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REVIEW

Evidence for multiple stressor interactions and effects on coral reefs

STEPHEN S. BAN*, NICHOLAS A. J. GRAHAM* and SEAN R. CONNOLLY*†

**Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, 4811 Qld, Australia,*
†School of Marine and Tropical Biology, James Cook University, Townsville, 4811 Qld, Australia

Abstract

Concern is growing about the potential effects of interacting multiple stressors, especially as the global climate changes. We provide a comprehensive review of multiple stressor interactions in coral reef ecosystems, which are widely considered to be one of the most sensitive ecosystems to global change. First, we synthesized coral reef studies that examined interactions of two or more stressors, highlighting stressor interactions (where one stressor directly influences another) and potentially synergistic effects on response variables (where two stressors interact to produce an effect that is greater than purely additive). For stressor-stressor interactions, we found 176 studies that examined at least 2 of the 13 stressors of interest. Applying network analysis to analyze relationships between stressors, we found that pathogens were exacerbated by more costressors than any other stressor, with ca. 78% of studies reporting an enhancing effect by another stressor. Sedimentation, storms, and water temperature directly affected the largest number of other stressors. Pathogens, nutrients, and crown-of-thorns starfish were the most-influenced stressors. We found 187 studies that examined the effects of two or more stressors on a third dependent variable. The interaction of irradiance and temperature on corals has been the subject of more research (62 studies, 33% of the total) than any other combination of stressors, with many studies reporting a synergistic effect on coral symbiont photosynthetic performance (n = 19). Second, we performed a quantitative meta-analysis of existing literature on this most-studied interaction (irradiance and temperature). We found that the mean effect size of combined treatments was statistically indistinguishable from a purely additive interaction, although it should be noted that the sample size was relatively small (n = 26). Overall, although in aggregate a large body of literature examines stressor effects on coral reefs and coral organisms, considerable gaps remain for numerous stressor interactions and effects, and insufficient quantitative evidence exists to suggest that the prevailing type of stressor interaction is synergistic.

Keywords: acidification, climate change, coral bleaching, coral disease, irradiance, meta-analysis, overfishing

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Introduction

Globally, biodiversity and ecosystem services are under threat from a suite of human activities (Dawson *et al.*, 2011), with climate change likely exacerbating existing stressors (Halpern *et al.*, 2008). The increased sense of urgency associated with these global threats adds to a long-standing call for a better understanding of the effect of multiple stressors on biodiversity and ecosystem function (Breitburg *et al.*, 1999). A stressor has been defined as any environmental change in a factor that causes some response by a population of interest (whether beneficial or deleterious) (Underwood, 1989); here we focus on deleterious effects at the community, population, or individual (including physiological) level, whether natural or anthropogenic in origin. However, despite the additional attention multiple stressors have received (Sutherland *et al.*, 2009; Blackwood *et al.*, 2011; Melbourne-Thomas *et al.*, 2011), our knowledge about their interactions remains nascent (Halpern *et al.*, 2008).

Much of the concern over multiple stressors stems from the potential for their combined effects to exceed their individual effects – often referred to as synergism (Folt *et al.*, 1999). If the combined effect of stressors is less than the sum of their individual effects, this is considered antagonistic. Additive effects occur when the combined effects are equal to the sum of the individual effects. Reviewing evidence for synergistic and antagonistic effects, Crain *et al.* (2008) found 202 experiments assessing direct impacts of multiple stressors in marine systems (33 of which applied to coral reefs), while Darling & Côté (2008) found 23 studies (112 experiments) across the terrestrial, marine, and freshwater ecological literature (although none pertained to coral reefs) that featured controlled factorial experiments with two stressors and mortality as the response

Correspondence: Stephen S. Ban tel. +61 07 4781 6063,
fax +61 07 4781 6722, e-mail stephen.ban@my.jcu.edu.au

variable. Both of these reviews concluded that the majority of studies investigating stressor interactions found nonadditive (i.e. either synergistic or antagonistic) effects. Crain *et al.* (2008) found synergistic effects in 36% of studies and antagonistic effects in 38%, with 26% additive. By contrast, Darling & Côté (2008) found synergistic effects in 35% of their sample and antagonistic effects in 23%, with 42% being additive. Furthermore, evidence for the existence of ecological surprises – where the behavior of a natural system sometimes drastically deviates from expectations or historic conditions – continues to mount (Lindenmayer *et al.*, 2010). In many cases, synergistic effects may have played a role in these ecological surprises (Hecky *et al.*, 2010). For example, Christensen *et al.* (2006) found that the interaction between temperature, dissolved organic carbon, and pH in temperate lakes had a positive, synergistic effect on consumer biomass, even though individually each variable exerted negative effects. In another example, Davis *et al.* (2010) found the combined effects of eutrophication, acidification, and salinization led to regime shifts between macrophyte-dominated and phytoplankton-dominated lentic (standing-water) systems.

Effective management responses to growing anthropogenic impacts on ecosystems requires an understanding of how stressors interact, and coral reefs are a particularly good example of the interplay between global and local stressors. Coral reefs are widely believed to be one of the world's most stressed ecosystems (Walther *et al.*, 2002; Hughes *et al.*, 2003; Carpenter *et al.*, 2008; Hoegh-Guldberg & Bruno, 2010), and hence understanding – and managing – multiple stressor interactions is particularly urgent. Coral reefs are also among the most biologically diverse and socioeconomically valuable biomes (Moberg & Folke, 1999), and face many natural, anthropogenic, and anthropogenically enhanced natural stresses. Identifying synergisms between stressors would allow prioritization of management to mitigate the most severe interactions, such as reducing sedimentation or fishing pressure to potentially enhance recovery from bleaching (e.g., Carilli *et al.*, 2009; Graham *et al.*, 2011), or improving water quality to enhance resistance to thermal bleaching (Wooldridge, 2009; Carilli *et al.*, 2010). Similarly, if signs or precursors of ecological surprises can be reliably detected, managers may be able to take early preventative action such as reducing fisheries catches (McClanahan *et al.*, 2011) or prohibiting fertilizer application in upstream watersheds (Brodie *et al.*, 2012). Thus, interactions of multiple stressors, and the resulting cumulative impacts, have been identified as a research priority or necessity by management and regulatory bodies (NOAA, 2012; PICES (North Pacific Marine Science Association) (2012), Great Barrier Reef Marine Park Authority, 2009; Fisheries & Oceans Canada, 2008; Council on Environmental Quality, 2005; Office of Research & Development, 2005) and researchers (Paine *et al.*, 1998; Vinebrooke *et al.*, 2004; Salbu *et al.*, 2005) alike. While the phenomenon of multiple stressors in coral reef ecosystems has been studied previously (Coles & Jokiel, 1978; Lesser *et al.*, 1990; Shick *et al.*, 1996; Darling *et al.*, 2010), to date little agreement exists about which stressors are likely to act synergistically, or how they should be managed where they do occur (Folt *et al.*, 1999; Dunne, 2010). Thus far, no reviews have specifically focused on the coral reef literature to assess the prevalence of synergistic effects.

The purpose of this study is to review the research on multiple stressor interactions in coral reef ecosystems, and we use two approaches to examine the problem of multiple stressors. First, we synthesize coral reef studies that examined interactions of two or more stressors and differentiate between stressor interactions (where one stressor directly influences another) and the effects of multiple stressors on another response variable. Our qualitative overview provides the state of current knowledge of multiple stressor interactions on coral reefs, allows for identification of research gaps, and highlights areas where sufficient data may exist for future meta-analyses. We apply a network-analysis approach to analyzing stressor interactions (Wenger *et al.*, 1999) to identify the most influential or most-influenced stressors. This approach may allow managers to focus on reducing those stressors whose interactions with other stressors are likely to have the most deleterious effects. Second, we perform a quantitative meta-analysis on one of the most-studied stressor interaction effects on coral organisms - irradiance and temperature - and assess whether sufficient evidence exists to draw general conclusions about this interaction. In this analysis, we consider three of the most commonly and consistently measured stress response variables from the coral reef literature: coral symbiont (zooxanthellae) density, photosynthetic efficiency (F_v/F_m), and chlorophyll *a* concentration.

Study Selection

To categorize research on stressor interactions, we identified 13 stressor categories through key review papers in the coral reef and multiple-stressor literature (Hoegh-Guldberg, 1999; Halpern *et al.*, 2007; Keller *et al.*, 2009) (Table 1). Some potential stressor categories [e.g., ocean mining, ecotourism, coastal development: (Halpern *et al.*, 2007)] manifest their effects indirectly through other stressors (e.g., nutrient loading, sedimentation), and hence we excluded these categories as

Table 1 List of stressor categories used to examine potential interactions between stressors

Stressor	Selected references
Ocean acidification	(Anthony *et al.*, 2008, Kleypas *et al.*, 1999)
Crown-of-thorns starfish outbreaks	(Done, 1992, Moran, 1986)
Eutrophication	(Bell, 1992, Szmant, 2002)
Fishing pressure	(Jackson *et al.*, 2001, Valentine & Heck Jr, 2005)
Increased ocean temperatures	(Carpenter *et al.*, 2008; Goreau & Hayes, 1994)
Irradiance	(Brown *et al.*, 1994)
Pathogen-induced disease	(Willis *et al.*, 2004)
Pollution	(Lewis *et al.*, 2009)
Reduced salinity	(Brown, 1997; Kerswell & Jones, 2003)
Storms	(Cheal *et al.*, 2002, van Woesik *et al.*, 1991)
Terrestrial sedimentation	(Dubinsky & Stambler, 1996, Fabricius, 2005)
Ultraviolet radiation	(Dunne & Brown, 1996, Lesser, 1997)
Sea level rise	(Przeslawski *et al.*, 2008, Selkoe *et al.*, 2009)

stressors *per se*. In the case of disease, to avoid conflating the stressor (i.e. pathogens) with the response of the host to the stressor (infection and associated symptoms) we differentiated studies that directly measured changes in pathogen abundance or virulence factors from those that observed disease symptoms or host mortality that were presumed to be disease-related. We searched each combination of stressors (using a combination of the Booleans *and* with *or* for synonymous terms – see Table S1) using the Topic search feature on ISI Web of Knowledge using the Science Citation Index (SCI-Expanded, 1972-Present) and the Conference Proceedings Citation Index (CPCI-S, 1990-Present). We used the Topic search because it is more comprehensive than using title or keyword searches. All studies up to September 2013 were included.

The studies returned from the searches were examined for their applicability, and entered into a database. If more than 150 results were returned from the topic search, we imported the search results into Endnote X4 (Thomson Reuters, New York, NY, USA, 1988–2010) and then filtered the results by searching only the keyword field. We manually screened this subset of results, and discarded studies that were outside the purview of our analysis (e.g., studies concerning 'sediment' in a geological context). If 150 or fewer results were returned, we manually screened each abstract to produce a subset of studies that explicitly examined (i.e. either manipulated or controlled for) the stressors of interest. To keep the number of search term permutations tractable, we confined our search to studies that pertained in some way to tropical or temperate hermatypic coral reefs or scleractinian coral organisms. Thus, studies on deep water and cold-water corals were excluded, as were organisms such as macroalgae, foraminifera, etc. Because marine reserves and no-take areas are a common management mechanism in coral reefs, we also included the effects of reef fisheries and stressors affecting reef-associated fish. We also disregarded studies that did not measure at least two stressors of interest. Both field and laboratory studies (including mesocosm studies) were included. Reviews and modeling studies without an experimental component were excluded. In this article, all of the response variables we discuss pertain to corals unless otherwise specified.

Meta-analysis approach

Qualitative meta-analysis. Studies were divided into two groups: those that reported the effect of one stressor on another, and those that reported the effect of two (or more) stressors on a response variable. In the first group, for each stressor combination, we first created a table where the number of studies examining a specific interaction were tallied according to the direction of effect one stressor had on another. We did not evaluate synergistic or antagonistic effects in these interactions, merely whether one stressor increases (reinforces) or reduces (mitigates) the level or incidence of another. These interactions were considered asymmetrically (e.g., sediment loading is typically associated with increased nutrients, but the converse cannot be assumed). To examine the relative stressor influences, we imported an unweighted (i.e. relationships were not weighted by the number of studies) version of the table into the software UCINET (Borgatti *et al.*, 2002) and NetDraw (Borgatti, 2002) for analysis and network diagram creation. Using this stressor 'network' of interactions, we calculated both in-degree centrality, out-degree, and betweenness to determine stressors with either the most influence on other stressors or that were affected by the highest number of stressors. In-degree centrality calculated the number of stressors that have a direct influence on each stressor; out-degree is the number of stressors influenced by a particular stressor, and betweenness is an indicator of how central a stressor is in terms of relationships to other stressors via indirect pathways.

For the studies that examined the effect of multiple stressors on a response variable, we identified the response variable for each stressor combination and the

Table 2 Effect of interacting stressors on response variables. Bold text denotes a *deleterious* effect on individual corals or the overall amount of coral cover; unbolded entries are either neutral or potentially beneficial. The first number reflects how many studies were found reporting the corresponding effect, whether qualitatively or quantitatively. The number that follows in parentheses is the number of studies that quantitatively tested for an interaction. Arrows denotes the direction of the change in response variable associated with an increase in both of the stressor variables; sideways arrows indicate that the response is either complex (e.g., U-shaped) or dependent on some other factor. Columns and rows containing no studies were removed: for columns, sea level rise, storms and UV; for rows, acidification, crown of thorns outbreaks, and disease

Stressor	Acidification	CoTS	Disease	Fishing	Irradiance	Nutrients	Pollution	(Reduced) Salinity	Sedimentation	Temperature
Fishing			**1↑Algal cover (0)**							
Irradiance	**1↑ Bleaching (1)** 3↔Calcification (3) **1↓Calcification (1)** **1↓Zoox. Photosynthesis (1)** ↑Photosynthesis (1)*									
Nutrients	**3↓Calcification (0)** 1↔Calcification (1) **2↑Pathogen growth (1)** **1↔Zoox. Photosynthesis (0)**			**1↑Algal cover (1)** 1↑Corallimorphs (0) **1↓Herbivory (0)** 1↑Sea urchin grazing (0)	1↑Microalgal production (0) **1↓Calcification (0)** 2↔ Zoox. Photosynthesis (2) 1↑ Zoox. density (1) 1↔Pigmentation (1) 1↓Photosystem damage (1)					
Pollution				**1↓Reef condition(1)**	**2↑Bleaching (0)** **1↓ Zoox. Photosynthesis (1)**					
(Reduced) Salinity					1↑ Zoox. Photosynthesis (1)	**1↓Fertilization (1)** **1↑Mortality (0)**	**1↓Zoox primary production (1)**			
Sediment				**1↓ Coral cover (0)** **1↔ Disease prevalence (0)** 1↔ Coral cover† (1)	1↓Coral mortality (1) **1↑UV penetration**	**2↓Coral cover (0)** **1↓Fert. (1) 1↓Growth rate (0)** **1↑Macroalgal growth (0)** **2↑Mortality (0)** 1↔Mortality (1) **1↓ Photosynthesis (0)**		**1↓ Coral cover (0)** **1↓ Fertilization (1)** 1↔ Growth rate (0) **1↑Mortality (1)** **1↓Photosynthesis (1)**		**1↑Mortality (1)**
SLR					1↔ Photosynthesis (0)			**1↓Growth rate (0)**		
Storms		**1↓Recovery (0)** 1↑Larval settlement (0)		**1↑Physical damage (0)**		1↓ Algal cover (0) 1↑Fish abundance (0)				**1↑Disease (0)**
Temp	**3↓Calcification (2)** 4↔ Calcification (4) **2↑Pathogenesis (2)** **1↓Nutrient uptake (1)** 1↓Aerobic scope of fish (1) 2↔ Photosynthesis (2) 1↔ Zoox density (1)		**1↓Zoox density (1)**	1↔Zoox growth rate	1↔ Antioxidant enzyme activity (1) 1↔Bleaching (1) **7↑Bleaching(1)** 1↑ Calcification (1) 1↔ Calcification (0) **3↑Coral mortality (2)**	**1↑Bleaching (0)** 1↔ Calcification (0) **1↑Disease (0)** 1↔ Disease (0) 3↔ Photosynthesis (3) **1↓ Photosynthesis (1)**	**1↓Larval metamorphosis (1)** **2↓ Photosynthesis (2)**	**1↑Bleaching (0)** **1↓Photosynthesis (1)**	**1↑Bleaching (0)** 1↓Mortality (1) **1↓Coral cover (0)** 1 ↔ Photosynthesis‡ (0)	

Table 2 (Continued)

Stressor	Acidification	CoTS	Disease	Fishing	Irradiance	Nutrients	Pollution	(Reduced) Salinity	Sedimentation	Temperature
	1↑Bioerosion (0) 1↓Fertilization (1) 1↔Fertilization (1) 1↔Photosynthesis (1) 1↔Coral mortality (1) **1↑Coral mortality (1)**				**4↑ Disease (4)** 1↔ Disease (1) 1↓ [Polyunsaturated FAs] (1) 2↑ [MAA] (0) **35↓ Photosynthesis (25)** 1↑ Photosynthesis (1) 5↔ Photosynthesis (4) 1↔ Symbiont clade (0)					
UV	**1↓ Calcification (1)** **1↓ Photosynthesis (1)**				**1↓Community productivity (0)** 1↔ Photosynthesis (0)		**1↑ Coral mortality (1)** **1↓ Photosynthesis (1)**			**1↑Bleaching (0)** **2↑ Coral mortality (2)** **1↓ Growth rate (0)** **7↓Photosynthesis (6)** 1↔Photosynthesis (1)

*This experiment compared subsaturating irradiance with saturating irradiance; the effects of higher irradiances were not tested.
†Possibly confounded by poaching in ostensibly protected areas.
‡This study was not unable to disentangle the effects of sedimentation from the effects of nutrient loading.

net direction of the response variable when stressor effects were combined. We also noted whether or not the experimental design (statistically and/or methodologically) allowed synergistic or antagonistic interactions to be detected quantitatively.

Quantitative meta-analysis. Using the database of multiple stressor studies, we tabulated the number of studies by dependent variable type to identify candidates for quantitative meta-analysis. We segregated studies by response variable to keep analysis subgroups as homogenous as possible. We also recorded genus, species, geographical region, and biographical information for each study. We then picked one of the most numerous response types (n = 31) to carry out a quantitative meta-analysis: the effect of temperature and irradiance on coral symbiont photosynthesis. Within this category, photosynthetic performance was most commonly measured by three different parameters. These parameters were (i) dark-adapted maximal chlorophyll fluorescence (F_v/F_m) (n = 20); (ii) symbiotic zooxanthellae density (n = 6); and (iii) chlorophyll *a* concentration (n = 16). We extracted data from electronic (PDF) versions of manuscripts using either Adobe Acrobat's on-screen measuring tools or directly from reported results. For studies reporting time series data, we used the last point in the experimental time series except in cases where complete mortality occurred before the end of the experiment, in which case we used the last nonzero point. If an experiment was long-term, we only used results from the acute stress phase of the experiment (i.e. we did not use values from a recovery phase). If multiple treatment levels (e.g., high and moderate temperature treatments) were applied, we only used the largest treatment differential to calculate effect size. In studies that included multiple species, we treated each species as a separate experiment. We discarded studies that were missing information about sample error, sample size, or did not manipulate each stressor both jointly and independently. After these screening steps, 17 studies for F_v/F_m, 6 studies for zooxanthellae density, and 3 studies for chlorophyll *a* concentration remained that were suitable for meta-analysis.

Ideally, meta-analysis of synergistic effects would analyze, from each study, an estimate of the interaction term from a statistical model (e.g., ANOVA or other linear model), and its associated SE. Unfortunately, most studies do not report this statistic. Consequently, previous meta-analyses have tended to use a 'two-interval' approach: inferring synergistic effects when the confidence intervals on the meta-analysis estimate of the combined treatment effect does not overlap with the confidence intervals on the estimate of the additive effect (Crain *et al.*, 2008; Darling & Côté, 2008). However, this approach is subject to potentially large Type II error—failure to detect a synergistic effect when one is, in fact, present (Schenker & Gentleman, 2001; Payton *et al.*, 2003)(see Appendix S1 and Table S2 for an illustration).

As an alternative to the two-interval approach, we instead use a Monte Carlo method, the parametric bootstrap (Efron & Tibshirani, 1994), to approximate the SE of the interaction term from each study, and we use those as our test statistics in the meta-analysis. The approach is similar to the better-known nonparametric bootstrap, but values are drawn from a probability distribution, rather than being resampled from actual observations. Specifically, we randomly draw a mean value for each treatment (control, irradiance only, temperature only, irradiance & temperature), from a normal distribution with a mean equal to the observed treatment mean, and a SD equal to the SD of the mean (i.e. the SE). We then calculate temperature, irradiance, and combined effects by taking the difference between the relevant Monte Carlo-sampled treatment mean value and the sampled mean of the control. The interaction term is then the difference between the combined treatment effect and the additive effect (temperature effect + irradiance effect). If the combined effect is larger than the additive effect (i.e. the interaction term is positive), this indicates synergy; if it is smaller than the additive effect, then antagonism is indicated. Finally, we convert this to an estimate of Hedges' g (Hedges, 1981), a measure of effect size, by dividing this interaction term by the pooled SD. We repeat this procedure 1000 times for each study, producing a frequency distribution of interaction term values. The SD of this statistic is the SE that we use in our meta-analysis for that study.

We calculated these bootstrap estimates of interaction terms for each response variable (i.e. maximal chlorophyll fluorescence (F_v/F_m), zooxanthellae density, chlorophyll *a* concentration), and evaluated subgroup heterogeneity using the I^2 index (Higgins & Thompson, 2002) in R (R Core Team, 2012) with the 'metafor' package (Viechtbauer, 2010). Heterogeneity measures provide an indication of whether the variation in effect size between studies is entirely due to measurement error around a single true effect size, or whether the true effect sizes being measured in each study actually vary around an overall mean (e.g., due to difference in how treatments were administered or to choice of study organism). As species and treatment conditions varied from study to study, we used a random-effects model (see Chan & Connolly, 2012 for more details) to estimate the combined effect size for each group of response variables and treatments. We also explored possible explanations for any heterogeneity by performing a meta-regression on the study characteristics of region of origin, genus of study species, and magnitude of temperature and irradiance treatments (absolute difference between treatment condition and control condition). Finally, we assessed whether a publication bias may exist (i.e. whether studies reporting large or significant effect sizes may be overrepresented relative to studies reporting no effect), by plotting reported effect sizes against the SE of each study to produce a funnel plot (Møller & Jennions, 2001). If no publication bias is present, this plot should show a larger variation in effect size as the SE increases (Fig. S1).

Multiple stressors on coral reefs: Much interest, few quantitatively comparable findings

Taken as a whole, there is an extensive body of literature concerning single and multiple stressor effects on coral reef ecosystems. However, we found that the number of studies that quantitatively examined combined stressor effects in a way that clearly demonstrates the presence or absence of synergistic effects was quite low (e.g., in the case of photosynthesis, only three studies examining temperature and nutrient interactions, and only one examining temperature and salinity interactions – see Table S3). Further complicating attempts to synthesize the literature is the diversity of response variables measured and the lack of consensus on what indicators or metrics best represent the state of coral reef health (e.g., coral cover, mortality, fecundity; Hughes *et al.*, 2010). Here, we describe some of the interactions between stressors themselves and between stressors and response variables in terms of their support (or lack thereof) in the literature. We also propose some ways in which managers could use these findings to assist in quantifying stressor interactions and help to identify those stressors with the most wide-reaching potential effects.

Qualitative Meta-analysis: Stressor-Stressor Interactions

Using our search criteria, we found 176 studies that examined the interaction of at least two of the 13 stressors (Table S4). The most frequently studied stressors were nutrient loading (37 studies, 21% of all studies), pathogen growth and virulence (32 studies, 18%), sedimentation (29 studies, 17%) and fishing pressure (29 studies, 17%). Some of the notable data gaps regarding stress-stressor interactions concern irradiance (other than interactions with sedimentation), salinity (other than interactions with nutrients), pollution, and

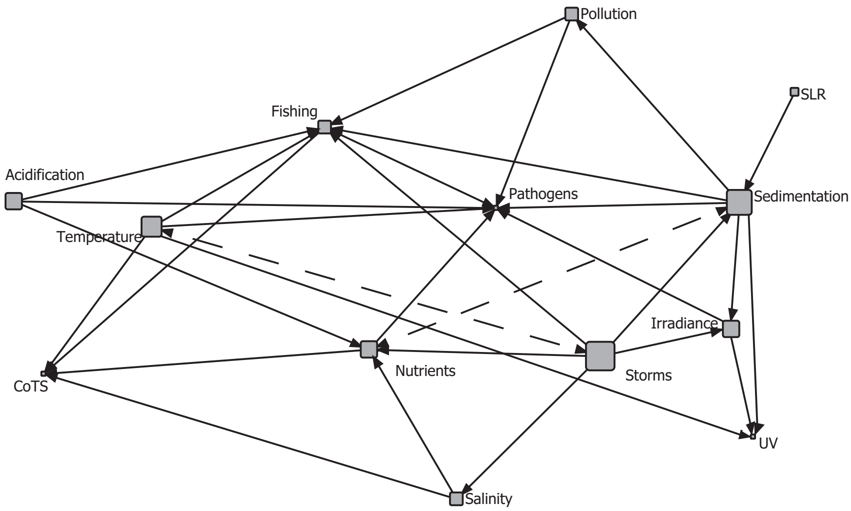

Fig. 1 Network diagram of stressor-stressor relationships. Node size reflects betweenness measure for that node, i.e. the number of other stressors that are directly or indirectly mediated by that node. Unidirectional relationships are depicted with solid lines; bidirectional relationships are depicted with dashed lines.

ultraviolet radiation. Converting the table into a network diagram (Fig. 1) and calculating the in-degree centrality (i.e. the number of other stressors directly affecting each stressor) and betweenness (i.e. number of other stressors that are directly or indirectly mediated by that node) of each node showed that pathogen loading had the highest in-degree and the highest betweenness measure. Nutrients also had a high in-degree, but a relatively low betweenness measure. Stressors with a high out-degree measure (i.e. those influencing the highest number of other stressors) were sedimentation, storms, and temperature. Weighting the network by the number of studies would reflect a bias in the topics that attract the most research interest, rather than the weight of evidence for (or against) a particular stressor interaction. In a weighted network, the degree centrality and betweenness metrics would be biased toward nodes that had a larger number of studies contributing to the linkages between nodes. Thus, in an unweighted network, both degree centrality and betweenness provide an unbiased way of quantifying the degree to which a stressor mediates or influences other stressors. However, betweenness reflects both direct and indirect linkages to other stressors, whereas in-degree and out-degree only measure direct linkages. The limitation of all these metrics is that additional interactions may exist that have not been reported in the literature. For example, increased irradiance is physically linked with increased water temperature, but this fundamental linkage is unlikely to be reported in the biological literature as a key finding. In addition, other linkages may exist that have not been reported simply because the studies have not been performed to test or verify their existence.

Most influential stressors: Sedimentation, storms, temperature

According to our network analysis of stressor relationships as reported in published studies, the stressors that were most influential on other stressors were sedimentation, storms, and temperature (Fig. 1). Sedimentation directly affected fishing (by affecting catches), irradiance, nutrient loading, pathogen loading, pollution, and ultraviolet exposure. Sedimentation correlates with or reinforces the effects of nutrients, disease, and pollution, but mitigates irradiance and UV exposure. Sedimentation effects on reef-associated fish and fisheries vary depending on the habitat association and prey composition of fish species. Storms (variously called cyclones, hurricanes, and typhoons, depending on the ocean basin in which they occur) directly influenced three of the same stressors as sedimentation (nutrients, ultraviolet exposure, and fishing) and three others (salinity, temperature, sedimentation). Storms, while causing direct and indirect damage to reefs, also potentially mitigate some stressors: they can reduce water temperatures (Manzello *et al.*, 2007; Carrigan & Puotinen, 2011), decrease irradiance (van Woesik *et al.*, 1995), and potentially reduce sediment burial (Manzello *et al.*, 2007; Carrigan & Puotinen, 2011).

Temperature was the most-studied influencing stressor, with ca. 23% of studies considering temperature and 57% of those reporting a reinforcing effect on another stressor. These reinforcing effects were seen with ultraviolet radiation (Anderson *et al.*, 2001) and pathogen growth (Bally & Garrabou, 2007) and virulence (Banin *et al.*, 2003) as well as fishing (by causing shifts in community structure or abundance; however, the aggregate response of reef fish populations to temperature increases appears to be complex and variable, resulting in changes in physiology, behavior, and recruitment (Lo-Yat *et al.*, 2011; Feary *et al.*, 2010; Gardiner *et al.*, 2010)). Potentially reinforcing effects were seen between increased temperature and cyclone and hurricane frequency (Pielke, 2005; Anthes *et al.*, 2006), and for low-salinity stress (Faxneld *et al.*, 2010), although the former is controversial (Hayne & Chappell, 2001; Hetzinger *et al.*, 2008; Kumar *et al.*, 2009) and there is conflicting evidence of the latter (Porter *et al.*, 1999). Potentially mitigating stressor interactions were seen for crown-of-thorns starfish, which appear to have a relatively narrow temperature tolerance during their larval stage (Johnson & Babcock, 1994), with adult mortality occurring at temperatures of 33–34 °C (Yamaguchi, 1974). In short, increasing water temperatures have a suite of effects on other stressors affecting coral reefs; on balance, most of these effects appear to be deleterious.

Most-influenced stressors: nutrients, crown-of-thorns starfish, pathogens

The stressors that were influenced by the greatest number of other stressors were nutrients, crown-of-thorns starfish, and pathogens (Fig. 1). Most of the stressors influencing nutrient loading were associated either directly or indirectly with flood events due to terrestrial runoff, and also sediment resuspension by storms (Delesalle *et al.*, 1993). Nutrient loading has been hypothesized to contribute to crown-of-thorns outbreaks (also known as the 'terrestrial runoff hypothesis' or 'larval survival hypothesis') (Birkeland, 1982), but evidence to date is mainly correlative (Brodie *et al.*, 2005; Fabricius, 2005). Pathogen growth and virulence can be enhanced by increased temperature (Ward *et al.*, 2007) and increased nutrient availability (Richardson & Ragoonath, 2008), while host susceptibility to infection can also be affected by stress due to increased irradiance (Griffin, 1998), acidification (Thurber *et al.*, 2008), pollution (Arboleda & Reichardt, 2009), and sedimentation (Vargas-Angel *et al.*, 2007) in addition to temperature stress (Ward *et al.*, 2007).

Although the network analysis is unweighted, it nevertheless will reflect any bias in research effort and subsequent publication. Thus, the stressors we have deemed as most-influential or most-influenced may not necessarily indicate the strength or ubiquity of these interactions. Furthermore, some stressors are difficult to quantify and measure due to their multifaceted and complex nature (such as crown-of-thorns outbreaks or fishing pressure), whereas others are more straightforward to measure and manipulate – at least in a laboratory setting (such as temperature and salinity). Thus, there is likely to be a bias in the literature toward stressors that lend themselves to experimental manipulation. This division between complex and simple stressors may partially explain why two of the most-influenced stressors are complex biological phenomena (crown-of-thorns and pathogens), whereas two of the most-influential stressors are relatively simple physical factors (sedimentation and temperature).

Qualitative Meta-analysis: Coral reef responses to multiple stressors

We found 187 experiments (some studies contained multiple experiments and thus contributed to more than one category) that examined the effects of two or more stressors on a third dependent variable (Table 2; Table S5). Coral calcification, coral bleaching/symbiont photosynthesis, coral cover, observations of coral disease symptoms, and coral mortality were among the most commonly studied response variables (Fig. 2) in multiple-stressor studies. Of the 187 experiments, 111 were assessed quantitatively in the original studies. Nearly all of the studies used an ANOVA to detect interaction effects, with some using techniques such as boosted regression trees (Cervino *et al.*, 2003), discriminant function analysis (Mumby *et al.*, 2001), or multi-model selection (Yee *et al.*, 2008; Yee & Barron, 2010). Of these 111 experiments with a quantitative basis, 60 reported a synergistic effect, 17 reported an antagonistic effect, and 33 reported an additive effect or no significant interaction (and one did not report either way regarding an interaction despite being designed to do so).

Examples of reported synergistic effects included nutrients and acidification enhancing the growth of the white plague pathogen *Aurantimonas coralicida* (Remily & Richardson, 2006), and increased sediment interacting with hyposaline conditions to depress fertilization and development of *Acropora millepora* (Humphrey *et al.*, 2008). Examples of antagonistic effects included increased nutrients offsetting the effects of acidification on coral calcification (Langdon & Atkinson, 2005; Holcomb *et al.*, 2010; Chauvin *et al.*, 2011), although the opposite effect has been more commonly reported (see Suggett *et al.*, 2013 for a list of all such studies). Similarly, sedimentation can reduce the effects of increased temperature and irradiance, either by augmenting

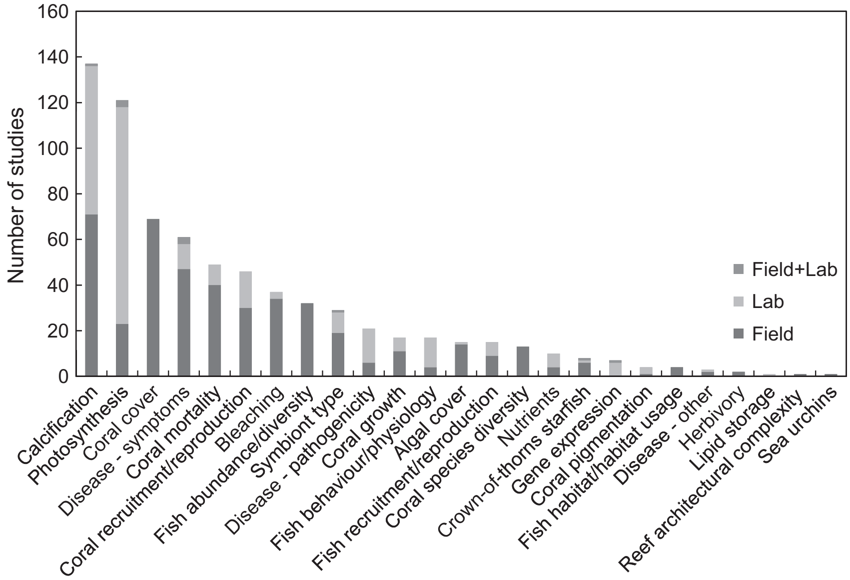

Fig. 2 Category of response variable of studies that fit two or more of the stressor search criteria listed in Table 1. Studies conducted in the field, lab or both are depicted by the different shading in the bars. Note that studies with response variables that we considered to be stressors in themselves (e.g., temperature, irradiance), are excluded. Search results are from ISI Web of Science from 1965 to September 2013. Note that if a study included more than one response variable category, it will contribute to the frequency distribution in all relevant categories.

heterotrophy or reducing light penetration (Anthony *et al*., 2007). The relatively low proportion of studies reporting either a strictly additive effect or no significant interaction at all may be due at least in part to publication bias, where studies that do not find deviations from additivity may be less likely to be submitted or published (although, as we note in the following section, we did not find evidence for such a bias in the case of temperature-irradiance-photosynthesis studies). Crain *et al.* (2008) also suggest that the literature in general is likely to be biased toward stressors that are amenable to factorial experiments (e.g., temperature is easier to manipulate than fishing pressure), and that stressors that are known or suspected to be synergistic (e.g., ultraviolet light and toxins) are more likely to attract research attention than those that are not.

The interaction of irradiance and temperature has been the subject of more research (62 studies, 33% of the total number of experiments) than any other combination of stressors. Including studies that examined the combination of ultraviolet radiation and temperature (n = 12), there are more than 10 times as many studies on the combined effects of irradiance and temperature than the next highest stressor combination of nutrients and sedimentation (n = 6 studies). Of these 62 irradiance-temperature studies, 47 used either qualitative bleaching or quantitative measures of photosynthesis as a response variable, and 27 of these 47 employed a fully factorial design. Most of the quantitative studies in the irradiance and temperature category reported a synergistic effect on photosynthetic performance (n = 19). Two studies found an antagonistic effect associated with conditioning or pre-exposure to stressful conditions (Dunne & Brown, 2001; Brown *et al*., 2002) and two (Venn *et al*., 2006; Yee *et al*., 2008) found that the response varied with either species or experimental conditions. Certain coral species such as *Porites astreoides* (Venn *et al*., 2006), *Porites porites* (Venn *et al*., 2006), *Pachyseris rugosa* (Yakovleva & Hidaka, 2004), and *Pavona divaricata* (Yakovleva & Hidaka, 2004) were resistant to bleaching even under the combination of high light and temperature. A similar variability in responses was found for ultraviolet radiation and temperature, with five studies finding synergistic increases in bleaching and mortality, but some finding no effect of UV on bleaching (Fitt & Warner, 1995) or even a mitigating effect (Fine *et al*., 2002). Again, conditioning or acclimation to stressful conditions appears to play a role in subsequent responses to these stressors (Rogers *et al*., 2010).

Bleaching was the most commonly reported response variable, with 52 studies reporting either a qualitative or quantitative bleaching metric. Many other studies measured other parameters that are either direct or indirect proxies for bleaching, such as mycosporine amino acid (MAA) composition, photosynthetic performance, or oxidative stress. While bleaching clearly has deleterious effects on individual coral organisms, even when it does not cause mortality, disagreement still exists about whether nonlethal bleaching may also play a role as an adaptive response to environmental stress (Fautin & Buddemeier, 2004; Jones, 2008).

The complex interactions between bleaching and disease are unusual in that they could be considered an example of an interaction between stressor responses. Some have hypothesized that bleaching is actually a result of infection by a pathogen that is facilitated by corals' response to environmental stress (Ben-Haim *et al.*, 2003; Rosenberg *et al.*, 2009), but reports of such a relationship are confined mainly to the Mediterranean region. In addition, there is some evidence – primarily from the Caribbean – that bleaching episodes may facilitate disease outbreaks, and vice-versa (Miller *et al.*, 2006; Brandt & McManus, 2009; Mydlarz *et al.*, 2009), or that sequential bleaching and disease outbreaks could have a synergistic effect on coral mortality (Harvell *et al.*, 2001; Miller *et al.*, 2006). However, it is unclear whether bleaching and disease are as tightly coupled in other regions, such as the Indo-Pacific (Maynard *et al.*, 2011; Ban *et al.*, 2013).

We found few studies that examined the effect on any response variable of interactions of any other stressor with pathogens ($n = 1$), crown-of-thorns ($n = 2$), sea level rise ($n = 2$), storms ($n = 4$), or pollution ($n = 6$). Thus, these areas may represent a potential research gap in terms of coral responses to multiple stressors. In addition, as with our stressor-stressor analysis, there are categories where it is reasonable to assume that interactions occur based on physical principles. For example, increased irradiance will increase temperatures, and sea-level rise will decrease irradiance for photosynthetic organisms with accretion rates slower than the rate of rise – as has occurred in the geologic past (Kendall & Schlager, 1981; Blanchon & Shaw, 1995; Zhao *et al.*, 2008) and may again in the future (Pittock, 1999; Knowlton, 2001; Grigg *et al.*, 2002). Indeed, Table 2 makes it clear that conspicuous gaps exist in the literature with respect to numerous interaction pairs. Some of these gaps include the interaction between nutrients and irradiance (including UV radiation), and between nutrients and pollution. The broad categories also belie the shortage of studies that examine interactions between stressors of the same type, e.g., between different herbicides, or between heavy metals and pesticides. One exceptional study (Negri *et al.*, 2011) not only examined the interaction between temperature and three different herbicides (diuron, atrazine, and hexazinone) independently, but also investigated the interaction between temperature and the simultaneous application of all three herbicides. Nevertheless, all of the herbicides in this study used the same mechanism of action, namely photosystem II inhibitors. Thus, as is the case with toxicology in general, much work remains to be done investigating interaction effects between specific compounds and even entire classes of compounds (Thompson, 1996). Given the paucity of studies on most interactions, relative to those concerning irradiance, temperature, and bleaching, there is a clear need to further explore many of these less well-understood stressors and responses.

Quantitative meta-analysis: Combined effect of irradiance and temperature on photosynthesis in corals

Of the 114 studies that measured one or more photosynthetic parameters of scleractinian corals as the response variable, 72 controlled or manipulated at least two factors and 45 examined the interaction between temperature and irradiance. Of these 45 studies, 26 used a fully factorial design that made them suitable for meta-analysis (see Table S3). From this quantitative meta-analysis, we found that although the mean of combined stressor effects predicted from the random-effect models tended to be larger than the predicted mean additive effect for each of the three response variables (F_v/F_m, [chl a], zooxanthellae density, Fig. 3a), the Monte Carlo estimate of the difference between these effect sizes was not significantly different from a purely additive effect for any of the response variables (Fig. 3b). Pooling all of the response variables ($n = 26$) also showed that the combined effect of temperature and irradiance stresses were not significantly different from the effect that would be predicted from the sum of the individual effects. Within this pooled group, there was a significant degree of heterogeneity ($I^2 = 89.2\%$); however, this heterogeneity was not well-explained by the magnitude of the temperature treatment, irradiance treatment, region of origin, nor genus of the study organism (Table S6). Given the relatively small sample size, though, the lack of statistical significance of the region and genus-level analyses should be interpreted with caution.

It is surprising to find a lack of statistical evidence for a synergistic effect between irradiance and temperature for the three photosynthetic variables we examined, given that photosystems that are already damaged or impaired by high temperatures are known to be more susceptible to photoinhibition at lower temperatures (Fitt *et al.*, 2001). However, there is considerable variety in species-specific responses (e.g., Abramovitch-Gottlib *et al.*, 2003; Zhu *et al.*, 2004; Abrego *et al.*, 2008; Yee *et al.*, 2008), as well as evidence for a possible mitigating effect of pre-exposure to irradiance on subsequent temperature exposure (Brown *et al.*, 2002; Brown &

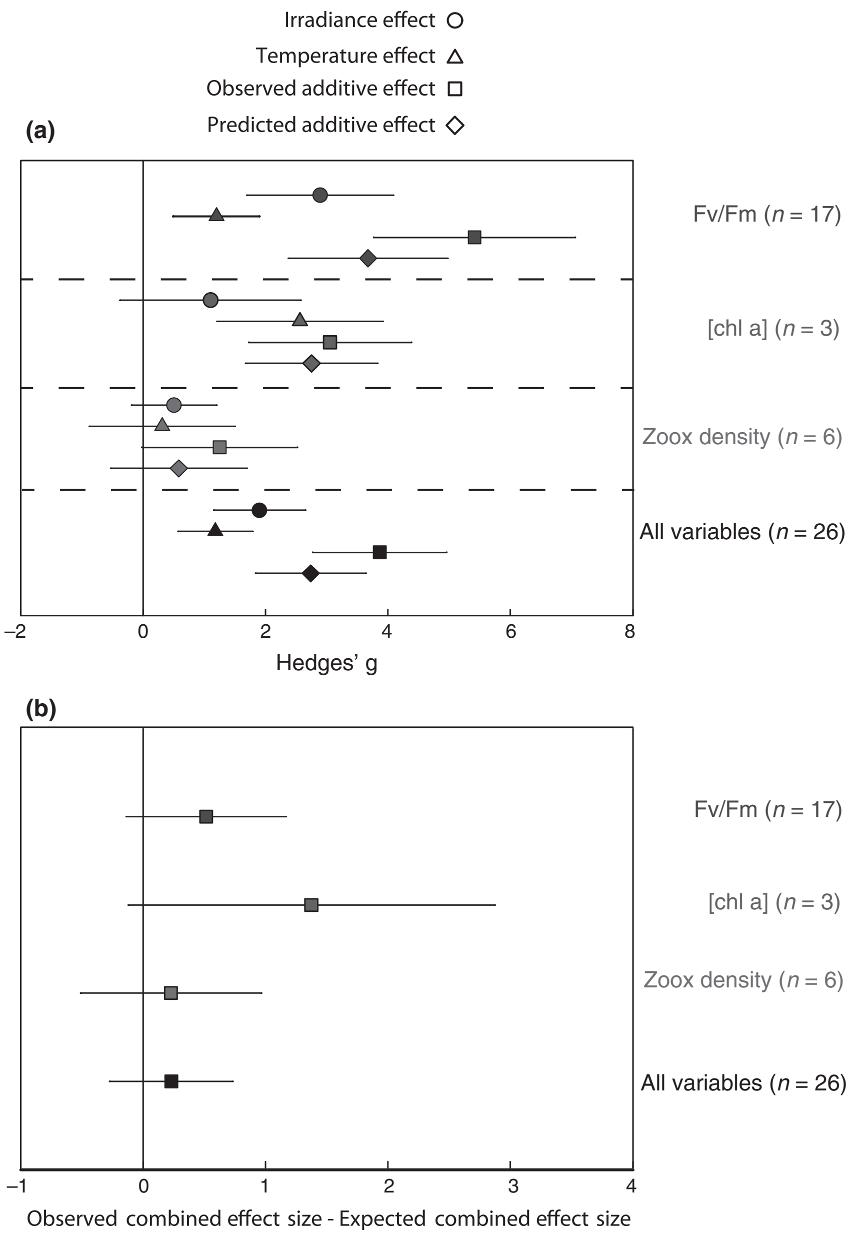

Fig. 3 (a) Mean effect sizes by response variable and stressor type, as predicted by a random effect model. Error bars represent 95% confidence interval. F_v/F_m is a measure of Photosystem II photosynthetic efficiency; [chl a] is chlorophyll a concentration; Zooxanthellae density is the density of symbiotic zooxanthellae contained within coral tissue. (b) Effect-size difference between observed and predicted (i.e. additive) combined effect using Monte Carlo simulation. Differences greater than zero indicate synergistic effect; differences less than zero indicate antagonistic effect.

Dunne, 2008), and acclimation to both temperature and irradiance (Robison & Warner, 2006; Visram & Douglas, 2007; Armoza-Zvuloni *et al.*, 2011). Factors such as heating rate (Middlebrook *et al.*, 2010) and preconditioning (Bellantuono *et al.*, 2012) also introduce additional variation into the stress response. Outside of a laboratory setting, temperature and particularly irradiance can be difficult to control (Brown, 1997). Thus, drawing broad conclusions about the irradiance-temperature-photosynthesis relationship poses a considerable challenge. Furthermore, given that few studies use more than one treatment temperature and/or irradiance level, determining the shape of an almost certainly nonlinear dose-response curve between these two factors will require more sophisticated experimental designs.

Lack of evidence for a synergistic effect at an aggregate level does not mean that synergistic effects were not present in individual studies or that synergistic effects do not exist. For example, in Darling & Côté's (2008) meta-analysis, the overall effect of multiple stressors was not synergistic despite more than a third of the individual experiments finding synergistic effects. In contrast, Crain *et al.* (2008) found evidence for an overall synergistic effect between stressors, despite the majority of individual stressor pairs having an additive effect. Both Crain *et al.* (2008) and Darling & Côté (2008) used the two-interval method, which increases the risk of type II error; hence, both may actually have underestimated the strength of evidence for an overall tendency toward synergistic effects. Here, we find that of the 45 studies that examined combined temperature and irradiance effects, 14 (31%) reported a synergistic effect on at least one of the response variables; seven reported no synergistic effect, and four reported a combination of synergistic and additive effects (Table S3). A further 18 studies had experimental designs that did not allow for the detection of potentially synergistic effects – generally because the stressors were not independently manipulated or controlled.

Conclusions

In general, the majority of stressor-stressor interactions – whether through reinforcing the incidence of another stressor or resulting in a synergistic effect on a response variable – have deleterious consequences for corals at both the organismal and ecosystem level, but considerable gaps in our understanding remain for numerous stressor interactions and interaction effects. There is some evidence of interactions between chemical pollutants (e.g., herbicides, pesticides, and heavy metals) and physical stressors such as increased temperature and irradiance, and between pathogen virulence and these physical environmental factors. We did not find any studies that quantitatively examined interactions between different kinds of the same type of pollutant (e.g., interactions between two herbicides). By contrast, irradiance and temperature effects are well-studied for a variety of response variables (e.g., bleaching, photosynthesis). However, differences in experimental design, protocols, and lack of consistency in choice of specific measures of response variables makes synthesizing the results of even well-studied interactions difficult. For example, we found only three studies that studied the effect of irradiance and temperature on chlorophyll a concentration using a fully factorial design.

Despite our study being one of the most comprehensive reviews on multiple-stressor effects in coral reef ecosystems to date, we found little data for many types of stressor interactions, particularly of the quality needed to perform quantitative meta-analyses. Thus, while the impacts of some stressor interactions have been well-described in the literature, many others remain unstudied and considerable knowledge-gaps remain, with particularly few studies examining interactions between crown-of-thorns starfish, disease, pollution, low-salinity events, and other stressors. In addition, interactions between (and within types of) nutrients and pollutants, and between both of these stressors and irradiance remain largely unstudied.

Despite more than a decade of research interest in multiple stressors across a variety of ecosystems and in both field and laboratory settings, it remains difficult to predict when and where synergistic effects may occur (Breitburg *et al.*, 1999; Folt *et al.*, 1999; Crain *et al.*, 2008; Darling & Côté, 2008; Dunne, 2010). Since our review was deliberately focused on stressors that affect corals and coral reefs, it likely under-sampled the body of literature concerning other reef-associated organisms (such as other invertebrate taxa and algae) that may have as-yet unknown interactions and effects on coral reef ecosystems. Furthermore, although we did include papers concerning reef-associated fish and fisheries where they met our search criteria, we did not extensively sample the considerable body of physiological, ethological, and fisheries science literature specific to coral reef fishes. It would thus be instructive to conduct reviews of multiple-stressor interactions for other specific coral reef-associated taxa to extend both our stressor-stressor and stressor-response matrices.

Relying on published literature to determine the relative importance of stressors is constrained by the existence of publication bias; although we attempted to minimize this by using an unweighted network analysis, there may be stressor interactions that exist that are not reflected in our network if no studies exist (or could be found) documenting these interactions. A lack of literature documenting a specific interaction could be due either to the difficulty or complexity associated with studying it, or due to the apparent self-evident nature of an interaction – such as between irradiance and temperature. Examples of gaps that deserve further investigation are whether changes in salinity, ultraviolet exposure, crown-of-thorns abundance, and fish abundance or diversity affect either disease pathogenicity or susceptibility. Salinity changes could affect the growth rate of pathogens or make corals more susceptible to disease through stress. Similarly, ultraviolet exposure could reduce pathogenicity by either causing DNA damage or inhibiting pathogen growth and/or increase host susceptibility. Finally, changes in fish community diversity and abundance (particularly corallivores) - as well as crown-of-thorns abundance - could affect the transmission of coral diseases if either fish or *A. planci* serve as carriers.

Additional attention also needs to be given to the question of whether the types of responses observed are sensitive to the choice of variables measured, and if so, whether the ways these variables are measured should be standardized. For example, Chan & Connolly (2012) demonstrated that the apparent response of calcification to acidification varied between studies depending on whether calcification was measured using the alkalinity anomaly or buoyant weighting technique, a difference they attributed to the time frame over which such measurements are typically taken.

Even though global climate change is an urgent issue, coral reef managers are mainly able to carry out local-scale management actions, and thus have to rely on local interventions to maximize coral reef resilience to climate change (Hughes *et al*., 2007; Carilli *et al*., 2009; Brown *et al*., 2013; Graham *et al*., 2013). Using local management actions to increase the potential resilience of an ecosystem is not limited just to coral reefs, however; others have recognized the utility of such an approach in rocky subtidal habitats (e.g., Przeslawski *et al*., 2005; Russell *et al*., 2009). Treating stressors as components of a network that is interconnected by reinforcing and mitigating relationships may help to identify the most influential components. By focusing management efforts on stressors that have a leverage effect on other stressors (e.g., sedimentation) and those that exert the largest or most frequent synergistic effects, it may be possible to maximize the effectiveness of those actions. Such efforts should include management of coral reef fisheries that considers effects beyond only target species' abundance (Mumby & Steneck, 2008). This will require broader implementation of ecosystem-based management and possibly management across multiple spatial scales (Hughes *et al*., 2005). Future research should not only attempt to fill the gaps with regard to under-studied stressors, but also investigate community-level responses to multiple stressors and whether synergistic effects are evident (e.g., Graham *et al*., 2011; Darling *et al*., 2013).

Identifying the most-influenced or most influential stressors at either an organismal or ecosystem level may be a useful monitoring and management tool. For example, our finding that disease is linked with so many other stressors means that disease outbreaks may serve as an early indicator of nonspecific ecosystem stress when it is otherwise difficult to determine when an individual stressor or combination of stressors are at harmful levels (e.g., Harvell *et al*., 1999; Knowlton, 2001). This approach of identifying indirect stressor effects has been used in both lacustrine and estuarine systems, where the recognition that eutrophication was directly or indirectly linked with issues of high turbidity, harmful algal blooms, anoxia, and loss of seagrasses allowed for rapid and effective ecosystem recovery following reductions in both phosphorus and nitrogen loading (Cloern, 2001). This recognition was partly a consequence of a shift in conceptual and management models that were based on single, direct responses to those that accommodated multiple, indirect responses (Cloern, 2001). A similar approach could be useful in coral reef systems. For example, nutrient loading and sedimentation could be managed to reduce susceptibility to bleaching (Wooldridge, 2009; Carilli *et al*., 2010). We are not the first to propose such an approach: a graph-theoretic analysis of ecosystem stressors was first proposed over a decade ago (Wenger *et al*., 1999), but it has seen little uptake thus far in management applications.

While our findings underscore both the lack of consensus about interacting stressor effects and the need for more consistency and structure in experimental design, they may also point a way forward by highlighting key research gaps on specific stressor interactions pertaining to coral reefs as well as the general need for study designs and protocols that allow for the identification of synergistic and antagonistic effects in all types of ecosystems. We believe that both the qualitative and quantitative approaches we have used are also readily applicable to the general problem of identifying and quantifying multiple stressor interactions.

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References

Abramovitch-Gottlib L, Katoshevski D, Vago R (2003) Responses of *Stylophora pistillata* and *Millepora dichotoma* to seawater temperature elevation. *Bulletin of Marine Science*, **73**, 745–755.

Abrego D, Ulstrup KE, Willis BL, van Oppen MJH (2008) Species-specific interactions between algal endosymbionts and coral hosts define their bleaching response to heat and light stress. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 2273–2282.

Anderson S, Zepp R, Machula J, Santavy D, Hansen L, Mueller E (2001) Indicators of UV exposure in corals and their relevance to global climate change and coral bleaching. *Human and Ecological Risk Assessment*, **7**, 1271–1282.

Anthes RA, Corell RW, Holland G, Hurrell JW, MacCracken MC, Trenberth KE (2006) Hurricanes and global warming - Potential linkages and consequences. *Bulletin of the American Meteorological Society*, **87**, 623–628.

Anthony KRN, Connolly SR, Hoegh-Guldberg O (2007) Bleaching, energetics, and coral mortality risk: Effects of temperature, light, and sediment regime. *Limnology and Oceanography*, **52**, 716–726.

Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 17442–17446.

Arboleda M, Reichardt WG (2009) Epizoic communities of prokaryotes on healthy and diseased scleractinian corals in Lingayen Gulf, Philippines. *Microbial Ecology*, **57**, 117–128.

Armoza-Zvuloni R, Segal R, Kramarsky-Winter E, Loya Y (2011) Repeated bleaching events may result in high tolerance and notable gametogenesis in stony corals: *Oculina patagonica* as a model. *Marine Ecology Progress Series*, **426**, 149–159.

Bally M, Garrabou J (2007) Thermodependent bacterial pathogens and mass mortalities in temperate benthic communities: a new case of emerging disease linked to climate change. *Global Change Biology*, **13**, 2078–2088.

Ban SS, Graham NAJ, Connolly SR (2013) Relationships between temperature, bleaching and white syndrome on the Great Barrier Reef. *Coral Reefs*, **32**, 1–12

Banin E, Vassilakos D, Orr E, Martinez RJ, Rosenberg E (2003) Superoxide dismutase is a virulence factor produced by the coral bleaching pathogen *Vibrio shiloi*. *Current Microbiology*, **46**, 418–422.

Bell PRF (1992) Eutrophication and coral reefs - Some examples in the Great Barrier Reef lagoon. *Water Research*, **26**, 553–568.

Bellantuono AJ, Hoegh-Guldberg O, Rodriguez-Lanetty M (2012) Resistance to thermal stress in corals without changes in symbiont composition. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 1100–1107.

Bellwood DR, Hoey AS, Ackerman JL, Depczynski M (2006) Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, **12**, 1587–1594.

Ben-Haim Y, Zicherman-Keren M, Rosenberg E (2003) Temperature-regulated bleaching and lysis of the coral Pocillopora damicornis by the novel pathogen *Vibrio coralliilyticus*. *Applied and Environmental Microbiology*, **69**, 4236–4242.

Birkeland C (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). *Marine Biology*, **69**, 175–185.

Blackwood JC, Hastings A, Mumby PJ (2011) A model-based approach to determine the long-term effects of multiple interacting stressors on coral reefs. *Ecological Applications*, **21**, 2722–2733.

Blanchon P, Shaw J (1995) Reef drowning during the last deglaciation: Evidence for catastrophic sea-level rise and ice-sheet collapse. *Geology*, **23**, 4–8.

Borgatti SP (2002) *NetDraw: Graph Visualization Software*. Analytic Technologies, Harvard.

Borgatti SP, Everett MG, Freeman LC (2002) *Ucinet 6 for Windows: Software for Social Network Analysis*. Analytic Technologies, Harvard.

Brandt ME, McManus JW (2009) Disease incidence is related to bleaching extent in reef-building corals. *Ecology*, **90**, 2859–2867.

Breitburg D, Seitzinger S, Sanders J (1999) Front matter. *Limnology and Oceanography*, **44** .

Brodie J, Fabricius K, De'ath G, Okaji K (2005) Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Marine Pollution Bulletin*, **51**, 266–278.

Brodie JE, Kroon FJ, Schaffelke B *et al*. (2012) Terrestrial pollutant runoff to the Great Barrier Reef: An update of issues, priorities and management responses. *Marine Pollution Bulletin*, **65**, 81–100.

Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs*, **16**, S129–S138.

Brown BE, Dunne RP (2008) Solar radiation modulates bleaching and damage protection in a shallow water coral. *Marine Ecology Progress Series*, **362**, 99–107.

Brown BE, Dunne RP, Scoffin TP, Letissier MDA (1994) Solar damage in intertidal corals. *Marine Ecology Progress Series*, **105**, 219–230.

Brown BE, Downs CA, Dunne RP, Gibb SW (2002) Exploring the basis of thermotolerance in the reef coral *Goniastrea aspera*. *Marine Ecology Progress Series*, **242**, 119–129.

Brown CJ, Saunders MI, Possingham HP, Richardson AJ (2013) Managing for Interactions between Local and Global Stressors of Ecosystems. *PLoS ONE*, **8**, e65765.

Carilli JE, Norris RD, Black BA, Walsh SM, McField M (2009) Local stressors reduce coral resilience to bleaching. *PLoS ONE*, **4**, e6324.

Carilli JE, Norris RD, Black B, Walsh SM, McField M (2010) Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Global Change Biology*, **16**, 1247–1257.

Carpenter KE, Abrar M, Aeby G *et al*. (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, **321**, 560–563.

Carrigan AD, Puotinen ML (2011) Assessing the potential for tropical cyclone induced sea surface cooling to reduce thermal stress on the world's coral reefs. *Geophysical Research Letters*, **38**, 1–5.

Cervino JM, Hayes RL, Honovich M, Goreau TJ, Jones S, Rubec PJ (2003) Changes in zooxanthellae density, morphology, and mitotic index in hermatypic corals and anemones exposed to cyanide. *Marine Pollution Bulletin*, **46**, 573–586.

Chan N, Connolly SR (2012) Sensitivity of coral calcification to ocean acidification: a meta-analysis. *Global Change Biology*, **19**, 282–290.

Chauvin A, Denis V, Cuet P (2011) Is the response of coral calcification to seawater acidification related to nutrient loading? *Coral Reefs*, **30**, 911–923.

Cheal AJ, Coleman G, Delean S, Miller I, Osborne K, Sweatman H (2002) Responses of coral and fish assemblages to a severe but short-lived tropical cyclone on the Great Barrier Reef, Australia. *Coral Reefs*, **21**, 131–142.

Christensen MR, Graham MD, Vinebrooke RD, Findlay DL, Paterson MJ, Turner MA (2006) Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biology*, **12**, 2316–2322.

Cloern JE (2001) Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series*, **210**, 223–253.

Coles SL, Jokiel PL (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Marine Biology*, **49**, 187–195.

Council on Environmental Quality (2005) *Guidance on the Consideration of Past Actions in Cumulative Effects Analysis*. (ed. Department of Energy), Washington D.C.

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, **11**, 1304–1315.

Darling ES, Côté IM (2008) Quantifying the evidence for ecological synergies. *Ecology Letters*, **11**, 1278–1286.

Darling ES, McClanahan TR, Côté IM (2010) Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conservation Letters*, **3**, 122–130.

Darling ES, McClanahan TR, Côté IM (2013) Life histories predict coral community disassembly under multiple stressors. *Global Change Biology*. **19**, 1930–1940.

Davis J, Sim L, Chambers J (2010) Multiple stressors and regime shifts in shallow aquatic ecosystems in antipodean landscapes. *Freshwater Biology*, **55**, 5–18.

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: Biodiversity conservation in a changing climate. *Science*, **332**, 53–58.

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27–year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 17995–17999.

Delesalle B, Pichon M, Frankignoulle M, Gattuso JP (1993) Effects of a cyclone on coral reef phytoplankton biomass, primary production and composition (Moorea Island, French Polynesia). *Journal of Plankton Research*, **15**, 1413–1423.

Done T (1992) Constancy and change in some Great Barrier Reef coral communities: 1980-1990. *American Zoologist*, **32**, 655–662.

Dubinsky Z, Stambler N (1996) Marine pollution and coral reefs. *Global Change Biology*, **2**, 511–526.

Dunne R (2010) Synergy or antagonism—interactions between stressors on coral reefs. *Coral Reefs*, **29**, 145–152.

Dunne RP, Brown BE (1996) Penetration of solar UVB radiation in shallow tropical waters and its potential biological effects on coral reefs; Results from the central Indian Ocean and Andaman Sea. *Marine Ecology-Progress Series*, **144**, 109–118.

Dunne RP, Brown BE (2001) The influence of solar radiation on bleaching of shallow water reef corals in the Andaman Sea, 1993-1998. *Coral Reefs*, **20**, 201–210.

Efron B, Tibshirani RJ (1994) *An Introduction to the Bootstrap*, Chapman & Hall/CRC Monographs on Statistics & Applied Probability, New York, NY.

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin*, **50**, 125–146.

Fautin DG, Buddemeier RW (2004) Adaptive bleaching: a general phenomenon. *Hydrobiologia*, **530**, 459–467.

Faxneld S, Jorgensen TL, Tedengren M (2010) Effects of elevated water temperature, reduced salinity and nutrient enrichment on the metabolism of the coral Turbinaria mesenterina. *Estuarine Coastal and Shelf Science*, **88**, 482–487.

Feary DA, Burt JA, Bauman AG, Usseglio P, Sale PF, Cavalcante GH (2010) Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future? *Journal of Fish Biology*, **77**, 1931–1947.

Fine M, Banin E, Israely T, Rosenberg E, Loya Y (2002) Ultraviolet radiation prevents bleaching in the Mediterranean coral *Oculina patagonica*. *Marine Ecology Progress Series*, **226**, 249–254.

Fisheries and Oceans Canada (2008) *Five-Year Research Plan*. Fisheries and Oceans Canada, Ottawa, Ontario.

Fitt WK, Warner ME (1995) Bleaching patterns of four species of Caribbean reef corals. *Biological Bulletin*, **189**, 298–307.

Fitt WK, Brown BE, Warner ME, Dunne RP (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs*, **20**, 51–65.

Folt CL, Chen CY, Moore MV, Burnaford J (1999) Synergism and antagonism among multiple stressors. *Limnology and Oceanography*, **44**, 864–877.

Gardiner NM, Munday PL, Nilsson GE (2010) Counter-gradient variation in respiratory performance of coral reef fishes at elevated temperatures. *PLoS ONE*, **5**, e13299.

Goreau TJ, Hayes RL (1994) Coral bleaching and ocean "hot spots". *Ambio*, **23**, 176–180.

Graham NAJ, Chabanet P, Evans RD *et al.* (2011) Extinction vulnerability of coral reef fishes. *Ecology Letters*, **14**, 341–348.

Graham NAJ, Bellwood DR, Cinner J, Hughes TP, Norström A, Nyström M (2013) Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment*, **11**, 541–548.

Great Barrier Reef Marine Park Authority (2009) *Great Barrier Reef Outlook Report 2009*, Great Barrier Reef Marine Park Authority. Townsville.

Griffin SP (1998) The effects of sunlight on the progression of Black Band Disease. *Revista De Biologia Tropical*, **46**, 175–179.

Grigg RW, Grossman EE, Earle SA, Gittings SR, Lott D, McDonough J (2002) Drowned reefs and antecedent karst topography, Au'au Channel, SE Hawaiian Islands. *Coral Reefs*, **21**, 73–82.

Halpern BS, Selkoe KA, Micheli F, Kappel CV (2007) Evaluating and ranking the vulnerability of global marine ecosystems to anthropogenic threats. *Conservation Biology*, **21**, 1301–1315.

Halpern BS, Walbridge S, Selkoe KA *et al.* (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.

Harvell CD, Kim K, Burkholder JM *et al.* (1999) Emerging marine diseases - Climate links and anthropogenic factors. *Science*, **285**, 1505–1510.

Harvell D, Kim K, Quirolo C, Weir J, Smith G (2001) Coral bleaching and disease: contributors to 1998 mass mortality in *Briareum asbestinum* (Octocorallia, Gorgonacea). *Hydrobiologia*, **460**, 97–104.

Hayne M, Chappell J (2001) Cyclone frequency during the last 5000 years at Curacoa Island, north Queensland, Australia. *Palaeogeography Palaeoclimatology Palaeoecology*, **168**, 207–219.

Hecky RE, Muginne R, Ramlal PS, Talbot MR, Kling GW (2010) Multiple stressors cause rapid ecosystem change in Lake Victoria. *Freshwater Biology*, **55**, 241–257.

Hedges LV (1981) Distribution theory for Glass's estimator of effect size and related estimators. *Journal of Educational Statistics*, **6**, 107–128.

Hetzinger S, Pfeiffer M, Dullo WC, Keenlyside N, Latif M, Zinke J (2008) Caribbean coral tracks Atlantic Multidecadal Oscillation and past hurricane activity. *Geology*, **36**, 11–14.

Higgins JPT, Thompson SG (2002) Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine*, **21**, 1539–1558.

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, **50**, 839–866.

Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science*, **328**, 1523–1528.

Holcomb M, McCorkle DC, Cohen AL (2010) Long-term effects of nutrient and CO2 enrichment on the temperate coral Astrangia poculata (Ellis and Solander, 1786). *Journal of Experimental Marine Biology and Ecology*, **386**, 27–33.

Hughes TP, Baird AH, Bellwood DR *et al.* (2003) Climate change, Human impacts, and the resilience of coral reefs. *Science*, **301**, 929–933.

Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution*, **20**, 380–386.

Hughes TP, Gunderson LH, Folke C *et al.* (2007) Adaptive management of the Great Barrier Reef and the Grand Canyon World Heritage Areas. *Ambio*, **36**, 586–592.

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution*, **25**, 633–642.

Humphrey C, Weber M, Lott C, Cooper T, Fabricius K (2008) Effects of suspended sediments, dissolved inorganic nutrients and salinity on fertilisation and embryo development in the coral Acropora millepora (Ehrenberg, 1834). *Coral Reefs*, **27**, 837–850.

Jackson J, Kirby M, Berger W *et al.* (2001) Historical over-fishing and the recent collapse of coastal ecosystems. *Science*, **293**, 629–638.

Johnson LG, Babcock RC (1994) Temperature and the larval ecology of the crown-of-thorns starfish, *Acanthaster planci*. *Biological Bulletin*, **187**, 304–308.

Jones RJ (2008) Coral bleaching, bleaching-induced mortality, and the adaptive significance of the bleaching response. *Marine Biology*, **154**, 65–80.

Keller BD, Gleason DF, McLeod E *et al.* (2009) Climate change, coral reef ecosystems, and management options for marine protected areas. *Environmental Management*, **44**, 1–20.

Kendall CGSC, Schlager W (1981) Carbonates and relative changes in sea level. *Marine Geology*, **44**, 181–212.

Kerswell AP, Jones RJ (2003) Effects of hypo-osmosis on the coral Stylophora pistillata: nature and cause of 'low-salinity bleaching'. *Marine Ecology-Progress Series*, **253**, 145–154.

Kleypas JA, Buddemeier RW, Archer D, Gattuso J-P, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science*, **284**, 118–120.

Knowlton N (2001) The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 5419–5425.

Kumar SP, Roshin RP, Narvekar J, Kumar PKD, Vivekanandan E (2009) Response of the Arabian Sea to global warming and associated regional climate shift. *Marine Environmental Research*, **68**, 217–222.

Langdon C, Atkinson MJ (2005) Effect of elevated pCO(2) on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research-Oceans*, **110**, S07.

Lesser MP (1997) Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral Reefs*, **16**, 187–192.

Lesser MP, Stochaj WR, Tapley DW, Shick JM (1990) Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs*, **8**, 225–232.

Lewis SE, Brodie JE, Bainbridge ZT *et al.* (2009) Herbicides: A new threat to the Great Barrier Reef. *Environmental Pollution*, **157**, 2470–2484.

Lindenmayer DB, Likens GE, Krebs CJ, Hobbs RJ (2010) Improved probability of detection of ecological 'surprises'. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21957–21962.

Lo-Yat A, Simpson SD, Meekan M, Lecchini DD, Martinez E, Galzin R (2011) Extreme climatic events reduce ocean productivity and larval supply in a tropical reef ecosystem. *Global Change Biology*, **17**, 1695–1702.

Manzello DP, Brandt M, Smith TB, Lirman D, Hendee JC, Nemeth RS (2007) Hurricanes benefit bleached corals. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 12035–12039.

Maynard JA, Anthony KRN, Harvell CD *et al.* (2011) Predicting outbreaks of a climate-driven coral disease in the Great Barrier Reef. *Coral Reefs*, **30**, 485–495.

McClanahan TR, Cinner JE, Maina J *et al.* (2008) Conservation action in a changing climate. *Conservation Letters*, **1**, 53–59.

McClanahan TR, Graham NAJ, MacNeil MA, Muthiga NA, Cinner JE, Bruggemann JH, Wilson SK (2011) Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 17230–17233.

Melbourne-Thomas J, Johnson CR, Fulton EA (2011) Regional-scale scenario analysis for the Meso-American Reef system: Modelling coral reef futures under multiple stressors. *Ecological Modelling*, **222**, 1756–1770.

Middlebrook R, Anthony KRN, Hoegh-Guldberg O, Dove S (2010) Heating rate and symbiont productivity are key factors determining thermal stress in the reef-building coral *Acropora formosa*. *Journal of Experimental Biology*, **213**, 1026–1034.

Miller J, Waara R, Muller E, Rogers C (2006) Coral bleaching and disease combine to cause extensive mortality on reefs in US Virgin Islands. *Coral Reefs*, **25**, 418–418.

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. *Ecological Economics*, **29**, 215–233.

Møller AP, Jennions MD (2001) Testing and adjusting for publication bias. *Trends in Ecology and Evolution*, **16**, 580–586.

Moran PJ (1986) The Acanthaster phenomenon. *Oceanography and Marine Biology*, **24**, 379–480.

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology & Evolution*, **23**, 555–563.

Mumby PJ, Chisholm JRM, Edwards AJ, Andrefouet S, Jaubert J (2001) Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. *Marine Ecology-Progress Series*, **222**, 209–216.

Mydlarz LD, Couch CS, Weil E, Smith G, Harvell CD (2009) Immune defenses of healthy, bleached and diseased Montastraea faveolata during a natural bleaching event. *Diseases of Aquatic Organisms*, **87**, 67–78.

Negri AP, Flores F, Rothig T, Uthicke S (2011) Herbicides increase the vulnerability of corals to rising sea surface temperature. *Limnology and Oceanography*, **56**, 471–485.

NOAA (2012) *NOAA's Integrated Assessment Program*. Available at: http://www.noaa.gov/iea/ (accessed: 22 October 2012)

Office of Research and Development (2005) *Wildlife Research Strategy*. (ed. United States Environmental Protection Agency), Research Triangle Park, NC.

Paine RT, Tegner MJ, Johnson EA (1998) Compounded perturbations yield ecological surprises. *Ecosystems*, **1**, 535–545.

Payton ME, Greenstone MH, Schenker N (2003) Overlapping confidence intervals or standard error intervals: What do they mean in terms of statistical significance? *Journal of Insect Science*, **3**, 1–6.

PICES (North Pacific Marine Science Association) (2012) *Working Group 28: Development of Ecosystem Indicators to Characterize Ecosystem Responses to Multiple Stressors*. North Pacific Marine Science Organization, Available at: http://www.pices.int/members/working_groups/wg28.aspx (accessed: 22 October 2012).

Pielke RA Jr (2005) Hurricanes and global warming. *Bulletin of the American Meteorological Society*, **86**, 1571–1575.

Pittock AB (1999) Coral reefs and environmental change: Adaptation to what? *American Zoologist*, **39**, 10–29.

Porter JW, Lewis SK, Porter KG (1999) The effect of multiple stressors on the Florida Keys coral reef ecosystem: A landscape hypothesis and a physiological test. *Limnology and Oceanography*, **44**, 941–949.

Przeslawski R, Davis AR, Benkendorff K (2005) Synergistic effects associated with climate change and the development of rocky shore molluscs. *Global Change Biology*, **11**, 515–522.

Przeslawski R, Ahyong S, Byrne M, Worheide G, Hutchings P (2008) Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biology*, **14**, 2773–2795.

R Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Remily ER, Richardson LL (2006) Ecological physiology of a coral pathogen and the coral reef environment. *Microbial Ecology*, **51**, 345–352.

Richardson LL, Ragoonath DN (2008) Organic carbon enhances dark survival of the cyanobacterium *Geitlerinema* sp. isolated from black band disease of corals. *Revista De Biologia Tropical*, **56**, 119–126.

Robison JD, Warner ME (2006) Differential impacts of photoacclimation and thermal stress on the photobiology of four different phylotypes of Symbiodinium (Pyrrhophyta). *Journal of Phycology*, **42**, 568–579.

Rogers JE, Marcovich DT, Jordan SJ, Gallaher SN (2010) Does temperature and UV exposure history modulate the effects of temperature and UV stress on Symbiodinium growth rates? *Bulletin of Marine Science*, **86**, 743–761.

Rosenberg E, Kushmaro A, Kramarsky-Winter E, Banin E, Yossi L (2009) The role of microorganisms in coral bleaching. *Isme Journal*, **3**, 139–146.

Russell BD, Thompson JI, Falkenberg LJ, Connell SD (2009) Synergistic effects of climate change and local stressors: CO_2 and nutrient-driven change in subtidal rocky habitats. *Global Change Biology*, **15**, 2153–2162.

Salbu B, Rosseland BA, Oughton DH (2005) Multiple stressors - a challenge for the future. *Journal of Environmental Monitoring*, **7**, 539–539.

Schenker N, Gentleman JF (2001) On judging the significance of differences by examining the overlap between confidence intervals. *The American Statistician*, **55**, 182–186.

Selkoe K, Halpern B, Ebert C *et al*. (2009) A map of human impacts to a “pristine” coral reef ecosystem, the Papahānaumokuākea Marine National Monument. *Coral Reefs*, **28**, 635–650.

Shick JM, Lesser MP, Jokiel PL (1996) Effects of ultraviolet radiation on corals and other coral reef organisms. *Global Change Biology*, **2**, 527–545.

Suggett DJ, Dong LF, Lawson T, Lawrenz E, Torres L, Smith DJ (2013) Light availability determines susceptibility of reef building corals to ocean acidification. *Coral Reefs*, **32**, 327–337.

Sutherland WJ, Adams WM, Aronson RB *et al.* (2009) One hundred questions of importance to the conservation of global biological biodiversity. *Conservation Biology*, **23**, 557–567.

Szmant AM (2002) Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? *Estuaries*, **25**, 743–766.

Thompson HM (1996) Interactions between pesticides; a review of reported effects and their implications for wildlife risk assessment. *Ecotoxicology*, **5**, 59–81.

Thurber RLV, Barott KL, Hall D *et al.* (2008) Metagenomic analysis indicates that stressors induce production of herpes-like viruses in the coral *Porites compressa*. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 18413–18418.

Underwood AJ (1989) The analysis of stress in natural populations. *Biological Journal of the Linnean Society*, **37**, 51–78.

Valentine JF, Heck Jr KL (2005) Perspective review of the impacts of overfishing on coral reef food web linkages. *Coral Reefs*, **24**, 209–213.

Vargas-Angel B, Peters EC, Kramarsky-Winter E, Gilliam DS, Dodge RE (2007) Cellular reactions to sedimentation and temperature stress in the Caribbean coral *Montastraea cavernosa*. *Journal of Invertebrate Pathology*, **95**, 140–145.

Venn AA, Wilson MA, Trapido-Rosenthal HG, Keely BJ, Douglas AE (2006) The impact of coral bleaching on the pigment profile of the symbiotic alga, Symbiodinium. *Plant Cell and Environment*, **29**, 2133–2142.

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, **36**, 1–48.

Vinebrooke RD, Cottingham KL, Norberg J, Scheffer M, Dodson SI, Maberly SC, Sommer U (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. *Oikos*, **104**, 451–457.

Visram S, Douglas AE (2007) Resilience and acclimation to bleaching stressors in the scleractinian coral *Porites cylindrica*. *Journal of Experimental Marine Biology and Ecology*, **349**, 35–44.

Walther G, Post E, Convey P *et al*. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Ward JR, Kim K, Harvell CD (2007) Temperature affects coral disease resistance and pathogen growth. *Marine Ecology-Progress Series*, **329**, 115–121.

Wenger RB, Harris HJ, Sivanpillai R, DeVault DS (1999) A graph-theoretic analysis of relationships among ecosystem stressors. *Journal of Environmental Management*, **57**, 109–122.

van Woesik R, Ayling AM, Mapstone B (1991) Impact of Tropical Cyclone Ivor on the Great Barrier Reef, Australia. *Journal of Coastal Research*, **7**, 551–558.

van Woesik R, DeVantier LM, Glazebrook JS (1995) Effects of cyclone ‘Joy’ on nearshore coral communities of the Great Barrier Reef. *Marine Ecology Progress Series*, **128**, 261–270.

Willis BL, Page CA, Dinsdale EA (2004) Coral Disease on the Great Barrier Reef. In: *Coral Health and Disease*, (eds Rosenberg E, Loya Y), pp. 69–104. Springer-Verlag, Berlin.

Wooldridge SA (2009) Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, **58**, 745–751.

Yakovleva I, Hidaka M (2004) Different effects of high temperature acclimation on bleaching-susceptible and tolerant corals. *Symbiosis*, **37**, 87–105.

Yamaguchi M (1974) Effect of elevated temperature on metabolic activity of coral reef Asteroid *Acanthaster planci* (L). *Pacific Science*, **28**, 139–146.

Yee SH, Barron MG (2010) Predicting coral bleaching in response to environmental stressors using 8 years of global-scale data. *Environmental Monitoring and Assessment*, **161**, 423–438.

Yee SH, Santavy DL, Barron MG (2008) Comparing environmental influences on coral bleaching across and within species using clustered binomial regression. *Ecological Modelling*, **218**, 162–174.

Zhao BC, Wang ZH, Chen J, Chen ZY (2008) Marine sediment records and relative sea level change during late Pleistocene in the Changjiang delta area and adjacent continental shelf. *Quaternary International*, **186**, 164–172.

Zhu BH, Wang GC, Huang B, Tseng CK (2004) Effects of temperature, hypoxia, ammonia and nitrate on the bleaching among three coral species. *Chinese Science Bulletin*, **49**, 1923–1928.

Supporting Information

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

Appendix S1. Type II error and the two-interval method.
Figure S1. Funnel plot of the light-temperature interaction term from studies with F_v/F_m, zooxanthellae density, or [chlorophyll a] as the response variable.
Table S1. Search terms used to identify studies using the Web of Science database.
Table S2. Table of hypothetical values illustrating the Type II error associated with using overlapping confidence intervals as indicator of significant differences.
Table S3. Multiple-stressor studies with photosynthesis as the response variable. N.f.f. = not fully factorial, i.e. experiment not designed to detected synergistic effects.
Table S4. Stressor-stressor interactions and direction of influence (↑ reinforcing, ↓ mitigating, ↔ mixed or no-effect). Empty rows/columns/rows omitted.
Table S5. Summary of multiple-stressor studies as listed in Table 2.
Table S6. Meta-regression of effect size for all photosynthetic response variables from multiple-stressor studies that examined both temperature and irradiance as stressors (n = 26).