments, where the difference between optimal and lethal conditions can be small (e.g. Peck *et al.*, 2004; Hoegh-Guldberg *et al.*, 2007). Compounding these biological limitations are physical constraints on dispersal for polar organisms which, in contrast to tropical and temperate organisms that can and do shift polewards (e.g. Parmesan & Yohe, 2003; Precht & Aronson, 2004; Greenstein & Pandolfi, 2008; Wernberg *et al.*, 2011b), have no-where to go to escape warming waters.

Benthic invertebrates such as sea urchins, mussels and crabs were by far the most studied groups of organisms, presumably because of their wide distribution, high diversity and ease of collection and experimentation. These animals have a long history as experimental models, and they continue to form the basis of our understanding of ecological response to marine climate change. However, this bias is a concern, as planktonic organisms play a crucial role in global biochemical cycles, including accounting for about half of the biosphere's primary production and exhibit high sensitivity to climate variability (Boyd & Doney, 2002; Doney, 2006). Moreover, marine macrophytes are some of the most productive primary producers in the world (Mann, 1973), and they are particularly important because of their critical contribution to the ecological function of many ecosystems through their diverse roles as the primary habitat providers, food sources and ecosystem engineers (e.g. Dayton, 1985; Wernberg *et al.*, 2005; Thomsen *et al.*, 2010). It is particularly important to understand how habitat-providing and-modifying species will be affected by climate change because habitat-mediated environmental amelioration is thought to become increasingly important to maintaining ecological function in the future (Halpern *et al.*, 2007).

It was apparent that for most organisms, only a single life stage had been considered – typically larval or juvenile stages for large organisms (e.g. fishes) and large or adult stages for organisms with very small propagules (e.g. seaweeds). However, juvenile and adult stages often have different tolerances to environmental stress (e.g. Gilman, 2006; Fredersdorf *et al.*, 2009) and without knowing which ontogentic stage is most vulnerable to a particular stressor, there is a risk of substantially under-estimating the potential ecological consequences (Russell *et al.*, 2012). Although logistically challenging, an increasing experimental effort is required for both small and large organisms (plankton, fishes, etc.) and on organisms from marginal or particularly vulnerable environments, to ensure a balanced understanding of how marine organisms might respond to climate change. Future experiments should focus on organisms that condition the existence of associated communities, and in particular on how climate change might influence the functions they provide. A focus on ecological function is particularly important where experiments and access to experimental organisms are limiting (e.g. polar regions, deep sea). Similarly, future experiments should explicitly contrast the vulnerability of different life stages to identify bottlenecks for population persistence under future environmental and biological conditions.

Experimental procedures

The physical forcing of climate change operates at regional scales, and interacts with processes at multiple spatial and temporal scales to impact local biota (Helmuth *et al.*, 2006; Wernberg *et al.*, 2011a). Global-change variables are therefore difficult to manipulate, particularly *in situ*. In the marine environment, the biophysical properties of water and the general inaccessibility of the underwater environment exacerbate these logistic constraints on experimentation. Still, experimental venue, selection of treatment levels, assignment to experimental units and the distribution of replicates among treatments (i.e. experimental design) have fundamental implications for the inferences that can be drawn from any experiment (Hurlbert, 1984; Underwood, 1997). In particular, it is critical that treatment levels capture the range and magnitude of variation that is relevant to the context, and that experimental units and replicates are independent, and integrate an appropriate level of 'random' non-treatment variation.

MCCEs had a high incidence of pseudoreplication (>40%) and this is perhaps surprising, given the strong traditions for experiments in marine ecology (Underwood, 1997) and the time since the issue was brought to the attention of ecologists (Hurlbert, 1984). However, the problem is not an isolated phenomenon of MCCEs as previous reviews of experiments in aquatic ecology have found up to 51% of experiments to be affected (Hurlbert, 1984; Hurlbert & White, 1993). Pseudoreplication is a problem because it limits the inference space and the ability to extrapolate the results. Technically, pseudoreplication covers a broad range of issues which influence the power structure of statistical tests by inflating the degrees of freedom in favour of the proposed hypothesis, thereby increasing the risk of type 1 error (Hurlbert, 1984; Hurlbert & White, 1993). Commonly this occurs by subsampling the same treatment thus failing to incorporate an appropriate amount of 'random' background variation (simple pseudoreplication) or by pooling treatments thus conflating 'random' background and 'treatment' variation (sacrificial pseudoreplication) (Hurlbert & White, 1993). Conceptually, pseudoreplication is akin to failing to incorporate autocorrelation into space- and time-series analyses, and this has been identified as one of the most prevalent issues with the analysis of observational evidence for impacts of climate change (Brown *et al*., 2011). It can perhaps be argued from a precautionary principle that pseudoreplication is not a serious problem because it implies that conclusions that climate change will have no effect are conservative. Nevertheless, it obscures an objective assessment of impact and may contribute to unnecessary spending on mitigation and adaptation.

Several MCCEs (6%) tested effects of climatic variables manipulated far beyond projections for 2100. While testing extreme values of relevant factors can be useful to delimit their impact-domain and identify worst case scenarios, or identify the impacts of discrete events such as heat waves or cyclones (reviewed in Jentsch *et al*., 2007), the outcomes of such studies are arguably of limited ecological relevance in relation to understanding impacts of overall climate change in the foreseeable future.

The overwhelming majority of MCCEs were *ex situ* studies (~90%), typically conducted in aquaria and small mesocosms. That these experiments have provided valuable information is beyond question (Benton *et al*., 2007). However, what makes these experiments useful and informative is also their Achilles heel: the confined and highly controlled nature of the physicochemical and biological environment in *ex situ* experiments reduces realism and limits the inference space to a highly artificial world (Carpenter, 1996). Species, populations and individuals in nature experience a constantly changing environment, where physio-chemical and biological influences fluctuate both predictably (i.e. over the cycle of a day or a year) and randomly. Moreover, biological communities are often connected across a range of spatial and temporal scales, which extend beyond the confines of an aquarium in a laboratory (e.g. Caley *et al*., 1996; Borthagaray *et al*., 2009). Consequently, ecological outcomes of selection and species interactions have been shown to differ fundamentally between highly controlled experiments and those with a greater similarity to natural conditions (Skelly, 2002; Van Doorslaer *et al*., 2010).

The lack of field-based MCCEs is a serious limitation because it exposes the artificial nature of the current experimental understanding. This shortcoming has undoubtedly been driven by difficulties with controlled manipulations of climate change factors *in situ*. However, other approaches such as 'opportunistic and natural experiments' (e.g. Schiel *et al*., 2004), 'comparative experiments' (e.g. Wernberg *et al*., 2010) and 'mensurative experiments' (e.g. Hall-Spencer *et al*., 2008) have long been advocated (Underwood, 1996; Menge *et al*., 2002; Dunne *et al*., 2004). Natural and opportunistic experiments can rarely be planned and are therefore not an efficient tool for systematic use in climate change studies. In contrast, comparative experiments, where identical manipulative experiments are carried out in different places characterised by different climates, are particularly useful (Menge *et al*., 2002; Dunne *et al*., 2004), especially to test how climate might modulate the impacts of additional factors (e.g. Wernberg *et al*., 2010). Comparative experiments can be criticised because they, strictly speaking, do not manipulate the climate factor and because it is impossible entirely to avoid confounding climate and non-climate factors. However, in carefully planned and cautiously interpreted experiments, this is no greater limitation to inference and extrapolation than the highly artificial conditions of enclosures and aquaria. It is important to recognise that these approaches can provide unique insights that are complementary in scope and scale to the prevalent *ex-situ* approaches, and to appreciate that even experiments with limitations on manipulation and replication *can* provide tests of hypotheses (Hurlbert, 2004). Future small-scale *ex-situ* experiments should focus on increasing their inference space through appropriate replication (i.e. avoid pseudoreplication), both in terms of the physical design of experimental units and in terms of increasing the power of subsequent analyses (see, for example, the detailed instructions in Riebesell *et al*., 2010). A more pragmatic approach is warranted for field experiments where it may be necessary to accept some level of pseudoreplication and confounding to gain the advantage of a substantially less artificial experimental venue (Hargrove & Pickering, 1992; Oksanen, 2001). In some cases, regression-based methods can alleviate difficulties of replication, and they should be used more widely in MCCEs particularly because they have the added benefit of a better parameterisation of the cause–effect relationship, which will facilitate projections into the future, with no loss of power (Cottingham *et al*., 2005) or ability to weight the relative importance of climate and non-climate drivers (see Brown *et al*., 2011 for a discussion relating to observational studies). As artificiality and limitations are inevitable, and probably more pronounced in MCCEs than in other experiments, a weighted evidence approach, where conclusions are driven by multiple pieces of independent evidence pointing in the same direction (Cleland, 2001), is a more productive approach towards understanding biological impacts of marine climate change than a quest for perfectly executed decisive experiments (*sensu* Platt, 1964).

Conclusions

Over the past decade, marine ecologists have conducted >100 experiments to establish a mechanistic understanding of how physical climate change will translate into ecological impacts. While these experiments have yielded many critical insights, it is clear that our current understanding is based almost entirely on simplified artificial model systems ruled by first-order environmental and biological effects (i.e. primary effects of a stressor on an organism as opposed to the effects that propagate from higher-order interaction webs of shifting environments and organisms). Moreover, there are striking biases in the scope of environments, organisms and levels of ecological organisation targeted, as well as limitations associated with the experimental procedures.

To strengthen the generality and accuracy of our understanding of climate change as a driver of biological change in marine ecosystems, it will be necessary for future research projects to increase the effort in five areas: (i) the combined effects of concurrent climate and non-climate stressors; (ii) responses of a broader range of species, particularly from tropical and polar regions as well as primary producers, pelagic invertebrates and fish; (iii) species interactions and responses of species assemblages; (iv) reducing pseudo-replication in controlled experiments; and (v) increasing realism in experiments through broad-scale observations and field experiments.

Where the current body of experimental evidence falls short in particular is in its integration of small-scale laboratory and broad-scale field studies. Indeed, the challenge for experimental ecologists is to provide real and realistic data that will expand the collective inference space of our mechanistic understanding of how the physical forcing of climate change translates into ecological changes. We believe, the most efficient path will be to use the entire experimental toolkit, reducing the artificiality of the experimental context by combining controlled and rigorous mesocosm and laboratory experiments (Benton *et al.*, 2007), novel field experiments (Morelissen & Harley, 2007; Smale *et al.*, 2011), with mensurative (Hall-Spencer *et al.*, 2008), comparative (Wernberg *et al.*, 2010) and opportunistic (Schiel *et al.*, 2004) field experiments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of all papers reviewed including brief results and classifications for this review.