Ivan Nagelkerken and Sean D. Connell
Global alteration of ocean ecosystem functioning due to increasing human CO₂ emissions
Proceedings of the National Academy of Sciences of the United States of America, 2015; 112(43):13272-13277

© The Author(s)
Originally published at: http://dx.doi.org/10.1073/pnas.1510856112

PERMISSIONS
http://www.pnas.org/site/aboutpnas/authorfaq.xhtml

6. Can I post my article on the Internet?
Yes, you may post the PDF of your article on a personal Web site, or portion of a site, either owned by you or at your institution (provided that the institution is nonprofit), and devoted to you and your work, provided that you include a link to the PNAS Web site.

24 August 2016

http://hdl.handle.net/2440/100658
Global alteration of ocean ecosystem functioning due to increasing human CO₂ emissions

Ivan Nagelkerken¹ and Sean D. Connell

Southern Seas Ecology Laboratories, School of Biological Sciences and The Environment Institute, The University of Adelaide, Adelaide, SA 5005, Australia

Edited by Nancy Knowlton, Smithsonian Institution, DC, Washington, and approved September 10, 2015 (received for review June 2, 2015)

Rising anthropogenic CO₂ emissions are anticipated to drive change to ocean ecosystems, but a conceptualization of biological change derived from quantitative analyses is lacking. Derived from multiple ecosystems and latitudes, our metaanalysis of 632 published experiments quantified the direction and magnitude of ecological change resulting from ocean acidification and warming to conceptualize broadly based change. Primary production by temperate noncalcifying plankton increases with elevated temperature and CO₂, whereas tropical plankton decreases productivity because of acidification. Temperature increases consumption by and metabolic rates of herbivores, but this response does not translate into greater secondary production, which instead decreases with acidification in calcifying and noncalcifying species. This effect creates a mismatch with carnivores whose metabolic and foraging costs increase with temperature. Species diversity and abundances of tropical as well as temperate species decline with acidification, with shifts favoring novel community compositions dominated by noncalcifiers and microorganisms. Both warming and acidification instigate reduced calcification in tropical and temperate reef-building species. Acidification leads to a decline in dimethylsulfide production by ocean plankton, which as a climate gas, contributes to cloud formation and maintenance of the Earth’s heat budget. Analysis of responses in short- and long-term experiments and of studies at natural CO₂ vents reveals little evidence of acclimation to acidification or temperature changes, except for microbes. This conceptualization of change across whole communities and their trophic linkages forecast a reduction in diversity and abundances of various key species that underpin current functioning of marine ecosystems.

Significance

People are not only concerned about climate change and its effects on plant and animal diversity but also about how humans are fundamentally changing the globe’s largest ecosystem that sustains economic revenue and food for many countries. We show that many species communities and ocean habitats will change from their current states. Ocean acidification and warming increase the potential for an overall simplification of ecosystem structure and function with reduced energy flow among trophic levels and little scope for species to acclimate. The future simplification of our oceans has profound consequences for our current way of life, particularly for coastal populations and those that rely on oceans for food and trade.

Author contributions: I.N. designed research; I.N. and S.D.C. performed research; I.N. derived metaanalysis; I.N. and S.D.C. conducted quantitative analyses; I.N. interpreted data; I.N. and S.D.C. wrote the paper. The authors declare no conflict of interest.

¹To whom correspondence should be addressed. Email: ivan.nagelkerken@adelaide.edu.au.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1510856112/-/DCSupplemental.
Results

Acclimation to warming, acidification, and their combination was small across the main effects we studied. In general, there was a trend of the effect sizes of longer-term experiments being equal or stronger than those of short-term experiments (Fig. 1 and Fig. S1). Likewise, suppressed species abundances and diversity at natural CO₂ vents, where organisms have been exposed to elevated CO₂ over extend time periods, are comparable to declines within laboratory experiments (Fig. 2 A and C). Only microorganisms, which are taxa with short generation times and occupy a wide range of (extreme) niches, showed population abundance increases at CO₂ vents in (sub)tropical regions (Fig. 2C).

Phytoplankton generate nearly half the planetary net primary production (13), which maintains the diversity and abundance of marine life, ecosystem services, and capacity for fishery yields and influences climate processes per se. Increasing temperature and CO₂ could enhance terrestrial primary production (14), although suitable plant-growing days, for example, decrease when changes in other abiotic factors are considered as well (15). In the ocean, elevated temperature has been predicted to increase primary production in polar regions and decrease production in tropical areas (16). Our metaanalysis reveals no effects of ocean acidification on pelagic production by tropical or temperate phytoplankton communities (Fig. 1 A and Tables S1 and S2). Single-species experiments, in contrast, show that ocean warming and acidification have a positive effect on primary production by temperate noncalcifying species but that acidification has a negative effect on production by tropical species (Fig. S2 A and B). However, warming also enhances oceanic stratification, exposing phytoplankton to the negative effects of greater levels of harmful UV light (17) and reduced transport of nutrients from ocean depths (18, 19). The disproportionately large contribution of phytoplankton to primary productivity (13) contributes substantially to the ocean’s net CO₂ uptake from the atmosphere (20). Changes in phytoplankton productivity attributable to ocean warming, through the contrasting direct effects of temperature and indirect effects of stratification, could, therefore, be a mechanism through which primary production might be altered in surface oceans. This alteration could consequently modify the demand for atmospheric CO₂ as a resource. However, there is no simple relationship between net primary production and net CO₂ uptake between the ocean and atmosphere, and a fraction of the production is rapidly respired to CO₂ and thus does not contribute to a net CO₂ sink.

Predicting the consequences of changing primary productivity is not simple because of the complex interplay among species interactions and their multiple drivers. Nevertheless, whereas warming increases consumption of primary productivity through higher metabolic rates (Fig. 1 C and D), secondary production by invertebrates in tropical as well as temperate regions decreases because of ocean acidification, as established by both single-species and multispecies studies (Fig. 1B and Table S1). Loss of secondary productivity under future scenarios forms a contrast with changing energetic demands of their predators, whose foraging and metabolic rates increase because of acidification as well temperature in tropical, temperate, and polar regions (Fig. 1 C and D and Table S1). Warming can intensify trophic cascades, leading to stronger control by top consumers (21), whereas a reduction in pH imposes energetic costs on acid–base balance (22) that may act as a stressor on many carnivores. Collectively, ocean warming and acidification showed contrasting effects on productivity and consumption at multiple trophic levels, but with higher-order carnivores at clear risk of not meeting increased energetic demands.

Our metaanalysis shows an overall decrease of tropical and temperate (but not polar) species abundances and diversity across multiple functional and species groups attributable to ocean acidification (Fig. 2 and Tables S1 and S2). Ocean acidification increases the potential for simplification of species communities for calcifying and noncalcifying species alike (Fig. 24). Of all taxa, benthic (sub)tropical microorganisms are the clearest “winners” from the effects of ocean acidification (Fig. 2 A and C). Simplification of trophic structure and reduced species diversity has been shown to lead to diminished functional redundancy, which has been coupled to lower ecosystem resistance.

Fig. 1. Effect of ocean acidification and warming on ecosystem processes and functional groups and scope for acclimation. (A–F) Mean effect size and direction of impacts from ocean acidification (OA) (blue) on species tested in multispecies experiments (Com OA) and of impacts from ocean acidification, warming (T) (orange), and their combined effects (OA×T) (red) on species tested in single-species experiments, for primary production (A), secondary production by invertebrates (B), foraging rate (C), metabolic rate (D), calcification rate (E), and DMS production (F). Scope for acclimation (Acclim.) compares short (<1 mo) vs. long (1–13 mo) experiments on the combined effects of warming and acidification. Error bars represent 95% confidence intervals. Numbers between brackets indicate sample size (no. of experiments). *P ≤ 0.05.
Fig. 2. Effect of ocean acidification on species diversity and abundances based on multispecies experiments. Mean effect size and direction of impacts of ocean acidification on species diversity (A and B) and abundances of species within communities, for multispecies studies only (C and D). (A and C, Center) Categorical effects where data are split for various functional groups: calcifying species alone (Cal), noncalcifying species alone (eukaryotes) (N-Cal), mixed communities of calcifiers and noncalcifiers (Mix), and microorganisms (Micro) (blue circles with gray filling). (A and C, Right) Effect sizes for short-term (≤1 mo.) vs. longer-term (1–13 mo.) vs. in situ studies on natural CO$_2$ vents, separated for microbes and all other species. (B and D) Effect sizes for different species groups. Error bars represent 95% confidence intervals. Numbers between brackets indicate sample size. *$P$ ≤ 0.05.

Ocean acidification has a greater negative effect on abundances of calcifying taxa (e.g., various species of crustaceans, molluscs, and calcifying macroalgae) than noncalcifiers (e.g., various species of noncalcifying macroalgae, sponges, autotrophic and heterotrophic plankton, and benthic invertebrates) (Fig. 2 C and D). A potential community shift toward noncalcifiers is reinforced by the differential effects that the combination of ocean acidification and increasing temperature have on primary and secondary production of noncalcifiers vs. calcifiers (Fig. 1 A and B). Such potential shifts to communities dominated by noncalcifying organisms have profound implications for pelagic and benthic systems.

For pelagic species, warming causes a shift toward smaller pico- and nanoplankton species (to the detriment of microplankton; Fig. S2C), which are less suitable as a food source for zooplankton (25). Furthermore, our results reveal a significant direct negative effect of CO$_2$ on dimethylsulfide (DMS) production by temperate phytoplankton communities (Fig. 1F and Table S1). DMS is a driver of food web structure (26), acting as an antigrazing defense mechanism in phytoplankton (27), while also providing chemical cues to attract predators (e.g., fishes, large zooplankton, birds) to prey that forage on phytoplankton (26, 28). DMS has the potential to mediate trophic interactions that span distances of millimeters (e.g., mesozooplankton attracted to grazing microzooplankton) to thousands of kilometers (e.g., seabirds attracted to oceanic areas with high plankton productivity). Alterations to oceanic DMS release can, therefore, alter the complex trophic interactions in the ocean (29). Reduced DMS production is also linked with potential increases in global temperature because it contributes to cloud formation as a climate gas (30, 31).

For tropical as well as temperate benthic species (Table S1), our analyses show a significant negative effect of acidification, warming, or their combination on calcification rates of key calcifying taxa that construct reefs, such as molluscs and tropical as well as cold water corals, and of calcareous algae that serve as a settlement substratum for coral larvae (Fig. 1E and Fig. S2D). Although there is broad agreement that calcification and abundance of tropical corals will decrease (9, 32), there is uncertainty of the overall effects on other foundation species. Mussel and oyster beds are the dominant reef-building taxa in estuaries and temperate coastal seas (33), whereas cold water corals construct large biogenic deep water reefs (34). A decline in such habitat-forming species at lowered pH and/or elevated temperature is likely to result in loss of secondary productivity, local extinctions, and reduced taxonomic distinctness (35, 36). The extent to which these indirect effects drive future change relative to direct effects is largely unknown (3, 21), although negative effects on habitat formers is likely to affect a greater number of species. Although our metaanalysis highlights negative effects for both habitat formers and users, it remains unclear how these effects will coincide.

**Discussion**

Ocean warming and acidification have received increasing focus as global change stressors, but marine species will also be impacted in their performance by other emerging stressors such as changes in sea surface height, UV, underwater irradiance, water salinity, and seawater oxygen content (7). Hypoxic zones are becoming widespread in oceanic as well as shelf environments because of climate change and local stressors such as eutrophication (37). Many species will be challenged by the interactive effects of ocean warming, acidification, and deoxygenation, but at present, hardly any (multistressors) studies exist to evaluate the effects of hypoxia on marine species and ecosystems (8, 38). For some species, there are opportunities to move to deeper waters or extend their ranges to higher latitudes, but not all species will be able to keep up with the pace of climate change, leading to alterations in current species distributions (39, 40). Moreover, species that have fewer generations (e.g., $k$ strategists with greater longevity and later maturation) have fewer opportunities to adapt to rapidly changing conditions forecast for
the next ~85 y. Unless longer-lived species relocate to climate re-
fugia, their persistence will rely more on mechanisms of acclima-
tion than adaption. Importantly, if acclimation and adaptation to climate have low potential, the probability for community change is heightened. Hence, variance for adaption among species (41), combined with low scope for acclimation (this study), jointly em-
phasize the potential for community change.

By integrating multispecies with multifactor experiments of
differing acclimation periods, we produce a conceptual insight into
how human greenhouse gas emissions may drive change to pelagic
and benthic ecosystems from different latitudes. Many of the
studies included in our metaanalysis manipulated temperature or
CO$_2$ to levels predicted for the end of this century (Table S1 and
Dataset S1). It is notable that despite variation in choice of ex-
perimental temperatures and CO$_2$ levels among studies, these
differences did not translate into detectable differences in the
effect size of most processes under study (Table S2). This finding
suggests that experimental outcomes are not only robust to such experimental choices but also that the magnitude of our forecast
responses are likely to be similar across the range of temperatures
and CO$_2$ levels anticipated at the end of the century. Although the
magnitude of future change in ocean temperature and pH will be
variable at local scales—potentially leading to different outcomes
at specific locations and for some species—there are emerging
patterns of change in ecosystem processes and species occurrences.
We find that ocean warming and acidification increase the poten-
tial for an overall simplification of ecosystem structure and
function, with reduced energy flow among trophic levels with little
scope for acclimation. Ocean acidification per se appears to have
the potential to bring penetrating modifications to ecological sys-
tems through changes in ecosystem processes and shifts in species
community structures. Although some ecosystem processes are
affected by ocean acidification only, others are affected by warming
alone or by the combination of the two stressors. These results,
therefore, provide a conceptual framework toward more inclusive
forecasts of future ecological change (Fig. 3).

Materials and Methods

Data Selection. We searched the literature for studies published through to
early 2014 on effects of ocean acidification on marine biota using Thomson
Reuters’ Web of Science. By using the search string “ocean acidification” we
explicitly incorporated studies that placed their experimental designs and
results within this broader context of climate change as distinct from those
testing the effects of changes in pH per se. We screened the titles and

![Conceptual diagram illustrating the main effects of ocean acidification, warming, and their combination on ecosystem processes and species groups, based on the metaanalysis results as shown in the various figures of our study. Circed arrows indicate the direction of change, and question marks (?) indicate less certain responses. The most likely feedback responses that exacerbate the direct effects of these two global stressors are indicated with white arrows. Two model ecosystems are shown here (reefs and surface-ocean) to visually capture potential change (present day (Upper Left and Upper Right) vs. future (Lower Left and Lower Right)) in species abundance, species diversity, and community shifts, as revealed by our metaanalysis for ecosystems in general. The changes shown here for reefs and surface-ocean are not exact outcomes of future states but merely emphasize overall responses for (relative) abundance of species.](image-url)
abstracts of ∼2,300 published articles, of which 151 studies (covering 632 experiments) met the requirements for inclusion (Dataset S1). We selected studying the individual effect of ocean acidification on species diversity, species community abundances, and DMS production and studies that investigated the effects of ocean acidification and warming on species performance (primary production, secondary production, foraging, metabolism, calcification). In addition to our own literature survey, we also cross-referenced our database with some more taxon-targeted metaanalyses on ocean acidification (S, 9, 10, 42), but this procedure added only a limited number of studies, suggesting that our search string in Web of Knowledge was very effective.

We focused our analyses on studies that used increases in CO2 and temperature, as predicted for year ∼2100, typically based on the representative concentration pathway (RCP) 8.5 emission scenario (business-as-usual). Under this scenario, global ocean surface temperatures are predicted to rise by an average (±1 SD) of ∼3.7 ± 0.7 °C (43) compared with the 1990s, whereas CO2 into the atmosphere will more than triple relative to preindustrial conditions, increasing from the current levels of ∼400 to ∼936 ppm by the end of the century. This scenario will lead to a decrease in ocean surface pH of approximately 0.33 ± 0.003 units by 2100 compared with the 1990s (43). Regarding the less likely high mitigation scenario RCP2.6, corresponding changes would be +0.7 ± (0.5) °C and -0.07 (±0.001) pH units, respectively. A few studies that we included used somewhat higher values than predicted for the RCP8.5 emission scenario, because their present-day conditions already showed above-average values for these stressors (e.g., enhanced acidification and to seasonal variations in shallow coastal areas that warm up faster during summertime), reflecting the variability as typically observed across ecosystems, latitudes, and water depths. Studies that used extreme temperature elevations or pH reductions that are well beyond the predictions for year 2100 were excluded from the analyses, following previous approaches (9). Average (SD) reduction in pH and enhancement of CO2 levels across all experiments included in our metaanalyses were +0.3 (0.1) units, +508 (230) ppm CO2, and +3.8 °C (1.1 °C), respectively, which closely match the average and range in projections for RCP8.5. Nevertheless, there was variability across studies in the treatment levels used. Elevation levels (Δ treatment vs. control of the experiment) and their SD for CO2 and temperature per main factor tested are shown in Table S1, and values per experiment are shown in Dataset S1. We did not normalize the data for experiments that used temperature or CO2 as a continuous variable, either simply averaging the seasonal averages or combining CO2 values for the different seasons into a new variable, the so-called seasonally averaged CO2 concentration. As our main focus was on the effects of acidification and warming, we excluded studies that investigated the effect of ocean acidification on species diversity, as those studies that specifically tested using metaanalysis, even though they are much more limited in number.

We investigated several categorical factors for the overall mean effect sizes that showed significant heterogeneity using a categorical random-effects model, which is analogous to a mixed-effects model in ANOVA. For this model, total heterogeneity Qc can be partitioned in the variance explained by the model (QM) and the residual variance not explained by the model (Qr). QM is the variance explained by a random-effects meta-analysis procedure (4,999 iterations), with a significant QM (Table S2) indicating statistical differences in the mean effects sizes among categories (within a factor).

We first tested for the effect of latitude as a categorical factor for all main response variables that showed a significant Qf (Table S2). Except for primary production, the response for the various main factors considered was similar for the different latitudes and the respective Qf was nonsignificant and/or very low, indicating other factors were more important. Hence, for secondary production, calcifiers vs. noncalcifiers was tested as a categorical factor instead (Table S2). For calcification rate, taxon was tested as a categorical factor, and the results are shown in Fig. S2D; in Fig. 1E, aggregated results are shown for comparative purposes only. For species diversity, functional group was tested as a categorical factor, and taxon-level responses were shown for comparative purposes only. For ocean acidification effects on species abundances, functional group level was tested as a categorical factor, and taxon-level responses were shown for comparative purposes only. For effects of temperature on species abundances, taxon was tested as a categorical factor. For primary productivity of single-species studies, either latitude or calcifiers vs. noncalcifiers or both categories were significant in independent categorical analyses, and therefore calcifiers vs. noncalcifiers was tested for the different latitudes separately (i.e., category calcifier within category latitude; the results are shown in Fig. S2A and B, whereas the aggregated results for calcifiers vs. noncalcifiers (across latitudes) are shown in Fig. 1A for comparative purposes only). In all other cases where Qf was nonsignificant, this finding implies that the various categories (functional groups/latitudes) showed a similar direction of response as the main effects analysis (either all positive or all negative); nevertheless, these responses are also plotted for some categories (Fig. 1) and reported (Table S2) to facilitate the understanding of the complex dataset.

To assess whether normalization of effect sizes to particular levels of altered pH or temperature would improve interpretive value, we performed a continuous random-effects metaanalysis on effect sizes across their different combinations using the relative differences between treatment and control as the explanatory variable. The relationship between effects sizes and predictor variables is calculated on the basis of a least-squares regression. In almost all cases, no significant correlations were detected (see regression results in Table S2) and the original data were analyzed without normalizing to pH or temperature.

To test for the potential of species to acclimate to changing stressors, we compared short-term experiments (<1 mo; range, 4–56 wk; mean ± SD: 11.6 ± 11.6 wk) as well as data collected
from natural CO\textsubscript{2} vents where many sessile or low-motility species have typically been exposed to decreased pH conditions over significant parts of their life cycle. For this specific analysis alone, we combined the data from single-species and multiple-species studies, and our interpretation is based on comparing the mean effect size and their 95% confidence intervals between short- and long-term experiments (rather than testing if their means differ from 0).

Sensitivity Analyses. Because data selection and weighing might affect the outcome of the overall effect size (44), we also calculated the unweighted effect sizes using a fixed-effects model. Because both approaches revealed similar trends and significances (test outcomes reported in Table S2), we report the weighted mean effect sizes. We tested for publication bias for main effects that were significant using Rosenthal's method of fail-safe numbers. The fail-safe number represents the number of studies with a nonsignificant outcome that needs to be added to change the effect sizes from significant to nonsignificant. Fail-safe numbers ranged between 7 and 1,151, with almost all cases > 19 (Table S2), which is relatively large compared with the sample sizes of main effects tested in our study.

ACKNOWLEDGMENTS. We thank T. Rossi for help with designing Fig. 3. This study was supported by Australian Research Council Future Fellowship Grants FT120100183 (to AJN) and FT0991993 (to S.D.C.).