INTERGOVERNMENTAL PANEL ON climate change

IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems

Bankoku Shinryokan
Okinawa, Japan
17–19 January 2011

Workshop Report

Edited by:
Christopher B. Field, Vicente Barros, Thomas F. Stocker, Qin Dahe,
Katharine J. Mach, Gian-Kasper Plattner,
Michael D. Mastrandrea, Melinda Tignor, Kristie L. Ebi

This meeting was agreed in advance as part of the IPCC workplan, but this does not imply working group or panel endorsement or approval of the proceedings or any recommendations or conclusions contained herein.

Supporting material prepared for consideration by the Intergovernmental Panel on Climate Change.
This material has not been subjected to formal IPCC review processes.

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Working Group II (WG II) – Impacts, Adaptation and Vulnerability

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WMO UNEP

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IPCC WGII/WGI Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems

17-19 January 2011
Okinawa, Japan

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Preface

Understanding the effects of increasing atmospheric CO_2 concentrations on ocean chemistry, commonly termed ocean acidification, as well as associated impacts on marine biology and ecosystems, is an important component of scientific knowledge about global change. The Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC) will include comprehensive coverage of ocean acidification and its impacts, including potential feedbacks to the climate system. To support ongoing AR5 assessment efforts, Working Group II and Working Group I (WGII and WGI) of the IPCC held a joint Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems in Okinawa, Japan, from 17 to 19 January 2011. The workshop convened experts from the scientific community, including WGII and WGI AR5 authors and review editors, to synthesise scientific understanding of changes in ocean chemistry due to increased CO_2 and of impacts of this changing chemistry on marine organisms, ecosystems, and ecosystem services.

This workshop report summarises the scientific content and perspectives presented and discussed during the workshop. It provides syntheses of these perspectives for the workshop's core topics: (i) the changing chemistry of the oceans, (ii) impacts of ocean acidification for individual organisms, and (iii) scaling up responses from individual organisms to ecosystems. It also presents summaries of workshop discussions of key cross-cutting themes, ranging from detection and attribution of ocean acidification and its impacts to understanding ocean acidification in the context of other stressors on marine systems. Additionally, the workshop report includes extended abstracts for keynote and poster presentations at the workshop.

We thank the Ministry of the Environment Japan, the National Institute for Environmental Studies, and the University of the Ryukyus for hosting the workshop and providing impeccable arrangements. The event could not have succeeded without the extensive efforts of Dr. Yukihiro Nojiri, as well as Claire Summers and Mizue Yuzurihara, at the National Institute for Environmental Studies. We also extend our gratitude to the members of the Scientific Steering Committee who contributed invaluable advice and considerable time in developing the workshop's scientific content and programme, in addition to the summaries contained in this report. Finally, we thank the workshop participants for their productive exchanges about current scientific understanding, which underpin this report.

We are convinced that this report, along with the workshop's scientific dialogues on ocean acidification and its impacts, will provide important input for the authors of the AR5 and the broader research community, as well as further stimulating collaboration across WGII and WGI of the IPCC.

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Executive Summary

Since the publication of the Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC), ocean acidification research has been advancing rapidly, evaluating the effects of increasing atmospheric CO_2 concentrations on ocean chemistry and the resulting biological impacts. Working Group II and Working Group I (WGII and WGI) of the IPCC held a joint Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems to summarize the body of science on ocean acidification and its impacts, as timely input to the IPCC Fifth Assessment Report (AR5).

The workshop consisted of four primary activities, interspersed with plenary discussion. First, through fourteen keynote presentations, invited experts provided a synthesis of the state of knowledge on ocean acidification and its impacts. The presentations summarized scientific understanding, identifying both what is known and what key uncertainties remain, for the overarching topics of the changing chemistry of the oceans, impacts of ocean acidification for individual organisms, and scaling up to ecosystems. Second, in six Breakout Groups, participants discussed and addressed questions related to cross-cutting themes: (i) detection and attribution of ocean acidification and its impacts; (ii) reconciling apparently contradictory observations; (iii) spatial and temporal scales of variability and rates of change; (iv) learning from the past and present to predict the future; (v) understanding the roles of multiple stressors; and (vi) scaling up to humans: the socioeconomics of ocean acidification. An additional ad hoc Breakout Group considered the glossary entries for "ocean acidification" that were used in the AR4, outlining considerations and potential improvements for the AR5. Third, workshop participants had the opportunity to provide brief oral highlights of their recent research results, discussing these results further during two poster sessions. Finally, the workshop concluded with three synthesis presentations that summarized the perspectives presented during the workshop for the overarching topics listed above, emphasizing the state of knowledge and important open questions.

This workshop report contains short reports written by the Chair and Rapporteur of each Breakout Group and by the presenters of the workshop's synthesis presentations. Additionally, it includes abstracts of all keynote and poster presentations, along with other workshop materials distributed to participants before the meeting. Below, short summaries of the discussions from the Breakout Group and synthesis presentations are given, with further details provided in the subsequent sections of this workshop report.

Summaries of Breakout Group Discussions:

Breakout Group I-1: Detection and attribution of ocean acidification and its impacts
(Chair: Chris Sabine, Rapporteur: Laurent Bopp)

This Breakout Group report summarizes participant discussions on detection and attribution of ocean acidification and its impacts. For the surface ocean, the whole water column, and specific ocean regions, the Breakout Group discussed the degree to which observed changes in ocean chemistry can be attributed to increases in atmospheric CO_2 -- as well as the degree to which biological impacts can be attributed to changing chemistry. Relevant detection and attribution approaches were considered, along with factors influencing their outcomes.

Breakout Group I-2: Reconciling apparently contradictory observations
(Chair: Jean-Pierre Gattuso, Rapporteur: Ulf Riebesell)

This Breakout Group report summarizes participant discussions on divergent observations of the effects of ocean acidification for marine organisms. For calcification in zooxanthellate corals and in plankton, as well as for other processes, the Breakout Group considered examples of contradictory observations, the level of disagreement among data sets, and possible explanations for apparently

conflicting results. From this evaluation, the Breakout Group investigated the complexity and species-specific nature of the coral calcification response to ocean acidification, the importance of clarifying present uncertainty about the responses of coccolithophores to ocean acidification, and the large inherent variability in the effects of ocean acidification for other processes considered.

Breakout Group I-3: Spatial and temporal scales of variability and rates of change
(Chair: Philip Munday, Rapporteur: Anne Cohen)

This Breakout Group report summarizes participant discussions of the relationships among physical, chemical, and biological processes on different spatial and temporal scales, with a focus on changing ocean chemistry and consequences for marine organisms and ecosystems. The Breakout Group considered mechanistic understanding across such scales and ways to improve this understanding, for example, through consideration of analogue or naturally variable systems and through use of varying experimental approaches to constrain sensitivities and investigate physiological mechanisms.

Breakout Group II-1: Learning from the past and present to predict the future
(Chair: Daniela Schmidt, Rapporteur: Christoph Heinze)

In the context of understanding and projecting future responses of marine ecosystems to ocean acidification, this Breakout Group report considers participant discussions of both the utility and the limitations of studying past changes in ocean chemistry including associated mass extinctions. The Breakout Group discussed the importance of such studies for evaluating acclimation, evolutionary adaptation, and ecosystem changes. Yet it also indicated the uniqueness of anthropogenic ocean acidification and the need to consider factors such as relevant timescales, amplitudes of change, and uncertainties in the paleoceanographic proxies.

Breakout Group II-2: Understanding the roles of multiple stressors
(Chair: Peter Haugan, Rapporteur: Gretchen Hofmann)

This Breakout Group report summarizes participant discussions of ocean acidification in the context of other stressors, ranging from temperature change to fishing pressure. The Breakout Group also identified a list of scientific studies on multiple stressors. Complications in and approaches for understanding interactions among stressors were considered, along with the potential for abrupt changes.

Breakout Group II-3: Scaling up to humans: the socioeconomics of ocean acidification
(Chair: Peter Brewer, Rapporteur: Carol Turley)

This Breakout Group report highlights the key elements of participant discussions about socioeconomic impacts of ocean acidification, focusing on the ways in which experimental findings and socioeconomic knowledge can be combined to project effects of ocean acidification for marine ecosystems, ecosystem services, and human communities and economies dependent upon marine resources. The Breakout Group focused on ecosystems, such as coral-reef systems, and ecosystem services, such as fisheries and tourism, at risk. The Breakout Group discussed limitations in understanding related, for example, to ecosystem-based modeling, to interactions among stressors, and to valuation of ocean goods and services.

Ad Hoc Breakout Group: Glossary entry for "ocean acidification"
(Chair: Chris Sabine, Rapporteur: Laurent Bopp)

This Breakout Group report summarizes participant perspectives on the glossary entry for "ocean acidification" in the WGI and WGII contributions to the AR5, building from WGI and WGII glossary entries in the AR4 and from key attributes identified for an effective glossary entry. The Breakout Group suggested the following glossary entry for "ocean acidification": "Ocean acidification refers to a reduction in the pH of the ocean over an extended period, typically decades or longer, which is caused primarily by uptake of carbon dioxide from the atmosphere, but can also be caused by other chemical additions or subtractions from the ocean. Anthropogenic ocean acidification refers to the

component of pH reduction that is caused by human activity." It also suggested that AR5 author teams might supplement this glossary entry with a more detailed discussion of the term in a chapter box.

Summaries of Synthesis Plenary Presentations:

Synthesis Plenary IV-1: The changing chemistry of the oceans: the state of knowledge, key uncertainties, and the way forward
(Richard Feely and James Orr)

This report summarizes discussions from the workshop on the changing chemistry of the oceans. Focusing on research completed since the Fourth Assessment Report, the presenters indicated workshop perspectives on using past ocean acidification events as analogues for current and projected future changes. They also summarized understanding of trends in changes in the surface and subsurface ocean and across oceanic regions and of future projections in ocean carbon chemistry. Finally, the presenters discussed gaps in knowledge that are currently limiting further understanding, as well as potential ways to address them.

Synthesis Plenary IV-2: Impacts of ocean acidification for individual organisms: the state of knowledge, key uncertainties, and the way forward
(Andreas Andersson, Anne Cohen and Yukihiro Nojiri)

This synthesis report summarizes scientific understanding, as presented and discussed at the workshop, for impacts of ocean acidification for microbial processes and biogeochemistry, for phytoplankton calcification and photosynthesis, for fishes, for calcification and dissolution of coral reefs and coral reef organisms, and for non-coral reef invertebrates. For each category of impacts and corresponding processes, the presenters characterized the state of knowledge as presented at the workshop. The presenters also indicated limitations in current understanding for each category and for organisms and biological processes overall, such as challenges in extrapolating from laboratory findings to future responses in natural systems.

Synthesis Plenary IV-3: Scaling up to ecosystems: the state of knowledge, key uncertainties, and the way forward
(Ken Caldeira, Philip Munday and Hans-Otto Pörtner)

This report synthesizes perspectives from the participants on scaling understanding of ocean acidification and its impacts to the level of ecosystems. The presenters focused on detection and attribution of ecosystem changes due to ocean acidification and on projection of the impacts of ocean acidification for ecological processes. They indicated ways in which a mechanistic framework, building from underlying biological processes, could allow further integration of experimental results obtained at different levels of biological organization and through varying research methods and systems.

Overall, the Breakout Group and synthesis presentation summaries contained in this report characterize core topics, research, and cross-cutting questions related to ocean acidification and its impacts, as extensively considered and discussed at the workshop. The WGII and WGI Co-Chairs are convinced that these summaries, as well as the material provided in the report annexes, will provide useful input to the author teams of the AR5, as well as to the broader community of scientists studying ocean acidification.

Breakout Group Reports

Breakout Group I-1: Detection and attribution of ocean acidification and its impacts

Chair: Christopher Sabine (NOAA Pacific Marine Environmental Laboratory, USA)
Rapporteur: Laurent Bopp (Laboratoire des Sciences du Climat et de l'Environment, CNRS, France)

The summary that follows, written by the Chair and Rapporteur, characterizes the main points of the discussion that took place during Breakout Group I-1 at the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems. Participants in the Breakout Group considered a series of questions focused on cross-cutting themes in ocean acidification research, which was developed by the Scientific Steering Committee for the workshop.

Ocean acidification is one of a number of stressors affecting the ocean's ecosystems. For present day and projected future changes, this BOG explored, using data and models, the degree to which ocean acidification and its impacts can be detected and attributed to anthropogenic increases in atmospheric CO_2. The BOG discussed the ability of the current generation of ocean carbon cycle models to reflect the observed spatio-temporal distribution of carbon system parameters and pH in the global oceans. In addition, the BOG evaluated when and where changes in carbonate chemistry, along with associated uncertainties, are expected to be quantified in the open ocean, coastal zones, and estuaries. Finally, the BOG evaluated when and where ocean acidification and its impacts are expected to be identified and understood, independent of other interacting stressors.

The discussion was developed around a set of questions provided by the Scientific Steering Committee so this report follows that format.

1. To what extent can changes in ocean chemistry be directly linked to increases of atmospheric CO_2?

The group discussed the links between the anthropogenic increase in atmospheric CO_2 and recent changes in ocean carbonate chemistry. The answer to this question is that recent changes in ocean surface water chemistry can be unequivocally linked to atmospheric CO_2. However, for the whole water column this is true only to some extent. Observations suggest that other processes (e.g., changes in ocean circulation) may have a stronger imprint on changes in ocean chemistry in some locations over interannual to decadal time scales.

The group then discussed the definition of "ocean acidification" that should be used when discussing the links with atmospheric CO_2. Several points of confusion may arise depending on the exact connotations of the term: Is ocean acidification only a consequence of human actions, or could it be caused naturally (e.g., Do we refer to ocean acidification when discussing specific events in the geological past)? Is ocean acidification linked to increase of atmospheric CO_2 by definition, or could it be caused by the addition of other substances (sulfur / nitrogen deposition) or by processes that are internal to the ocean?

Recommendation to the IPCC AR5 authors: Discuss a common WGI-WGII definition for "ocean acidification" to be proposed as a common glossary entry to be used by both WGs.

An ad hoc breakout group was established to propose one or more candidate glossary entries (see the Ad Hoc Breakout Group Report). The glossary entry agreed by the Ad Hoc BOG and then discussed in the plenary was:

Ocean Acidification. *Ocean acidification refers to a reduction in the pH of the ocean over an extended period, typically decades or longer, which is caused primarily by uptake of carbon dioxide*

from the atmosphere, but can also be caused by other chemical additions or subtractions from the ocean. ***Anthropogenic ocean acidification*** *refers to the component of pH reduction that is caused by human activity.*

2. How do the various components of climate change in the ocean (warming, circulation changes, etc.) affect detection and attribution of direct CO_2-induced changes?

In the context of ocean acidification, detection and attribution methods should be applied as a multi-step process: from atmospheric CO_2 to changes in ocean chemistry, and from changes in ocean chemistry to the potential impacts of ocean acidification on marine organisms, ecosystems, and ocean biogeochemistry. The group discussed the first of these points (from atmospheric CO_2 to changes in ocean chemistry).

Using observations (repeated CO_2 surveys), a ΔpH signal can be separated into an anthropogenic component due to atmospheric CO_2 and another component due to changes in circulation / ventilation (e.g., using extended multiple linear regression (eMLR) methods applied in the North Pacific). These methods should be applied to other ocean basins, but one should keep in mind that they rely on strong assumptions (e.g., constant Redfield ratios, that is, constant stoichiometric ratios) that remain to be tested in other places.

Using the suite of CMIP5 simulations with climate & carbon cycle models on the historical period, it will soon be possible to separate the different components (internal climate variability, natural forcing, anthropogenic forcing including atmospheric CO_2) of changes on ocean chemistry.

Recommendation to the research community: Apply more formal detection and attribution methods to ocean acidification, for changes in ocean chemistry (as discussed above) but also for the potential impacts of ocean acidification (see discussion point 5.)

3. Are different approaches for determining atmospheric sources of ocean acidification required for coastal zones and estuaries, as compared to the open ocean?

Impacts of ocean acidification may have a more immediate and noticeable impact in coastal zones, but WGI science is traditionally not focused there. Additional points made during the discussion that extend the range of the question are: (1) that not only coastal zones and estuaries, but also marginal seas, should be considered, and (2) that the role of coastal zones and estuaries is also a key point for the global carbon cycle as these regions strongly contribute to a natural preindustrial outflux of carbon from the ocean estimated at 0.4 PgC yr^{-1} but with large uncertainties. This area of research should however benefit from recent developments in (1) data compilation of carbon variables in the global coastal ocean, (2) improvements in monitoring, modeling, compilation of river input (NEWS II project, estuaries classification, …), and (3) regional coastal modeling.

Recommendation to the research community: Consider working on a synthesis paper on ocean acidification in coastal zones, following the work done on air-sea carbon fluxes in these regions (e.g., Borges et al., 2005).

4. How well do observations and ocean carbon cycle models agree on the spatial distributions of aragonite and calcite saturation? What are the uncertainties of the present-day estimates of carbonate saturation from these models? How will model-data biases affect future projections of carbonate saturation and of ocean acidification in general?

Observations and ocean carbon cycle models broadly agree on the spatial distributions of aragonite and calcite saturation. This is true at the exception of some specific regions (e.g., North Pacific) where global models have much more difficulties in representing these quantities. It was noted that

the evaluation should not be restricted to these variables as good results/scores could be obtained from wrong reasons. The group agreed that not only simulated carbonate saturations should be compared and evaluated, but that ocean physics and circulation, and other carbon-related variables (pH, CO_2, dissolved inorganic carbon (DIC) and alkalinity, particle fluxes, …) should also be included. These evaluations will be made much easier thanks to the standard output variables in the CMIP5 protocol that will be made available for all models participating.

It was also made clear in the discussion that model results have proven to be much more consistent for simulating changes than for the generating the proper mean state. An alternative and useful approach to estimate future changes in ocean chemistry is based on adding simulated changes obtained from a series of model simulations to the mean state obtained from observations (e.g., Orr et al., 2005). The impact of the mean-state biases on feedbacks is however clearly unknown.

Recommendation to the research community: Consider working on a synthesis paper on model - observation comparisons (saturation state but also DIC, alkalinity, pH, …), identifying not only the model biases but also the reasons for the biases.

5. What are key considerations in detection and attribution of ocean acidification and its impacts in the context of multiple changes?

The primary point of discussion under this question was how one might go about trying to actually detect biological changes and then attribute those changes to ocean acidification. As discussed in previous sections, the changes in ocean chemistry are relatively straightforward to measure and document. However, most of the evidence of the impacts of elevated CO_2 comes from laboratory or mesocosm studies not from field observations. Very few studies, with the exception of areas with naturally high CO_2 because of bubbling from the seafloor, have actually documented ecosystem changes that can be directly attributed to ocean acidification. This is because there are multiple stressors on marine ecosystems that confound the attribution of changes to ocean acidification.

The group discussed ways that geochemical measurements might be used to detect biological changes that might then be attributed to ocean acidification. For example, changes in alkalinity might provide insights into potential changes in biocalcification and carbonate dissolution. Other types of measurements that could prove useful include radionuclides, particle flux measurements, remotely sensed observations of production, or specific species distributions and abundances. The impression of the group was that little effort had been put into determining when ocean acidification impacts on marine ecosystems might be detectable using geochemical approaches. Scoping studies are still needed to determine what might be feasible and how long it might be before signals are detectable. The group also noted that, although it may be more than a decade before there are detectable global geochemical signals, there may be specific regions where the signals may be detected sooner.

Recommendation to the research community: Consider the ocean acidification impacts that should be detectable using geochemical methods to answer questions like - what are the most appropriate measurements, where should the measurements be made, and how long it is expected to take before an ocean acidification signal may be detectable?

6. To what degree can impacts expected from ocean acidification be detected and linked to the changing chemistry of the oceans? To what degree can these impacts be formally attributed (e.g., through a formal multi-step attribution approach) to ocean acidification, as well as to anthropogenic increases in atmospheric CO_2?

This question builds from the last. As noted above, it is not clear that biogeochemical changes expected from ocean acidification can actually be detected in the field yet, much less formally attributed to ocean acidification. At the Hawaii Ocean Time-series site, for example, there is no

obvious trend in total alkalinity which one might expect if there has been a decrease in calcification over the 20 year record. Some modeling studies suggest that it may take at least 20–30 years to see a change in surface water alkalinity even with a substantial decrease in calcification. The group was not aware of similar modeling studies to determine when the shoaling of the aragonite saturation horizons should be detectable with a change in alkalinity. Given the variety of processes affecting ocean biogeochemical signals, it will be very difficult to attribute any observed changes specifically to ocean acidification.

Recommendation to the research community: In addition to the research recommended under question 5, further research is needed in the key regions where the first detectable signals are expected to determine what other processes will influence the attribution process and what additional observations or controls might help with the final attribution effort.

7. How do the interacting processes of calcification, dissolution, and organic matter remineralization impact feedback mechanisms for carbon cycling to the atmosphere?

The answer to this question strongly depends on the time scale being considered. On short time scales (<100 years), there are more than a dozen possible feedbacks related to ocean acidification and climate change that have been postulated. In the list of possible feedbacks, there are both positive and negative feedbacks. The majority of the models, however, suggest that the combination of feedbacks will have a slightly net negative feedback (decreased ocean uptake of CO_2). Most feel that the effects of ocean acidification on atmospheric CO_2 will be relatively small. On the other hand, on time scales of 10,000 years or more the dissolution of carbonate sediments due to the acidification of the ocean will provide one of the strongest positive feedbacks, ultimately removing as much as 90% of the anthropogenic CO_2 from the atmosphere and storing it in the ocean.

The science is less certain at intermediate time scales on the order of 1,000 years. Some of the uncertainty comes from the ambiguity in the rate of CO_2 buildup over the next few centuries, but there is also large uncertainty in how the ecosystem structure and geochemical cycling might change over these time scales. It was noted, for example, that we do not even have a well constrained budget for the calcium carbonate cycle at the moment. Estimates of global marine calcification vary by a factor of 4 or more, and there is disagreement over which organisms are the primary contributors to global calcification. There is also uncertainty where the pelagic calcification is remineralized (at what depth in the water column or possibly in the surface sediments). How quickly can dissolution occur in marine sediments? Additional work is needed to evaluate the processes affected by rising CO_2 and climate change so that these processes (including the calcium carbonate cycle) can be accurately incorporated into models that can project how these processes might change over the next few thousand years.

Recommendation to the research community: Consider working to develop a new global carbonate budget. Work to include a more accurate carbonate cycle into ocean and earth system models.

8. Other Issues

The group discussed the most productive ways to move forward from here. On the data side there was consensus that more effort was needed to collect biogeochemical measurements relevant to ocean acidification. This means fully constraining the inorganic carbon distributions (at least two parameters measured together) as well as collecting the relevant associated biological measurements at the same time and space scales. Additional biological and ecological assessments are needed including developing new techniques to assess ecosystem processes (e.g., pelagic calcification rates). In particular, more measurements are needed to constrain all aspects of the calcium carbonate cycle if we hope to be able to detect and attribute changes in calcification/remineralization resulting from ocean acidification.

On the model side, progress is needed on incorporating ocean acidification impacts on processes already in the models (e.g., productivity, species composition, carbon / nutrient uptake ratios) as well as adding processes that are not represented in most models (e.g., aragonite cycle). Development of coastal models that include ocean acidification will be particularly useful as the ocean acidification effects are likely to be confounded by many other climate change and anthropogenic factors and because the coastal zones are regions of great interest for economic reasons (e.g., fisheries and tourism). Coastal ocean acidification models will likely have to include interactive sediment and river components that will be a challenge to develop.

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Breakout Group I-2: Reconciling apparently contradictory observations

Chair: Jean-Pierre Gattuso (Centre National de la Recherche Scientifique, France)
Rapporteur: Ulf Riebesell (Leibniz Institute of Marine Sciences, Germany)

The summary that follows, written by the Chair and Rapporteur, characterizes the main points of the discussion that took place during Breakout Group I-2 at the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems. Participants in the Breakout Group considered a series of questions focused on cross-cutting themes in ocean acidification research, which was developed by the Scientific Steering Committee for the workshop.

Task: In the burgeoning fields of study related to ocean acidification, some experimental results (for example, from oceanic or regional observations, lab and mesocosm studies, observations of natural responses, and modeling) have been apparently contradictory. Following guidance provided by the Scientific Steering Committee, this Breakout Group (BOG) attempted to identify areas of controversy and provide possible explanations for them. In the interest of time, the group focused on three broad areas, as suggested in the BOG proposal from the Scientific Steering Committee:

1. Coral calcification
2. Planktonic calcification (forams, coccolithophorids)
3. Effects on processes other than calcification

Setting the stage: The BOG participants acknowledged that recent work on the effects of ocean acidification on marine organisms has revealed a wide range of variability in species-specific response patterns, including responses with opposite signs (reduced versus stimulated metabolic rates with decreasing pH/increasing pCO_2). Whereas some of these divergent observations may be due to misinterpretations of the data, measurement errors, or flaws in the experimental design and call for reconciling, others may simply reflect taxon-specific differences in responses to ocean acidification. While unravelling the mechanisms underlying these divergent response patterns will be of critical importance for our ability to predict the overall impacts of ocean acidification, the BOG participants felt that these should not be considered *contradictory observations* if they occur between organisms that are not taxonomically-related.

With this in mind, the BOG participants defined contradictory observations as:

- divergent response patterns for the same species or closely related taxa
- conflicting observations between laboratory experiments, *in situ* experiments, and field observations
- inconsistencies between perturbation experiments and retrospective studies

Observations were not considered contradictory when they differ with respect to:

- variability in the magnitude of the response of the same species or closely related taxa
- divergent responses of species of different taxonomic groups

Level of disagreement: The BOG participants decided that a helpful criterion in looking at contradictory findings can be the number of data sets supporting each side of the opposing observations. As established at the beginning of the BOG discussion, three levels of disagreements were distinguished according to the following scheme:

Table 1: Level of disagreement as determined by the percentage of opposing data sets.

Level of Disagreement	Percentage of Data Sets Supporting: Opposing Observation
High	50:50
Medium	70:30
Low	90:10

1. Calcification in zooxanthellate corals

General trend: As discussed by the BOG participants and more precisely quantified subsequently, in a set of 48 experimental studies (including 24 species – 13 genera) and 6 field studies, the vast majority indicates a decrease in calcification under elevated pCO_2 (reduced pH) (Erez et al., 2011). In a small number of experiments no effect was recorded or the effect was only significant under very low pH. A clear stimulatory effect of high pCO_2 was never observed. In spite of a general inhibitory effect of the calcification process, the BOG participants indicated that there is a high inter- and intra-specific variability, ranging from –3 to –85% decrease in the rate of calcification in response to a 2-fold increase in pCO_2 compared to pre-industrial values. The inhibitory process may be exacerbated by temperature increase.

Lab experiments versus field studies: BOG participants pointed out that the vast majority of studies were performed under lab condition during short-term incubations (67% of the experiments lasted less than 1 month; 27% less than 6 hours; only 8% lasted more than 1 year and only one more than 3 years). Only 6 field studies were specifically designed to test the effect of ocean acidification on coral calcification. All these experiments recorded a decrease of coral calcification with increasing pCO_2.

The BOG discussed the fact that divergent observations have been obtained from retrospective studies using cores of the long-lived massive coral, *Porites*. Pelejero et al. (2005), using boron isotope as a proxy of seawater pH, observed that in spite of a wide range of pH (~0.3 pH unit) experienced by corals over a 300-year period, no significant change of calcification rates was detected. Lough and Barnes (2000) as well as Bessat and Buigues (2001) reported an increase in calcification in recent decades. In contrast, Cooper et al. (2008) and De'ath et al. (2009) found a reduction of the rates of extension and calcification over a period ranging from 10 to 436 years which was attributed to both temperature increase and Ω_{arag} (aragonite saturation state) decrease. However, pH was not estimated in these studies. BOG participants noted that these discrepancies may be due to other interacting factors in the field.

Form of carbon used for calcification: The BOG discussion indicated that the major discrepancy between the available results lies in the form of inorganic carbon used for calcification. While some studies (Jury et al. 2009) demonstrate that HCO_3^- is used as a source of carbon for calcification and that addition of bicarbonate stimulates the rate of calcification (Herfort et al., 2008; Marubini and Thake, 1999), others suggest that metabolic CO_2 is the major form (Furla et al., 2000). While the source of carbon is mainly a mechanistic problem, BOG participants indicated that it may have important implications for understanding the biological basis of sensitivity and tolerance of corals. For example, if some species utilize bicarbonate whereas others use carbonate or CO_2 then the response to ocean acidification will be species-specific rather than universal. Curiously, in most perturbation experiments, the increase of CO_2 and HCO_3^- is associated with a decrease of calcification, which would be unexpected if these carbon species were really the major source of carbon.

BOG participants pointed out that most data show a correlation between the CO_3^{2-} concentration and the rate of coral calcification, suggesting that CO_3^{2-} ion may be the source of carbon. However, there is no physiological proof for such a process and the existence of a carbonate transporter has not been demonstrated in animals so far.

Carbonate chemistry parameter relevant for observed responses: A second major discrepancy discussed in the BOG, linked to the previous point, is the choice of parameter used in describing the effect of ocean acidification on coral calcification. Most of the data sets show positive correlation between Ω_{arag} and the rate of calcification (calcification increases linearly with Ω_{arag}). However about 40% of the data sets exhibit curvilinear relationships with Michaelis-Menten kinetics or relatively constant rates up to a threshold value of Ω_{arag}. In some studies, no correlation is observed between Ω_{arag} and the rate of calcification, but yields a better correlation with HCO_3^- concentrations. The BOG

participants concluded that these contrasting observations suggest that the coral calcification response to ocean acidification may be quite complex and species-specific.

The conclusions of the discussion for this first broad area considered are summarized in Table 2.

Table 2: Contradictory observations in zooxanthellate coral calcification.

Contradictory Observation (observational basis)	Level of Disagreement	Possible Explanations
Laboratory experiments vs. field observations / retrospective studies *perturbation experiments demonstrate a decline of calcification that is not always found in field or retrospective studies*	High	• Retrospective studies may not have a resolution good enough to detect the decline of calcification estimated for the past 200 years (about 10%) • Lack of ecological interactions in laboratory experiments; only a few experiments investigated multiple stressors • Stress resulting from the transplantation of colonies to laboratory conditions
Form of carbon used for calcification *respiratory CO_2 vs. HCO_3^- vs. CO_3^{2-}*	High	• Lack of understanding of the calcification mechanism • Parameters co-vary
Carbonate chemistry parameter relevant for observed responses *driving parameter: HCO_3^- vs. CO_3^{2-} (vs. pH)*	Medium	• Parameters co-vary • Confounding factors • Lack of data sets • Less than 2 parameters of carbonate system reported

2. Planktonic calcification

The BOG participants discussed that most planktonic calcifying organisms tested so far, such as foraminifera, pteropods, and planktonic larvae of echinoderms, show a decrease in calcification in response to elevated CO_2/reduced pH. A wide range of responses to ocean acidification has been obtained for coccolithophores. Whereas calcification of *Emiliania huxleyi*, *Gephyrocapsa oceanica*, and *Calcidiscus quadriperforatus* decreases to varying degrees with increasing pCO_2, *C. leptoporus* shows an optimum curve with reduced calcification at pCO_2 levels below and above present conditions and *Coccolithus pelagicus/braarudii* appears to be insensitive to elevated pCO_2. In a comparison of different strains of *E. huxleyi* either no change or a decrease in calcification rate was observed with increasing pCO_2. In all 14 studies on coccolithophores the ratio of calcium carbonate to organic matter production (PIC:POC) decreases or remains unchanged with elevated pCO_2 (reviewed by Riebesell and Tortell, 2011). The results of two mesocosm experiments are consistent with the majority of laboratory experiment, showing a decrease in calcification and in the PIC:POC ratio with increasing pCO_2.

The BOG considered two studies on coccolithophores that reported a stimulating effect of ocean acidification on calcification. Iglesias-Rodriguez et al. (2008) reported strain NZEH of *E. huxleyi* to double its calcification in response to pCO_2 increasing from 280 to 750 µatm which was interpreted as a response to an increase in the concentration of bicarbonate. They claimed that this increase was not identified before because prior studies used an inadequate approach to manipulate the carbonate chemistry (acid/base addition versus gas bubbling; Iglesias-Rodriguez et al., 2008b). BOG participants indicated that it was later suggested that methodological differences are unlikely to explain the differences (Gattuso and Lavigne, 2009; Ridgwell et al., 2009; Schulz et al., 2009). Riebesell et al. (2008) interpreted the results of Iglesias-Rodriguez et al. (2008a) differently. Their main comment was that, due to difference in size of the cells incubated in the different CO_2 treatments, cells grown at high CO_2 had an initial biomass two to three times greater than low CO_2^-

grown cells (possibly due to differences in pre-cultures). They concluded that a comparison between CO_2 treatments cannot be performed on a per cell basis and that the trends in calcification and primary production with increasing pCO_2 disappear when normalized to algal biomass. As pointed out in BOG discussion, this interpretation was discounted by Igleasias-Rodriguez et al. (2008b). A re-analysis of strain NZEH of *E. huxleyi* used by Iglesias-Rodriguez et al. (2008) by Hoppe (2010) revealed no effect on growth rate and a moderate decrease in calcification with increasing pCO_2.

The BOG discussion indicated that, in a study by Shi et al. (2009), both growth rate (cell division rate) and the cellular POC and PIC content of *E. huxleyi* (strain NZEH) were higher at pH_T 7.8 compared to pH_T 8.1, yielding higher rates of organic carbon production and calcification at elevated pCO_2. The ratio of PIC:POC was slightly lower in cultures maintained at lower pH levels. Increased carbon cell quota and cell size are frequently observed in coccolithophores at elevated pCO_2. However, the results reported by Shi et al. (2009) differ from all other studies on coccolithophores in showing an increased cell division rate at elevated pCO_2. Using the same strain of *E. huxleyi*, Hoppe (2010) found no effect on growth rate.

At the end of this discussion, the BOG participants suggested that the present uncertainty about the response of coccolithophores to ocean acidification is a critical issue preventing future projection of the impact of ocean acidification on community structure, food-webs, and biogeochemical cycles. The BOG discussion pointed out that further studies by the research community could clarify the issue in the peer-reviewed literature.

The conclusions of the discussion for this second broad area considered are summarized in Table 3.

Table 3: Contradictory observations in coccolithophore calcification.

Contradictory Observation (observational basis)	Level of Disagreement	Possible Explanations
Direction of response *decline vs. increase in calcification*	Low	• Inappropriate data normalization • Difference in experimental design

3. Processes other than calcification

The BOG participants discussed that, as observed for calcification, a large variability in response to ocean acidification appears to be the rule ranging from negative to positive effects, sometime in closely related species. These differences are widely accepted as reflecting natural variability in species sensitivity related to environmental history, ontogeny, taxa-related differences in physiology, or life-history traits. As a consequence the level of controversy is generally low. Nonetheless, the BOG identified five apparently contradictory results.

Respiration in the pteropod *Limacina helicina:* The BOG participants pointed out that Comeau et al. (2010) reported a 10% increase in respiration rate in pteropods acclimated for 24 h at 760 µatm. This is in apparent contradiction with Fabry et al. (2008) showing a 26% decrease in respiration rate in pteropods exposed to 789 µatm. BOG participants thought that it is probable that these differences relate to experimental conditions. Different temperatures were used and very little information on experimental design (replications, exposure time, method used, sampling period, etc.) is provided in Fabry et al. (2008) making comparison difficult. On the other hand, pteropods are difficult animals to keep in the laboratory and results are highly dependent on general health of individual used.

Fertilization in the sea urchin *Heliocidaris erythrogramma*: The BOG discussed that many studies are documenting the impact of ocean acidification on fertilization, and the general trend is the absence of a significant effect (Dupont et al., 2010, for review). However, one study (Havenhand et al., 2008) reported a 20% decrease in fertilization success for *Heliocidaris erythrogramma* when

gametes were exposed to a 0.4 pH unit decrease. Working on the same species, Byrne et al. (2009a,b) reported no effect within a similar range of pH changes. These contrasting results may be the consequence of different experimental conditions (polyandry vs. single male–female crosses, sperm concentration, stability of pH, inappropriate sperm-egg contact times, number of replicates, etc.), none of these studies being ecologically relevant (Reuter et al., 2011). The BOG concluded that this controversy is a good illustration of the need to design biologically relevant experiments. Inappropriate experimental design can lead to apparent contradiction and false results.

Bacterial production: BOG participants indicated that only a few studies have investigated the impact of ocean acidification on bacterial production. Two publications presented no effect on cell specific protein production (Allgair et al., 2008; Tanaka et al., 2008) during mesocosm experiments. In contrast, one study documented a stimulation and an increase in cell specific production of attached bacteria with rising pCO_2 during a bloom of coccolithophorids and diatoms in a mesocosm study (Grossart et al., 2006).

Nitrogen fixation in *Nodularia*: BOG participants indicated that nitrogen fixation in the heterocystous cyanobacterium *Nodularia spumigena* was observed to decrease with increasing pCO_2 in a study by Czerny et al. (2009), while the opposite response was reported by Isensee et al. (2009). For the non-heterocystous species *Trichodesmium* a rather consistent response pattern with increased nitrogen fixation at elevated pCO_2 was observed in eight independent studies.

Production of dimethyl-sulphide (DMS): BOG participants discussed that the effect of ocean acidification on DMS production was addressed in five studies, of which three showed a decrease, one showed no effects, and one study an increase with increasing pCO_2. This response pattern was consistent with the observed production dimethylsulfoniopropionate (DMSP), the precursor of DMS. The BOG suggested that possible explanations for the observed discrepancy are differences in phytoplankton species composition between studies and between different treatments of the same experiment.

The conclusions of the discussion for this third broad area considered are summarized in Table 4.

Table 4: Contradictory observations in processes other than calcification.

Contradictory Observation (observational basis)	Level of Disagreement	Possible Explanations
Respiration rate of pteropods *one study found an increase at elevated pCO_2, another study a decrease*	High	• Different feeding history • Experimental differences
Fertilization *no effect vs. decrease (sea urchin)*	Low	• Experimental differences • Different sperm concentration
Bacterial production *no effect vs. stimulation*	Medium (2:1)	• Experimental differences
Nitrogen fixation *decreases in Nodularia – recent work shows increase*	High for *Nodularia* 2 studies	• Experimental differences
DMS production *some show increase, some no effect, some decrease with increasing pCO_2*	Medium	• Differences in phytoplankton species composition between experiments and between treatments of the same experiment

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Breakout Group I-3: Spatial and temporal scales of variability and rates of change

Chair: Philip Munday (James Cook University, Australia)
Rapporteur: Anne Cohen (Woods Hole Oceanographic Institute, USA)

The summary that follows, written by the Chair and Rapporteur, characterizes the main points of the discussion that took place during Breakout Group I-3 at the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems. Participants in the Breakout Group considered a series of questions focused on cross-cutting themes in ocean acidification research, which was developed by the Scientific Steering Committee for the workshop.

The processes associated with and the influences of ocean acidification occur across a wide variety of spatial and temporal scales: from specific ocean regions to whole ocean basins, from molecular and cellular mechanisms to organisms and ecosystems, and from short-term variability to changes over deep evolutionary time. Fully understanding processes and resulting scientific complexities across these scales will take a long time, yet people, including policymakers, will need to make decisions based on limited information.

In this BOG, we explored how physical, chemical, and biological processes on different spatial and temporal scales relate to each other, as relevant to changing ocean chemistry and consequences for marine organisms and ecosystems. Overall, we discussed how we can develop increased mechanistic understanding over spatial and temporal scales, or adopt other strategies, that can improve the ability to project changes in ocean chemistry and resulting biological and ecological impacts over the time scales relevant to decision-makers. For each question considered, the BOG participants identified what is known and outlined strategies that could be used to provide better or more certain answers, especially as would inform decision-making over the next few decades.

1. What insights can we gain from natural and experimental "analogues" (e.g., naturally varying systems, CO_2 seeps, short and long term experimental systems)?

The BOG participants indicated that there are clear advantages to using natural and experimental analogues to gain insight into the potential impacts of anthropogenic-induced ocean acidification on organisms and ecosystems. However, there are important caveats to consider if analogue systems are used to extrapolate into the future. Analogue systems provide chronic, naturally high pCO_2 conditions and gradients in those conditions which can be used to identify i) threshold tolerances of different organisms to CO_2 stress (e.g., Hall-Spencer, 2008), ii) potential winners and losers, iii) community -scale effects, and iv) better understanding of adaptive capabilities. Highly variable environments (those with natural pH/pCO_2 fluctuations on daily and seasonal timescales) can also be used to investigate species responses and acclimation potential.

However, as discussed in the BOG, for analogues such as CO_2 seeps and mesocosm experiments, both of which are spatially constrained, the scale of connectivity is usually larger than the study unit, limiting insights into both population dynamics and adaptation potential. Mobile organisms moving in and out of a high CO_2 region don't face the same selection pressure as sessile organisms or those experiencing chronic conditions; in addition, larvae of many species are recruited from an external, unaffected population (e.g., Cigliano et al., 2010). Because source populations outside the high CO_2 region are unaffected, the potential exists to under- and overestimate the impact of a real, global-scale acidification of the oceans.

The BOG discussion pointed out that more spatially extensive analogue systems exist, such as upwelling, naturally high CO_2 systems in the eastern tropical Pacific and southern Oman. The advantages here are similar, but with different caveats. Mainly, the challenge presented by multiple co-varying factors such as pCO_2, temperature, and nutrients and their interactions, all of which are known to influence the health of coral reef organisms and ecosystems (e.g., Kleypas et al., 1999). For

this reason, it is difficult, if not impossible, to resolve the influence of high pCO_2 from that of low temperature or elevated nutrient levels because these conditions co-occur. Furthermore, the strength of the analogy between upwelling systems today and the tropical oceans in a high CO_2 world is debatable. Rising sea surface temperatures under global warming are projected to increase stratification and reduce delivery of nutrients to the surface (e.g., Boyd and Doney, 2002). This scenario is counter to that characterizing upwelling systems today which experience very high levels of inorganic nutrients and, as a result, productivity that may offset, at least partially, the impact of high pCO_2 on some physiological processes such as calcification (e.g., Holcomb et al., 2010). Indeed, recent work suggests that for some species, coral growth in these upwelling regions may be as fast or faster than that of their conspecifics in nearby higher saturation state, non-upwelling regions (Manzello, 2010). Other factors influencing species composition and coral reef development include biogeography (e.g., there is a gradational rather than abrupt attenuation of species diversity from the Indo-Pacific center of biodiversity to the eastern Pacific; Veron, 1995) and processes involved in the accretion, cementation, and bioerosion of biogenic and abiogenic $CaCO_3$. For example, the well developed Australian Great Barrier Reef system experiences some of the highest known $CaCO_3$ dissolution rates (Tribollet et al., 2008). Thus, low species diversity and poor reef development in the eastern tropical Pacific might not be explicable solely in terms of naturally high pCO_2 conditions; BOG participants concluded that the complexity of these systems must be considered if analogies are drawn between them and coral reefs under ocean acidification.

Recommendation to the research community: The BOG participants suggested that the value of analogue systems is that they provide – in a very general sense - insights into what is possible in a high CO_2 world: the types of organisms that could be favored, the types of behaviors that could be favored, the potential for adaptation. Further, comparing species living under chronic naturally high CO_2 conditions with conspecifics living under ambient conditions provides a unique opportunity to identify the specific combination of environmental conditions that enables normal physiological functioning in a high CO_2 world (e.g., nutrients, turbidity, temperature) and through molecular or experimental work, the possibility to identify acclimation and adaptation to high CO_2 conditions.

2. What are the advantages as well as pitfalls inherent in scaling up experimental and natural responses to understanding change at the ecosystem level?

BOG participants stated that there are many advantages to small-scale, single organism laboratory-based manipulation experiments. Manipulating one variable (e.g., aragonite saturation state, Ω_{arag}) and experimenting with one species at a time enables accurate and unambiguous quantification of its impact on organism physiology, without confounding effects of temperature and other environmental parameters, and species interactions including predator-prey and intra-specific competition. For the same reasons, BOG participants indicated that single organism single variable manipulations enable identification of threshold responses (e.g., Ries et al., 2010; de Putron et al., 2010), to address questions about the relative sensitivity of different life history stages and to identify critical life history stages. These types of experiments also provide the best opportunities to investigate the mechanisms by which ocean acidification influences organism physiology. However, as discussed in the BOG, extrapolating results of single organism, single variable experiments to predicting ecosystem level responses is challenging. Higher level ecosystem properties cannot be tested for in small scale experiments yet may be critical in determining outcome. Species interactions cannot be tested and the role of natural cycles in growth and reproduction are usually not considered due to the short duration of such experiments. BOG participants discussed that mesocosm experiments can better capture interactions and field based mesocosms (e.g., the Coral Proto - Free Ocean Carbon Enrichment system (CP-FOCE), as described further in the abstract for Poster 13 in Annex 6 of this Workshop Report) can effectively capture natural diurnal & seasonal variability in light, pCO_2, nutrients as well as cycles in growth and reproduction. Field-based mesocosms also have great potential for long-term experimentation; however, they are generally expensive and labor-intensive hence the statistical problem of replication. BOG participants discussed that, although larger in scale

than single organism experiments or tank mesocosms, field based mesocosms are usually still too small to capture some important components of ecosystem dynamics including larval supply, recruitment and population connectivity.

Recommendation to the research community: The BOG's participants indicated that a portfolio of approaches from small scale, single organism experiments, through field-based mesocosms and natural analogues will allow us to constrain sensitivities, identify thresholds, and investigate physiological mechanisms and how they're affected by multiple, co-varying environmental variables, species interactions, and cycles in growth and reproduction in an ecologically relevant setting. Systematic investigations that involve i) small scale, single parameter experiments to provide the initial framework for understanding and quantifying species-specific responses at all life history stages should be followed by ii) small scale multi-parameter experiments to identify interactions amongst physico-chemical variables e.g., temperature and Ω_{arag}; and iii) larger-scale field-based mesocosms to test hypotheses formulated in the lab and to investigate organism responses in a relevant ecosystem setting and over relevant time-scales. Finally, analogue sites provide unique opportunities to test hypotheses in established ecosystems.

3. Does plasticity (physiological, behavioral, morphological) play a significant role in coping with the warmer and more acidic oceans of today?

The BOG's conclusion: probably yes. Many organisms exhibit plasticity in response to temperature change, and BOG participants thought that it seems likely that some organisms will also exhibit plasticity in response to ocean acidification. Decades of research on thermal acclimation (acclimation is a type of plasticity) and adaptation tell us that species and populations living in thermally variable environments, such as temperate ocean and intertidal zones, tend to exhibit a greater capacity to cope with thermal challenge than species and populations from more thermally stable environments. Organisms in some environments experience large fluctuations in pCO_2 on tidal, diurnal and seasonal timescales, which suggests that some plasticity to respond to ocean acidification is likely.

The BOG discussed that the capacity of physiological process to adjust will vary within and between species and life stages depending on environmental variability currently experienced and in their evolutionary history. Species from more variable environments are expected to exhibit more plasticity. Plasticity might involve an energetic cost to the organism, which could be expressed as reduced tissue growth, calcification, longevity, reproductive output, or behavioural changes. However, costs of plasticity are poorly described for any environmental variable.

Recommendation to the research community: Some species naturally experience variable CO_2 and pH environments, and BOG participants recommended that greater consideration should be given to this fact when researchers design experiments, interpret results, and consider species' plasticity and potential to adapt. The BOG noted that affordable sensors and other in-situ methods for measuring pCO_2 were becoming more available, making it easier to match natural environmental measurements with experimental manipulations.

4. Is there evidence for genetic variability to influence how organisms and ecosystems respond to ocean acidification?

The BOG's conclusion: yes. BOG participants indicated that there is increasing evidence from experimental studies of variation among species and among individuals in their responses to CO_2 and acidification (e.g., Ries et al., 2010 and Munday et al., 2010). Some calcifying species, for example, appear more tolerant to reduced Ω_{arag} that others. Other experiments exhibit variation among individuals in CO_2 treatments that overlaps with variation in controls. Variation among individuals indicates potential for selection of more tolerant genotypes. Importantly, many marine species are

highly fecund and spawn repeatedly; therefore a few tolerant breeding individuals could potentially produce many tolerant offspring that might be favored in future populations, even among long-lived species. The BOG also noted that most studies to date involve acute stressors, which may elicit different response from chronic exposure to ocean acidification.

Recommendation to the research community: BOG participants recommended that researchers should pay more attention to variation amongst individuals within a treatment, and not dismiss it as experimental noise – it could be real and important adaptive genetic variability.

5. Are there examples from experimental manipulations that demonstrate potential for acclimation to ocean acidification?

The BOG's conclusion: yes. The BOG discussion indicated that, for example, bicarbonate ions acquired from shell dissolution are thought to be used for the short-term regulation of extracellular pH in many marine invertebrates. Spicer et al (2007) showed that this mechanism was used by the crab *Necora puber* during a 14 day exposure to elevated CO_2. However, Small et al. (2010) showed that, in the same species, the surrounding seawater is used as an alternative source of bicarbonate after longer-term exposure (30 days). This suggests an acclimation of the crab's acid-base and calcification physiology through time. Several other good examples of longer term capacity for acclimation to ocean acidification were discussed by the BOG.

The BOG noted that some species only express plasticity to environmental change when juveniles experience the new environment (called developmental acclimation) (e.g., Donelson et al., 2011). Furthermore, acclimation can occur across generations as a result of parental effects (called transgenerational acclimation). BOG participants suggested that this demonstrates the need for long term experiments that allow the full range of plasticity to be expressed.

Recommendation to the research community: The BOG indicated that long term experiments that rear organisms through their entire life, and across generations, are needed to allow the full potential capacity for acclimation to ocean acidification to be expressed and explored.

6. Are there examples from experimental manipulations that demonstrate potential for adaptation to ocean acidification?

Three studies that illustrate population- or strain-specific difference in response to ocean acidification were discussed by the BOG. One of these unambiguously illustrated that adaptive genetic selection to high CO_2 can occur. Fitness of the alga *Chlamydomonas* evolved when exposed to high CO_2 for 320 generations (Collins, 2010). Species with short generation times and large populations sizes, and those from spatially and temporally variable environments, should have the greatest potential for adaptation. Recent experimental evidence indicates that there is a correlation between physiological plasticity and capacity to adapt, and this relationship could potentially be used to predict species with better prospects for adaptation. The BOG indicated that whether species with longer generation times have the capacity to evolve to keep pace with the rapid pace of change in ocean chemistry is currently unknown.

7. Are there circumstances where organisms have adapted to spatial differences in ocean acidity?

The BOG's conclusion: probably yes. The BOG discussed, for example, Antarctic krill embryos that migrate vertically from 1,000 m depth to the surface, and experience a change in pCO_2 from ~600 to 300 ppm during development, which were shown to be completely tolerant of high CO_2 conditions >1,000 ppm; however, embryo development was completely inhibited at 2,000 ppm CO_2 (Kawaguchi et al., 2010). In another example, the BOG indicated that calcification by *Porites* species in the eastern Pacific can be as high as that of conspecifics in the western Pacific despite low

aragonite saturation states (Ω_{arag}) in the eastern Pacific (Cohen, unpublished data). Further, calcification by *Pavona* species across the eastern Pacific does not correlate with gradients in Ω_{arag} even though linear growth of branching *Pocillopora* does (Manzello, 2010). However, other factors that covary with low Ω_{arag} in the eastern Pacific, such as temperature and nutrient gradients, make it difficult to assign reasons for why calcification is maintained by some species at these locations and even to identify whether Ω_{arag}, temperature, nutrients, or combinations of these parameters, is the primary driver of calcification/linear growth. The BOG noted increasing evidence that local adaptation to other environmental parameters can occur in marine species, including species with planktonic larval dispersal (Sanford and Kelly, 2011), and therefore the potential for local adaptation to spatial variation in pCO_2, pH, and Ω should not be ignored. BOG participants indicated that local adaptation is best tested using long-term, common-garden manipulation experiments. Good candidates for this approach include corals and other organisms that experience a large natural range of CO_2 within their geographic distributions.

8. Specific problems for adaptation

A number of specific problems and issues regarding the potential for rapid adaptation to ocean acidification were discussed by the BOG. First, clear evidence for adaptation to ocean acidification is very weak, although it must be recognized that few studies have been conducted to date. The rates of change in ocean chemistry are very fast and whether adaptation can keep pace is unknown, especially for organisms with long generation times, such as most coral species. Also, rapid selection for one environmental factor (e.g., reduced pH) tends to reduce genetic variability, which might potentially limit the capacity to adapt to other ecological stresses, such as ocean warming or eutrophication. This makes it challenging to predict how species will cope with rapid changes in multiple stressors.

The BOG noted that we have the tools for testing local adaptation and speed of selection, as evidenced by research into thermal adaptation. Selection experiments and population genetic approaches will be useful; however, we are missing basic information in most cases (e.g., population size and recombination rates) to properly assess adaptation potential.

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Breakout Group II-1: Learning from the past and present to predict the future

Chair: Daniela Schmidt (University of Bristol, United Kingdom)
Rapporteur: Christoph Heinze (University of Bergen, Norway)

The summary that follows, written by the Chair and Rapporteur, characterizes the main points of the discussion that took place during Breakout Group II-1 at the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems. Participants in the Breakout Group considered a series of questions focused on cross-cutting themes in ocean acidification research, which was developed by the Scientific Steering Committee for the workshop.

Introduction to the topics discussed

Ocean chemistry has varied in the past, resulting in conditions that have had consequences for life on Earth including fast turnovers of ecosystems and mass extinctions. Understanding these changes and their influence on past organisms and ecosystems has the potential to help understand and project future responses in ocean ecosystems. Relevant changes of past ocean chemistry occurred at very different times – from past deep time at the Permo-Triassic boundary 251.4 Ma to historical records from the past decades and centuries. In order to use evidence from past oceans for predicting the impact of ongoing and further evolving anthropogenic ocean acidification, one has to keep in mind the different time scales and forcings of the processes, the different amplitudes of the changes, uncertainties in the paleoceanographic proxies, and the overall different environmental conditions as compared to the present and expected near future.

On the other hand, the Earth system as such provides the possibility to assess acclimation, evolutionary adaptation, and ecosystem changes -- processes difficult or impossible to study in idealized modern laboratory studies or mesocosm-experiments which are by nature short lived shock experiments and highly influenced by the measurement set-up and techniques.

As an overall outcome of the discussion in this BOG we can state the following key issues:

1. There is no perfect past analogue for the human-induced ocean acidification. This is information of crucial importance: It sets the uniqueness of the anthropogenic perturbation in the correct perspective.
2. There are no relevant high rate of change, low pH events documented by high resolution sedimentary records.
3. For the Holocene, high resolution records are available, but the rates of pCO_2/pH change during all of the past 10,000 years are small as compared to modern ocean acidification.
4. Nevertheless, past changes in pCO_2/pH/carbonate saturation may be used as calibration points for predictive models, though these calibration points would be located fairly far away from present day conditions.

The discussion was developed around a set of questions provided by the Scientific Steering Committee, and this report also follows that format.

1. What can be learned from palaeontological perspectives?

Past changes in ocean chemistry differ considerably in character, timing, and strength. It is, therefore, practical to consider relevant events or periods in time, which have the potential to provide us with information on ocean acidification impacts. We list those in Table 1 starting with the oldest first.

Table 1: Evidence for ocean chemistry changes from the palaeontological record.

Event, Time Period	Age	Potentially Supporting Evidence	Disadvantages
Permian/Triassic boundary	251 Ma	• 92% of species went extinct, paleo-physiology agrees with ocean acidification as a possible extinction mechanism	• No pH or saturation state reconstruction
Cretaceous/Paleogene boundary	65 Ma	• Possibly fastest perturbation of surface chemistry • Several 10 Ma recovery times for diversity/community structures	• No good analogue as attribution will likely be impossible • Too many other stressors to identify acidification signal
Paleocene Eocene Thermal Maximum (PETM)	55 Ma	• Large changes in carbonate compensation depth • Extinction in the deep sea • After models strong sea surface carbonate saturation state variations unlikely • High resolution records potentially feasible • "Good" global coverage of cores (order of 20 cores)	• Attribution difficult: temperature, ocean acidification, nutrient inventories, hydrological cycle, circulation, weathering • Duration of onset of PETM unclear by a couple of 1000 years • Large error bars on rates of change
Pliocene	3 Ma	• Quasi-analog for warm world (ca 400 ppm) • Boron isotopes and excess partial pressure of CO_2 ($epCO_2$) reconstructions	• No rapid approach to 400 ppm level • Not of great use for ocean acidification • Attribution problem: ocean acidification vs. changes in circulation, temperature and O_2
Glacial/Interglacial cycles	LGM 20 kyr BP	• Good data coverage • $CaCO_3$ Lysocline, CCD • Boron isotopes, ε_p, pCO_2 • Some evidence for change in surface mean pH with limited time resolution available (useful for pelagial)	• Small and slow change led to acclimation or migration of species (100 ppm in a few thousand years) • No hard evidence for shelf environments yet available for pH. • Attribution problem: pH changes vs. changes in circulation, temperature and nutrient cycles.
Holocene: change now much larger than during past 10,000 years	10 kyr BP until pre-industrial	• High resolution cores available • Very good data constraints	• Rates of pCO_2/pH change are small

2. What are the observational uncertainties from the paleo-record?

The BOG discussed that, concerning pH reconstructions for the open ocean, the glacial/interglacial precision using boron isotopes is about 0.05 pH units (i.e., half of the anthropogenic signal so far). The time resolution is generally low except for a few Holocene records. There is hardly any useable evidence for higher trophic levels available for ocean acidification studies from sedimentary records as these rarely contain proxies for macrofossils, though fish scales may be found. The BOG noted that recent high resolution records on pH from microfossils or corals are useful for putting the human induced changes into an Earth system perspective: these changes stand out as extreme on the natural background.

3. Can evolutionary models help inform an understanding of past changes, and help project future changes?

The BOG discussed that, based on evidence from the paleo-record, evolutionary concepts are around for only few species. So far, no integrated evolutionary predictive concept for ecosystems is available. There are hints that a higher degree of specialisation hampers the ability to adjust to changing environmental conditions.

The BOG noted that, so far, the paleo-record does not give any conclusive answer to the question of how many generations complex organisms need to be able to adapt during perturbation. Here studies from actually newly forming environments, such as, e.g., rapid species evolution as observed in African rift lakes, may help.

Experiments are often not performed on species which can be found in the geological record thereby reducing possible synergies.

Recommendations to the research community

From the discussion in the BOG, a few concrete suggestions for further paleoceanographic studies evolved:

1. There is evidence that certain species survived the PETM event. Studying the physiology of the species that lived during the PETM which still exist today may provide insight into the mechanisms that allowed adaptation. These species should be added to mesoscsom as well as laboratory studies on the impact of pH change/$CaCO_3$ saturation in order to observe their behaviour concerning resilience as compared to other species.
2. Paleontologists and paleoceanographers should explore whether there is any evidence for foodweb dynamic changes/higher trophic levels/ecosystem levels from the paleo-record.
3. Researchers should try to establish a geologic record for physiology: Can we deduce a trend of biotic reaction to acidification for the past 50–100/200 years? Coral species that can live longer than 100 years could be a suitable study object for stable isotope analysis (on the living organism). Alternatively, historical collections available since the end of the 19th century could be used for samples. Research could aim to use the international network to assess the availability of these collections.
4. Modelling: So far generally, ocean acidification studies using global general circulation models do not allow any assessment for coastal regions. Modellers should discuss whether regional models could help here, especially for time slice computations. Upcoming CMIP5[1] last millennium runs with global GCMs can help to provide an open ocean baseline for the Holocene, the LGM, and the climatic optimum at 6 kyr BP. A long term aim is attribution of environmental factors to past perturbations to de-convolve the abiotic stressor.

[1] http://cmip-pcmdi.llnl.gov/cmip5/

Breakout Group II-2: Understanding the roles of multiple stressors

Chair: Peter Haugan (University of Bergen, Norway)
Rapporteur: Gretchen Hofmann, University of California Santa Barbara, USA)

The summary that follows, written by the Chair and Rapporteur, characterizes the main points of the discussion that took place during Breakout Group II-2 at the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems. Participants in the Breakout Group considered a series of questions focused on cross-cutting themes in ocean acidification research, which was developed by the Scientific Steering Committee for the workshop.

Ocean acidification is one of many stressors relevant to ocean ecosystems. In almost all regions, acidification is occurring in concert with changes in other key parameters such as temperature, circulation patterns, nutrient concentrations, other forms of pollution, invasive species, and trophic alterations associated with fishing. The nature and magnitude of the impacts from ocean acidification on marine organisms and ecosystems may be different (exaggerated or modulated) when coupled with these other changes. Furthermore, questions remain regarding the degree to which unexpected or abrupt changes and regime shifts will occur and the degree to which ocean acidification might affect when these thresholds would be surpassed. This BOG discussed the role of ocean acidification in the context of other stressors, such as temperature, nutrients, disease, pollution, and fishing pressure, taking into consideration the potential for abrupt changes and the role of complex system feedbacks.

1. What do we know today about the way ocean acidification interacts with other stressors in the marine environment?

Under what circumstances or sets of circumstances do combinations of stressors enhance or modulate one another?

The BOG noted that this was a particularly broad question and considered the following:

- There was consensus in the BOG that listing stressors in an order (major-minor) would be useful; factors listed by the BOG (not in any particular order) were changes in: temperature, oxygen, freshwater and nutrient inputs from the land, ice melt, stratification, trace metals, light, fishing, solar radiation, and ultraviolet radiation (UV).
- Although the BOG noted this to be a complex question, there were representative examples that could have large effects in an ocean acidification context. For example, in nature, variable nutrient levels (access to food) may interact with temperature and CO_2. Here, it was suggested that the BOG produce a table of examples from the literature where stressors have interacted (see Table 1).
- The BOG noted that physical elements should also be considered. For example, changes in upwelling could play a key role as well as an increase in the stratified areas of the ocean, which could have a significant impact on local biology.

Are interactions between these variables and the carbon chemistry of seawater synergistic, antagonistic or irrelevant?

The BOG noted there was a great deal of variation in the published literature depending upon species and experimental conditions. A specific mention was made regarding the fact that this is a multi-dimensional problem; further, the process under study would influence the interpretation of what is important. For example, a particular stressor's effect on fitness may be different than its effect on spawning. There could be a range of responses across normal ambient exposure to the environmental extremes. In addition, it was noted that knowledge of a species' natural history, its ambient conditions, and relative use of thermal ranges would be necessary. Finally, life history and life history traits would matter when interpreting the outcome of multiple stressor studies on a single species. (See Table 1.)

Table 1: A non-comprehensive listing of illustrative examples of multiple stressor studies.

Stressors	Organism
Temperature and ocean acidification	Reef fishes (Munday et al., 2009)
	Pteropods (Comeau et al., 2010)
	Phytoplankton (Feng et al., 2009)
	Urchins (Brennand et al., 2010; Byrne et al., 2009; O'Donnell et al., 2009)
	Kelp (Connell and Russell, 2010)
	Coccoliths (De Bodt et al., 2010)
	Barnacles (Findlay et al., 2010)
	Oysters (Lannig et al., 2010; Parker et al., 2009)
	Sea stars (Gooding et al., 2009)
	Cuttlefish (Lacoue Labarthe et al., 2009)
	Phytoplankton (Feng et al., 2009; Rose et al., 2009)
	Corraline algae (Martin et al., 2009; Anthony et al., 2008)
	Gastropods (Melatunin, et al., 2009)
	Bryozoans (Rodolfo-Metalpa et al., 2010)
	Crabs (Walther et al., 2009, 2010)
	Brittle stars (Wood et al., 2010)
	Corals (Rodolfo-Metalpa et al., 2010b; Reynaud et al., 2003; Anthony et al., 2008)
Nutrients and ocean acidification	Coral (Holcomb et al., 2010; Silverman et al., 2007)
	Subtidal algae (Russell et al., 2009)
	Phytoplankton (Hopkinson et al., 2010)
	Dinoflagellates (Fu et al., 2010)
UV/Light and ocean acidification	Phytoplankton (Wu et al., 2010; Gao et al., 2009)
	Corraline algae (Gao et al., 2010)
	Cyanobacteria (Kranz et al., 2010)
Oxygen and ocean acidification	Squid (Rosa and Seibel, 2008)
Ice melt and ocean acidification	Arctic Ocean organisms (Yamamoto-Kawai et al., 2009)

Progressive versus threshold responses: Are abrupt changes expected?

The BOG's conclusion: probably. The BOG discussed that some examples of abrupt changes have been seen already with (1) abrupt changes in fish behaviour (Munday et al., 2010) and (2) losses in oyster aquaculture on the US West coast (in the states of Oregon and Washington) where sudden drops in production may be linked to low carbonate, corrosive water entering major hatcheries (Feely et al., 2010).

Can we associate regime shifts with ocean acidification scenarios (future)?

The BOG's conclusion: yes. The BOG noted that regime shifts are expected in response to future ocean acidification scenarios, but presently there are not many examples that meet the criteria for a direct causal relationship. The BOG noted the following potential directions for research:

- Naturally occurring oceanographic changes can drive ecosystem regime shifts; for example, North Pacific Pacific Decadal Oscillation shifts have been shown to alter sardine and anchovy distributions (Chavez et al., 2003). Researchers could consider the potential for regime shifts as a result of ocean acidification in the future.
- Oyster hatcheries and other coastal aquaculture activities may be the best option for exploring the effects of altered carbonate chemistry.

- While much work has been undertaken on warm water corals, the effects on and consequences of loss of cold water corals could be further explored.
- CO_2 vents show strong shifts in distribution. These natural observations support that ocean acidification shifts could occur. Studies of such systems, with their strong CO_2 gradients, could be undertaken.
- Time-series locations (e.g., Hawaii Ocean Time-series (HOT) Program[1], Bermuda Atlantic Time-series Study (BATS)[2], European Station for Time Series in the Ocean (ESTOC)[3]) provide valuable opportunities where we should attempt to explore possible links between CO_2 changes and shifts in ecology or biology.

Are there certain groups of organisms (ecosystem engineers, primary producers, predators) or certain types of ecosystems more likely to show amplification of ocean-acidification-induced effects through synergistic interactions of multiple stressors?

The BOG's consensus was generally: yes. Groups that were highlighted, without comprehensive consideration, include:

- Deep sea ecosystems (here, specifically, cold water corals)
- Coralline algae in tropical and temperature ecosystems
- Tropical stony corals
- Coccolithophores

2. How can the roles of multiple stressors be untangled using in situ observations of real ecosystems?

The BOG had suggestions but acknowledged this would be a difficult task. This challenge would be greatly aided by resources and approaches as follows:

- Good time series data
- Effective use of multivariate analysis
- Better use of modelling – stronger linkage of experimental approach with modelling
- Networks of experiments
- The use of examples in other ecosystems (e.g., terrestrial investigations)

3. How do we resolve the relative importance of multiple co-varying factors – solar radiation, water flow, temperature, nutrients, food availability, carbonate saturation, pH, community composition – on organism and ecosystem function in the field?

The BOG noted that free-ocean carbon dioxide enrichment (FOCE) approaches are perhaps best here: learning more about how FOCE experimenters balance these elements was considered to be an option that could be more carefully explored. One confounding issue to pay attention to was that of interpretation of complex multiple stressor experiments. For example, phytoplankton cells experience changes even during a daily cycle in physical (solar PAR and UV, temperature, stratification) and chemical (changes in nutrients, CO_2 and acidity) conditions.

Notably, in these types of experiments, what is the driver? This becomes difficult to determine because many factors are changing at once and they may interact non-linearly. It was suggested to pair FOCE experiments with much more tightly controlled lab experiments and systematic manipulations of covarying factors.

[1] http://hahana.soest.hawaii.edu/hot/hot.html
[2] http://bats.bios.edu/
[3] http://www.estoc.es/

4. What experiments, observations and modelling are needed to improve our understanding of how ocean acidification will interact with other stressors in marine ecosystems? What parameters not considered "stressors" under ambient conditions could behave as stressors under elevated CO_2?

The following were listed as experiments and experimental approaches that are needed:

- FOCE systems in more critically threatened habitats (known locations for ocean acidification FOCE experiments are currently deep-sea (Monterey Bay Aquarium Research Institute (MBARI)[4] and Heron Island[5] experiments)
- Multifactor experiments in the lab and in the field, including studies that examine more than just pairwise interactions.
- The inclusion of comparative approaches.
- Observations: Long-term observatories should be supported and ensure that these include physical, chemical, and biological measurements
- Integrated approach for modelling: Modelling needs to be planned alongside experiments and observations.
- Models that predict the evolution of multiple stressors (ocean acidification, temperature, eutrophication, pollutants, fishing, etc.), along with models that integrate the effects of multiple stressors on individuals, species and communities are needed.

Parameters that are not considered stressors under ambient conditions but that may behave as stressors under elevated CO_2 were listed by the BOG: temperature, mixing patterns, oxygen, and the ratio of CO_2 and O_2. The BOG noted that the ratio of partial pressure of each gas, food availability, changes in bioavailability of metals, and UV and high levels of PAR can become stressful as CO_2 increases.

Recommendations from BOG II-2 to research community

Ocean acidification version of the 'Burning Embers' diagram. This product could:

- Address/indicate whether there are thresholds
- Highlight interactions of ocean acidification with other factors
- Highlight penetration of factors into the food web, reaching out to food security

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Breakout Group II-3: Scaling up to humans: the socioeconomics of ocean acidification

Chair: Peter Brewer(Monterey Bay Aquarium Research Institute, USA)
Rapporteur: Carol Turley (Plymouth Marine Laboratory, United Kingdom)

The summary that follows, written by the Chair and Rapporteur, characterizes the main points of the discussion that took place during Breakout Group II-3 at the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems. Participants in the Breakout Group considered a series of questions focused on cross-cutting themes in ocean acidification research, which was developed by the Scientific Steering Committee for the workshop.

This BOG explored the socioeconomic impacts of ocean acidification. It evaluated the ways in which experimental results from ocean acidification research and socioeconomic knowledge can be combined to project consequences of ocean acidification for ocean ecosystems, for corresponding ecosystem services, and for human communities and economic systems dependent on ocean resources. The discussion was developed around a set of questions provided by the workshop organizers. This report follows that format.

1. What ecosystems, and what ecosystems services provided by these ecosystems, are at greater risk from ocean acidification? In what ways are humans dependent on these ecosystems and ecosystem services?

The BOG participants discussed that ecosystems at risk this century are those provided by corals (temperate-, cold-, and warm-water corals), certain upwelling dominated ecosystems, Arctic and Southern Ocean ecosystems, coastal and benthic ecosystems including estuaries, deep water ecosystems, and those in the open ocean (where future changes are greater than natural variability). It was noted that the vulnerability of mangroves and salt marshes had not yet been studied.

Ecosystem services identified as at risk were fisheries (sport, commercial, and subsistence); tourism where shore lines are dependent on reefs; land integrity, coastal protection, and associated structures and infrastructure; heritage and cultural value associated with biodiversity and habitat; and regulatory services such as nutrient regeneration and carbon sequestration and storage.

The degree and timing of ecological impacts of ocean acidification and the subsequent socio-economic impacts and risks were discussed and found to vary with ecosystem type. To help synthesize understanding of the consequences of ocean acidification, BOG participants suggested a table listing the following information for each ecosystem type: ecological impacts of ocean acidification expected over specified time frames, human dependency on the affected ecosystems, and resulting socioeconomic impacts and risks.

2. In order to understand and anticipate possible socioeconomic consequences of ocean acidification, (i) what existing socioeconomic knowledge and (ii) what understanding of past ocean-ecosystem collapse is available and could be used?

The BOG noted that there are a number of useful existing documents on socio-economics but few if any that combine impacts on ecosystems and both the economic and social consequences: e.g., the Millennium Ecosystem Assessment[1] defines categories of goods and services that can be used in socio-economic assessments; the Stern Review (Stern, 2006) focuses on the economics but not on social science; the Census of Marine Life[2] assesses biodiversity but not socio-economic impacts and

[1] http://www.maweb.org/
[2] http://www.coml.org/

consequences. The Economics of Ecosystems and Biodiversity[3] (TEEB) initiative hosted by the UN Environment Programme may be especially useful for linking economics of ecosystems and biodiversity; national reporting documents via the National Communications to the UNFCCC are focused on climate change, but that methodology could be useful and the BOG suggested they be updated to include acidification. Similarly, national and regional assessments of stressors like harmful algal blooms (HABS) (e.g., Jewett et al., 2007) could provide useful frameworks for considering ocean acidification. The OSPAR Quality Status Report (OSPAR, 2010) may also be useful, as too is *Ocean Acidification. A National Strategy to Meet the Challenges of a Changing Ocean* by the US National Research Council of the National Academies of Science (NAS, 2010); the UNEP Emerging Issues Bulletin: *Environmental Consequences of Ocean Acidification: A Threat to Food Security*[4] (UNEP, 2010); the forthcoming report and conclusions from The Monaco Environment and Economics Dialogue on Economics of Ocean Acidification International Workshop, 16-18 November 2010[5]; and a small number of scientific papers may help link ocean acidification and socio-economics (see BOG II-3 Appendix A).

To further understand socioeconomic consequences of ocean acidification, BOG participants indicated that the following past ocean ecosystem collapses could be used: studies of loss of keystone species (e.g., in the Caribbean or in intertidal temperate zones), impacts by invasive species (e.g., in the Mediterranean), physical loss due to catastrophic or extreme events (e.g., bleaching, tsunamis, fishing damage), fisheries collapse (e.g., northern cod), regime shifts and ecosystem restructuring (due to urbanisation, changing watershed and climate drivers), and species survival, adaptation, or extinctions seen in ocean acidification events in the geological record.

3. What are consequences of ocean acidification for fisheries and food security? Are there organisms and fisheries/aquaculture systems that are more or less vulnerable to ocean acidification and changing seawater chemistry?

The BOG discussed the UNEP Emerging Issues Bulletin: *Environmental Consequences of Ocean Acidification: A Threat to Food Security* (UNEP, 2010), which examines the risks to future fisheries and aquaculture. Fisheries "hotspots" such as some upwelling regions, coral reefs, coastal seas, fronts, estuaries, and sub-polar regions often supplying the main protein source for coastal communities may be particularly vulnerable to ocean acidification. Some aquaculture species show vulnerability to ocean acidification within their life cycle. This is an area needing further research. At the moment, scientific understanding includes species-by-species evidence of ocean acidification impacts, but there is a large need for ecosystem-based modelling studies to place individual responses to ocean acidification in the context of food webs, population behaviour, and the ecosystem as a whole. These studies will then allow better projections of specific species that will be most vulnerable because of their total responses to changing ocean chemistry, ecosystem pressures, and all the factors that may change because of ocean acidification.

4. Do projected impacts of acidification have consequences for shoreline protection by coral reefs and the ability of coral reefs to support coastal tropical fisheries? Do smaller/thinner shells matter for commercially important shellfish, and can we quantify the impacts for these shellfish and their fisheries?

Large effects of ocean acidification and synergies with other stressors such as rise in sea level and seawater temperature may affect coral reefs this century, with consequences for shoreline protection supplied by reefs and those coastal tropic fisheries reliant on reef ecosystems.

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[3] http://www.teebweb.org/

[4] http://www.unep.org/dewa/pdf/ Environmental_Consequences_of_Ocean_Acidification.pdf

[5] http://www.iaea.org/nael/meeting/csm2010/The%20Monaco%20Workshop%20Public%20Conclusions.pdf

Shells of species of shellfish may be thinner or smaller in a future high CO_2 ocean but the total consequences on organisms and populations are unknown in either wild or commercially important shellfish used in aquaculture.

5. What are implications for tourism and economic development?

The BOG participants all thought that change could be expected on economies dependent on tourism of reefs via reduced tourism and the allied spending. However, the BOG noted that scales of economic impact are likely to be different from small-island to global – one size does not fit all. For example, for some small islands 10–15% of GDP is directly dependent on coral reef tourism with additional indirect economic benefits (Cooley et al., 2009) which approximately double this figure but the global economic value of coral reefs will be relatively minor in terms of combined GDP.

6. For decision-making related to the socioeconomic impacts of ocean acidification, what are the most important questions? Which of these questions are scientifically tractable and could be answered in the next one to two decades to inform decision-making?

BOG participants indicated that some of the questions listed below can be quickly addressed (1-3 years), and others will take longer. Bringing in the human dimension and impacts of ocean acidification on socio-economics is a challenge, but addressable, and needs method development to couple society, ecosystems and earth systems.

Are the goods and services provided by the ocean changing due to ocean acidification?

What are the synergistic impacts of ocean acidification and other human activities (e.g., fisheries, pollution, climate change)? Will species be able to migrate along established pathways and what is the subsequent impact on socio-economics? What is the potential for socio-economic adaptation and mitigation? What is the long-term viability of coral reefs and other ecosystems in relation to stabilization pathways? Will the trajectory of aragonite saturation track status of coral reefs and their socio-economic benefits? Can we scale up from individual organism responses to multispecies interactions, and ecosystem responses, including trophic responses?

Is future global food security at risk?

What is the status of marine protein production and its quantity and quality in a future high CO_2 ocean with an increasing human population? Which are the most vulnerable geographical areas and populations? What are the socio-economic impacts on regional scales?

As ocean acidification is the consequence of human CO_2 emissions choices does full accounting of socioeconomic risks require nesting ocean acidification impacts in climate change impacts assessments?

What are the key non-monetary values of goods and services provided by the ocean? Multi-metric valuation that also takes account of non-market benefits, ethical and societal concerns is missing from current capability.

What impacts are uniquely associated with ocean acidification, aside from impacts identified by climate change impact studies already carried out?

Does mitigation of dangerous ocean acidification require lower CO_2 emissions than that required to avoid dangerous climate change?

Are assessments of geoengineering solutions (e.g., Asilomar Report (ASOC, 2010); Royal Society Report (Shepherd et al., 2009) taking full account of ocean acidification?

Ocean acidification has mainly emerged in developed countries but what is the understanding of the issue, its scales of impacts, recovery and implications, in potentially more vulnerable developing countries?

What is the research and capacity in the regions that are most vulnerable? What are the communication vehicles to bring ocean acidification to decision makers and society in these countries? Is there a mechanism to help fund these countries and develop capacity in ocean acidification research?

In the BOG report back to the all workshop participants, it was suggested that a "traffic light" figure showing CO_2 emission trajectories and both species/ecosystem and regional vulnerability could be developed, providing information similar to that in Figure 3 in Turley et al. (2010).

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BOG II-3 Appendix A: Selection of scientific publications connecting ocean acidification and socio-economics.

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Cooley, S.R., N. Locey, H. Kite-Powell, and S.C. Doney, 2011: Nutrition and income from mollusks today imply vulnerability to ocean acidification tomorrow. *Fish and Fisheries* (in press).

Hattam, C., B. Laverock, S. Mangi, and S. Widdicombe, 2011: The impact of ocean acidification on the socioeconomic value of marine benthic ecosystems. In: *The Other Carbon Dioxide Problem: Ocean Acidification Science, Law, and Policy* [W.C.G. Burns, and J. Firestone, (eds.)]. Cambridge University Press (in review).

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Ad Hoc Breakout Group: Glossary entry for "ocean acidification"

Chair: Ken Caldeira (Carnegie Institution for Science, USA)

The summary that follows, written by the Chair, characterizes the main points of the discussion that took place during the Ad Hoc Breakout Group at the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems. Participants in the Breakout Group considered a possible joint-WG AR5 glossary entry for "ocean acidification."

During discussions at the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems, participants indicated the utility of considering a glossary entry for the term "ocean acidification" and the benefits of all IPCC Working Groups adopting a uniform entry for this term. In response to this perceived need, the Ad Hoc BOG was established to propose one or more candidate glossary entries. A suggested glossary entry was presented back to plenary. The proposed glossary entry received widespread but not universal assent.

The glossary entry agreed to by at least some members of the BOG was:

Ocean Acidification. *Ocean acidification refers to a reduction in the pH of the ocean over an extended period, typically decades or longer, which is caused primarily by uptake of carbon dioxide from the atmosphere, but can also be caused by other chemical additions or subtractions from the ocean.* ***Anthropogenic ocean acidification*** *refers to the component of pH reduction that is caused by human activity.*

Initially, there were two main dimensions of disagreement:

1. Is ocean acidification defined to be a consequence of human actions, or is it at least logically possible that ocean acidification could be caused naturally?
2. Is ocean acidification defined to result from additions of substances to (or subtractions of substances from) the ocean, or could ocean acidification result from processes that are purely internal to the ocean (e.g., ocean circulation changes)?

The BOG was able to reach consensus on both of these points, but a universal consensus on the second point was not achieved in plenary.

The BOG presented a definition (see above) that opened up the possibility of natural ocean acidification events (i.e., not anthropogenic) but limited ocean acidification to result from processes that add or remove materials from the ocean.

Several important points came up in the discussion that are recorded here:

1. A goal of a glossary entry is to orient the non-expert reader. Since the central case of current concern involves a reduction in pH from the absorption of carbon dioxide from the atmosphere, it was felt that this should be mentioned in the glossary entry to fulfill this "orienting" function.
2. Addition of other acids or removal of bases can also cause a decline in pH. Furthermore, additions or removals may occur from underwater pipes or other means that do not involve transfer from the atmosphere. For these reasons, the phrase "*caused primarily by uptake of carbon dioxide from the atmosphere, but can also be caused by other chemical additions or subtractions from the ocean"* was included.
3. Short term natural variability should not be construed as "ocean acidification", thus the importance of "*over an extended period, typically decades or longer*".
4. There was a desire, where practicable, to echo the glossary entry for "climate change".
5. Some felt that it was important to leave open the logical possibility that ocean acidification could be caused by natural processes, perhaps during events in Earth's distant past. Some felt it

was important that statements like "ocean acidification is today being caused by human actions" be the result of empirical scientific investigation and not a tautological statement that flows purely from the definition of terms.

Note that other subtle issues were raised, including whether ocean acidification is really the reduction in pH or should instead refer to broader chemical changes characterized by a reduction in pH. For example, one can say "the reduction in pH is 0.3" but typically people do not say "the ocean acidification is 0.3", which indicates that ocean acidification is not exactly the reduction in pH. One option to deal with this would be to say "ocean acidification is a process involving a reduction in pH …". While this may be more accurate, some felt that this added accuracy came at an unacceptable cost to felicitous expression. There was some discussion of whether the glossary entry should be a precise definition or a pointer to the core meaning. The BOG participants felt that it would be good to have a clear and understandable short glossary entry, but that this should be supplemented by a box within a report chapter that would explore some of these details with greater specificity.

In the plenary, if the comment was properly understood, at least one person felt that the term "ocean acidification" could be applied to any process that would tend to decrease ocean pH. Thus, under this understanding, the natural "steady-state" process of remineralization of organic matter in an oxygen minimum zone would be a process that contributes to ocean acidification, despite the fact that it is a process that is internal to the ocean and does not reflect a change in the overall state of the ocean. This viewpoint, which may be a minority viewpoint, differs from the consensus achieved by the Ad Hoc BOG defining ocean acidification to require (a) a change in state and (b) a change in the overall composition of the ocean, thus the phrasing "*Ocean acidification refers to a reduction in the pH of the ocean over an extended period … caused by ... chemical additions or subtractions from the ocean.*"

Recommendation to the IPCC AR5 authors: It is the recommendation of the chair of the Ad Hoc BOG that IPCC AR5 authors consider adopting the glossary entry for ocean acidification specified above, following a discussion of the relevant issues. Furthermore, the BOG chair believes there was a consensus among the Ad Hoc BOG participants that IPCC authors should consider placing a box in one of the report chapters that contains a more detailed discussion of the meaning of the term "ocean acidification."

Ad Hoc Breakout Group Appendix A: Additional background for reference

The IPCC AR4 glossary entry for "ocean acidification" from Working Group I was:

> ***Ocean acidification.*** *A decrease in the pH of sea water due to the uptake of anthropogenic carbon dioxide.*[1]

The IPCC AR4 glossary entry for "ocean acidification" from Working Group II was:

> ***Ocean Acidification.*** *Increased concentrations of CO_2 in sea water causing a measurable increase in acidity (i.e., a reduction in ocean pH). This may lead to reduced calcification rates of calcifying organisms such as corals, molluscs, algae and crustacea.*[2]

The main weakness in these glossary entries is that they are not the same. The WGI definition requires an anthropogenic cause and requires that addition of CO_2 be the cause. The WGII definition might be interpreted as including cases where a change in ocean circulation briefly causes a local increase in CO_2 concentration.

IPCC AR4 WGI definition of "climate change" (relevant to point 4):

> *Climate change refers to a change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forcings, or to persistent anthropogenic changes in the composition of the atmosphere or in land use. Note that the Framework Convention on Climate Change (UNFCCC), in its Article 1, defines climate change as: 'a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods'. The UNFCCC thus makes a distinction between climate change attributable to human activities altering the atmospheric composition, and climate variability attributable to natural causes. See also Climate variability; Detection and Attribution.*[1]

IPCC AR4 WGII definition of "climate change" (relevant to point 4):

> *Climate change refers to any change in climate over time, whether due to natural variability or as a result of human activity. This usage differs from that in the United Nations Framework Convention on Climate Change (UNFCCC), which defines 'climate change' as: 'a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods'. See also climate variability.*[2]

Other definitions for ocean acidification, found on the web, include:

> *Ocean acidification is the name given to the ongoing decrease in the pH of the Earth's oceans, caused by their uptake of anthropogenic carbon dioxide from the atmosphere.*[3]
>
> *the process whereby atmospheric carbon dioxide dissolves in seawater producing carbonic acid, which subsequently lowers pH of surrounding seawater.*[4]
>
> *Decrease in ocean pH due to higher levels of dissolved carbon dioxide.*[5]

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[1] http://www.ipcc.ch/publications_and_data/ar4/wg1/en/annexessannex-i.html
[2] http://www.ipcc.ch/publications_and_data/ar4/wg2/en/annexessannex-i.html
[3] http://en.wikipedia.org/wiki/Ocean_acidification
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Synthesis Plenary Reports

Synthesis Plenary IV-1: The changing chemistry of the oceans: the state of knowledge, key uncertainties, and the way forward

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Richard Feely (Pacific Marine Environmental Laboratory, USA)

The summary that follows, written by the presenters of the Synthesis Plenary IV-1 presentation, synthesizes perspectives of the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems, especially as presented during Plenary Session I: The Changing Chemistry of the Oceans but also as discussed during the workshop's breakout group, poster, and other plenary sessions.

The Synthesis Plenary IV-1 presentation focused on presentations and discussions at the workshop concerned with past, present, and future changes in ocean carbonate chemistry, particularly regarding current knowledge, remaining uncertainties, and future work. This synthesis was based on four presentations and subsequent discussions in Plenary Session I, as well as on Breakout Group discussions on the changing chemistry of the oceans. The four presentation in Plenary Session I were (1) Controls on ocean carbon chemistry: a paleo perspective (Richard Zeebe); (2) Changes in ocean carbon chemistry since pre-industrial times (Kitack Lee); (3) Future projections of ocean carbon chemistry (Fortunat Joos); and (4) Ocean acidification in coastal waters and other vulnerable ocean regions (Rik Wanninkhof).

For brevity, this summary focuses on a synthesis of discussions in the following three main areas: (1) what the research community has learned since the IPCC Fourth Assessment Report (AR4); (2) gaps in knowledge that are limiting further understanding; and (3) the way forward.

1. What has the research community learned since the IPCC AR4?

Workshop participants indicated that past "acidification events" are poor analogs of the fast ongoing anthropocene event, but their continued study allows the present-day event to be placed in a geological context. Generally, long-term paleo-scale (> ~10,000 years) changes in saturation state are well regulated and decoupled from changes in pH. These longer-term changes are buffered by $CaCO_3$ sediment dissolution and formation, and on even longer time scales by continental erosion. The projected anthropogenic perturbation is considered to be unprecedented during the past several hundred million years. Paleo-acidification events, such as the most recent Palaeocene-Eocene Thermal Maximum (PETM, 55 million years ago), are large perturbations that occur on time scales of less than about 10,000 years, but they cannot be attributed only to an increase in atmospheric CO_2, thus complicating the interpretation.

As discussed at the workshop, the modern surface-ocean pCO_2 increase generally follows the atmospheric CO_2 increase, thus driving corresponding changes in surface ocean pH and $CaCO_3$ saturation states (via well established thermodynamic equilibrium equations). But there are regional differences across the surface ocean. Surface waters in the subtropics remain at the surface for longer periods, a year or more, enough time to equilibrate with atmospheric CO_2, whereas surface waters in the high latitudes often spend less time at the surface (e.g., in the Southern Ocean waters upwell and are later subducted). Additionally, on interannual time scales, trends in surface ocean pCO_2 in some regions may be decoupled from those in the atmosphere due to natural variations in climate, such as those driven by El Niño. In some areas such as the Southern Ocean, it has been suggested that the ocean carbon sink may be saturating due to climate-induced changes in wind patterns.

As described by participants, subsurface changes in pH generally lag behind those in the surface ocean. These lags are explained by incomplete equilibrium with atmosphere, and they are affected by changes in circulation (ventilation, advection, stratification), which alters temperature, nutrients, oxygen, productivity and remineralisation. However, the maximum change in pH is often not at the surface. In both observations and models, the maximum anthropogenic pH change has been found to occur at between 200–300 m depth in the subtropics (Dore et al., 2009; Byrne et al., 2010; Ishii et al., 2011; Orr, 2011).

Some regions are more vulnerable to low $CaCO_3$ saturation and pH. Of particular concern are the polar oceans where cold temperatures maintain only low natural levels of $[CO_3^{2-}]$ and thus saturation. The problem is exacerbated further in the high northern latitudes, particularly the Arctic, where saturation states and pH are further reduced because of enhanced freshwater input and melting of sea ice and river runoff. Some coastal regions are also particularly vulnerable due to seasonal upwelling of subsurface waters that are naturally rich in inorganic carbon and may be already affected by anthropogenic CO_2 invasion (Feely et al., 2008). Acidification is also more adverse in some river mouths and estuaries (Salisbury et al., 2008; Feely et al., 2010) due to combined effects from freshwater input, eutrophication, hypoxia, and sulphur and nitrogen deposition.

Although anthropogenic changes in pCO_2, pH, and $CaCO_3$ saturation states are measureable at time series stations and along repeated ship transects, discussions held during the workshop indicated that detecting changes in total alkalinity from potential reductions in calcification or enhanced $CaCO_3$ dissolution is still not possible. One model study (Ilyina et al., 2009) suggests that such changes may remain undetectable for at least two decades.

2. What gaps in knowledge are limiting further understanding?

To further understanding, workshop participants emphasized a need for a wider global perspective from a broader synthesis of long-term observations. In addition, they discussed a need for models that are as accurate as possible in their projected changes of acidification and circulation (ventilation, stratification, deoxygenation, export, and remineralisation), not only for the surface but also subsurface waters, and not only for the open ocean but also for nearshore regions (Rykaczewski and Dunne, 2010). Furthermore, discussions reflected a need for improved approaches based on chemical sensors (e.g., DIC, alkalinity, pH, and O_2) on moorings, floats and gliders to better identify anthropogenic impacts and distinguish natural changes in carbon species.

3. What is the way forward?

First, from the perspective of the participants, the most basic requirement to move forward on the needs identified above is to increase spatiotemporal coverage of chemical and biological observations covering daily, seasonal, interannual and decadal time scales. Data coverage must be increased in the most vulnerable regions, particularly coastal regions and the high latitudes, as well as in the lower-latitudes of the open ocean. As a starting point, it is important to synthesize recent data acquired during the ongoing CLIVAR/GO-SHIP repeat section surveys, time-series stations, the growing SOCAT surface-ocean pCO_2 global data, the RECCAP comparison, and the US Ocean Acidification program.

Second, participants discussed the benefits of strengthening ties between observationalists and modellers, reemphasizing the need for an international observing system and data-model comparison of both surface and subsurface changes in pH, DIC, total alkalinity, O_2, and saturation states along with other key physical and biogeochemical variables.

Third, discussions reflected the importance of adequately modelling ocean acidification simultaneously with other anthropogenic stressors (stratification, hypoxia, eutrophication, etc.) in coastal regions and marginal seas, while also building model frameworks to focus on the connection between coastal and global ocean.

Finally, participants indicated that there would be benefit from models being made more complex where necessary. For example, it would be important to include the sensitivity to increasing CO_2 in more of the fundamental biogeochemical processes (e.g., iron chemistry, nutrient ratios, productivity, calcification, dissolution, hypoxia). Models should also address how acidification affects metal speciation as well as production and consumption of climate relevant gases such as N_2O and DMS.

Many of these forward-looking themes -- from strengthening ties between observationalists and modellers, to accounting for the role of multiple stressors, to making models more complex where necessary -- also emerged in discussions on organism and ecosystem level considerations, as summarized in other sections of this Workshop Report.

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Synthesis Plenary IV-2: Impacts of ocean acidification for individual organisms: the state of knowledge, key uncertainties, and the way forward

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The summary that follows, written by two presenters of the Synthesis Plenary IV-2 presentation, synthesizes perspectives of the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems, especially as presented during Plenary Session II: Impacts of Ocean Acidification for Individual Organisms but also as discussed during the workshop's breakout group, poster, and other plenary sessions.

Objective: We, as presenters of the Synthesis Plenary IV-2 presentation, aimed to summarize the current state of knowledge and to identify key uncertainties and ways to move forward, as presented and discussed at the *IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems*. We focused on the following areas: (1) microbial processes and biogeochemistry; (2) phytoplankton calcification and photosynthesis; (3) fishes; (4) calcification and dissolution of coral reefs and coral reef organisms; (5) non-coral reef invertebrates; and (6) additional impacts on invertebrates. We approached our synthesis of participant perspectives by summarizing the state of knowledge for each organism group, working from the expert keynote-presentation syntheses and individual contributions to other workshop sessions.

1. State of knowledge, as discussed at the workshop

1.1 Impacts on microbial processes and biogeochemistry

This section of the Synthesis Plenary IV-2 presentation and the corresponding summary here synthesizes the material presented during Plenary Session II, Keynote II-6: Impacts on microbial processes and biogeochemistry, by Nicola Wannicke. It also incorporates some points raised during the workshop's breakout group, poster session, and plenary discussions.

As discussed at the workshop, microbes and microbial communities are ubiquitous in the ocean and play central roles in the cycling of major and minor elements. For example, primary production by prochlorococcus and syneccochocus constitutes most of the production in the subtropical gyres; cyanobacteria fix nitrogen gas in its most inert form, N_2, and make it bio-available. Other microbes remineralize organic material and release nutrients and DOM back into the seawater while others oxidize reduced forms of nitrogen through the process of nitrification.

Perspectives presented at the workshop indicated that most microbial processes will be affected by ocean acidification and that changes in microbial processes will have an effect on biogeochemical cycles. The processes studied to date (number of studies in parenthesis) are primary production (29), nitrogen fixation (10), element ratios such as C:N (27), species composition (3), bacterial turnover (3), and aggregation and sedimentation (3). With few exceptions, most experiments report an increase in processes under study except bacterial turnover and nitrification, which decrease (Beman et al., 2010). Evidence for increased primary production under experimental conditions is strong and consistent, especially for non-heterocystous cyanobacteria. However, extrapolation to the real oceanic environment will depend on the availability of nutrients. Similarly, evidence for increased nitrogen fixation in experiments is strong and consistent for non-heterocystous cyanobacteria, while there are only two studies available for heterocystous cyanobacteria, which are contradictory concerning the trend under high CO_2 (Czerny et al., 2009; Isensee et al., 2009).

Remaining uncertainties: Perspectives presented at the workshop indicated that it is particularly difficult to ascertain how changes in microbial processes will play out in the real world where

multiple parameters and multiple processes change simultaneously. The challenges are amplified because these processes have complex links and feedbacks with one another. For example, an increase in TEP production will accelerate the biological carbon pump whereas an increase in bacterial degradation will slow it down.

1.2 Impacts on phytoplankton calcification and photosynthesis

This section of the Synthesis Plenary IV-2 presentation and the corresponding summary here synthesizes the material presented during Plenary Session II, Keynote II-2: Impacts on phytoplankton calcification and photosynthesis, with consideration of evolutionary responses, by Debora Iglesias-Rodriguez. It also incorporates some points raised during the workshop's breakout group, poster session, and plenary discussions.

In general, discussions indicated that ocean acidification enhances photosynthetic carbon fixation by marine phytoplankton (e.g., diatoms - Tortell et al., 2000, 2008; coccolithophores - Riebesell et al., 2000; Iglesias- Rodriguez et al., 2008; Shi et al., 2009). Calcification responses under experimental conditions are variable, but more negative (9 studies) than positive (2 studies) or neutral (3 studies) responses have been reported. Interpretation of results is complicated by evidence for strain-specific responses in growth rate, organic and inorganic carbon production. This implies a genetic basis for the response variability (Langer et al., 2009). Additional community level effects have been identified including synergistic interactions between temperature and CO_2 that can control the composition of phytoplankton populations (Tortell et al., 2008). In addition, the availability of Fe, a key nutrient for phytoplankton, can be affected by ocean acidification (Shi et al., 2010). Finally, pH-induced shifts in nutrient stoichiometry can also influence community structure, the ratio of nutrient (Si:N:P) utilization, and productivity (Tortell et al., 2002; Blackford, 2010).

Remaining uncertainties: The reduced level of confidence in experimental data comes partly from the different experimental approaches employed amongst the different groups**.** Also, older studies did not report CO_2 parameters so interpretation of data is difficult. Limited understanding of calcification physiology amongst phytoplankton groups and taxa, specifically, carbonate versus bicarbonate usage, and mechanisms of pH control, has emerged as an important limitation to interpreting and predicting responses.

1.3 Impacts on fishes, their life histories, and evolutionary responses

This section of the Synthesis Plenary IV-2 presentation and the corresponding summary here synthesizes the material presented during Plenary Session II, Keynote II-5: Impacts on fishes, their life histories, and evolutionary responses, by Atsushi Ishimatsu. It also incorporates some points raised during the workshop's breakout group, poster session, and plenary discussions.

Discussions during the workshop indicated that, by far, the majority of data on ocean acidification impacts on fishes comes from research with aquaculture species, which are typically resistant and hardy. From these data, it is apparent that growth and survival of adult Atlantic salmon, spotted wolfish, rainbow trout and white sturgeon are unaffected by seawater pCO_2 levels as high as 15,000 µatm (Ishimatsu et al., 2005), and initial data suggest spawning and early development are unaffected up to 1000 µatm. However, observed physiological effects such as ventilator and cardiovascular responses (e.g., skate and rainbow trout: Graham et al., 1990; McKendry and Perry, 2001), increased tissue lactate concentrations (Michaelidis et al., 2007), and increased energy demand of ion exchange and protein and RNA synthesis in gills of two Antarctic species, *G. gibberifrons* and *N. coriiceps*, at 10,000 µatm pCO_2 (Deigweiher et al., 2009) suggest that the metabolic costs to fishes under elevated CO_2 might be elevated. Furthermore, recent work has documented impacts on the predator avoidance mechanism of tropical fishes through the effect of acidification on olfaction and the ability to recognize predators by smell (Munday et al., 2010).

Remaining uncertainties: Workshop participants noted that there is concern about the relevance for wild species of data collected on domesticated fishes and limited understanding of "downstream" effects, such as impacts of ocean acidification on prey species (food web alterations), and of "sublethal and behavioral effects" including impacts on migration, social interactions, spawning, predator avoidance, and prey capture.

1.4 Impacts on calcification and dissolution for coral reefs and coral reef organisms

This section of the Synthesis Plenary IV-2 presentation and the corresponding summary here synthesizes the material presented during Plenary Session II, Keynote II-1: Impacts on calcification and dissolution for coral reefs and coral reef organisms, by Jean-Pierre Gattuso. It also incorporates some points raised during the workshop's breakout group, poster session, and plenary discussions.

This group is relatively well-studied with more than 63 publications for corals alone (Gattuso and Hanson, 2011). The majority of experiments to date have focused on the calcification response to elevated CO_2 of corals and coralline algae in single organism tank experiments, as well as that of mixed coral reef assemblages in mesocosms and field-based studies. More recent studies have expanded to study effects of elevated CO_2 on reproduction and recruitment, bleaching susceptibility, dissolution/erosion, and symbiont photosynthesis. Also, the number of experiments that combine multiple parameters (temperature, CO_2, nutrients) has recently increased. There is a paucity of data on reef-scale responses to Ω_{arag} and pCO_2, and there is little information about impacts of ocean acidification on $CaCO_3$ dissolution and erosion.

Workshop participants indicated that, in general, calcification by corals, coralline algae and coral assemblages in tank experiments has been observed to decline with increasing seawater pCO_2 (see reviews by Langdon and Atkinson, 2005; Kleypas and Yates, 2009; Doney et al., 2009; Andersson et al., 2011; Erez et al., 2011). Some of these results have been drastic with potentially large implications for coral reef ecosystems. For example, Langdon and Atkinson (2005) report an 85% decline in coral calcification under a near doubling of pCO_2, and Kuffner et al. (2008) observed an 85% decrease in recruitment of crustose coralline algae (CCA) under doubled ambient pCO_2. However, and probably by virtue of the large number of studies that have been conducted on coral reef organisms, there is clearly significant variability in the sensitivity of the calcification response amongst different experiments. For example, de Putron et al. (2011) and Reynaud et al. (2003) reported no change and a slight increase in coral calcification respectively, under a near doubling of pCO_2, and Ries et al. (2009) observed increased calcification by coralline algae under doubled ambient pCO_2. As discussed at the workshop, these contradictory results highlight the complexity of organism and ecosystem responses to ocean acidification and the importance of other environmental and biological factors in modulating or exacerbating the CO_2 effect. Some factors that have been identified include concentrations and ratios of dissolved inorganic nutrients (e.g., Langdon and Atkinson, 2005; Holcomb et al., 2010), water temperature (Reynaud et al., 2003; Anthony et al., 2008), energetic status of the coral host (Cohen and Holcomb, 2009), and reproductive status of coral host (Holcomb, 2010). Jury et al. (2010) observed an increase in coral calcification when bicarbonate ion concentrations (and total DIC) were significantly increased under experimental conditions leading to suggestions that calcification could increase under ocean acidification; however these results are not borne out by the majority of studies including Schneider and Erez (2006) and de Putron et al. (2011), who observed decreased calcification as bicarbonate ion concentrations (and total DIC) increased. Results of Rodolfo-Metalpa (2010) and Ries et al. (2009, 2010), which show no response from temperate coral species to increasing pCO_2 until $\Omega_{arag}<1$ (Ries et al., 2009, 2010), hint at species-specific responses and potentially decreased sensitivity of temperate species, but this hypothesis has yet to be directly tested. Recent studies using geochemical tools to quantify conditions within the isolated (from seawater) extracellular space where calcification occurs, show that coral reef organisms (corals and algae) exert control over the pH (de Beer et al., 2000; Al Horani et al., 2003; Trotter et al., 2011; Venn et al., 2011) and saturation state (Cohen et al., 2009; Cohen and Holcomb, 2009) of the calcifying fluid, possibly through a combination of Ca ion pumping and H^+

removal. Differences amongst species and amongst different taxa, in their ability to control conditions at the site of calcification, may account for some of the observed variability.

Discussion at the workshop indicated that, in general, field studies of reef calcification versus Ω_{arag} based on alkalinity depletion method (e.g., Broecker et al., 2001; Yates and Halley, 2006; Silverman et al., 2007; Bates et al., 2010; Shamberger et al., in review) suggest significantly greater sensitivities than have been observed in single organism or tank mesocosm experiments. As seawater Ω_{arag} decreases, the net reef calcification (=sum of calcification – sum of dissolution) declines significantly. These studies also highlight the significant differences in baseline net calcification rates amongst different reef systems. When comparing across reef systems, net reef calcification rates do not correlate with Ω_{arag} (Shamberger et al., 2011, in review). These observations highlight the difficulties involved in resolving the relative influences on calcification of multiple co-varying factors (light, temperature, nutrients, hydrography, community composition) in the field.

As discussed at the workshop, there is a paucity of data on the effects of ocean acidification on non-calcification processes in coral reef organisms. Three studies have specifically addressed these effects, and the results are mixed. Albright et al. (2008) and Jokiel et al. (2008) reported no effect on settlement or gamete production (*P. astreoides*, *P. damicornis, M. capitata),* but a significant reduction was observed in sperm motility and settlement rates amongst new recruits of *A. palmata* (Albright et al., 2010).

Relatively few studies have investigated the impact of ocean acidification on carbonate reef dissolution. Available results suggest that dissolution could increase (e.g., Andersson et al., 2003, 2009; Yates and Halley, 2006). Tribollet et al. (2009) reported a 48% increase in bioerosion rates between 400 and 750 µatm CO_2 and increased activity of microborers.

Remaining uncertainties: Participant perspectives indicated that there is a paucity of data on reef-scale responses to Ω_{arag} and pCO_2 and on impacts of ocean acidification on $CaCO_3$ dissolution and bio-erosion. Multi-parameter experimental manipulations are needed (e.g., pCO_2, temperature, light and nutrients). To date, there is no information on behavioral/species interactions and few data on non-calcification effects (e.g., spawning, egg production). There has been no attempt to expand single organism responses to community level effects e.g., impact of reduced extension rates on coral cover. There are significant contradictions between laboratory and field observations in the sensitivity of calcification to changes in Ω_{arag}, and the reasons for this are unclear. One might be the difficulties involved in distinguishing and quantifying gross calcification and gross dissolution in natural reef settings. Results to date report only the net of these two processes.

1.5 Impacts on non-coral-reef invertebrates

This section of the Synthesis Plenary IV-2 presentation and the corresponding summary here synthesizes the material presented during Plenary Session II, Keynote II-3: Impacts on non-coral-reef invertebrates, by Sam Dupont. It also incorporates some points raised during the workshop's breakout group, poster session, and plenary discussions.

Workshop presentations and discussions indicated that this group is relatively well-studied using single species perturbation experiments, multi-species mesocosms, field manipulations, and observations and modeling studies. Single-species studies have been conducted on approximately 80 non-coral reef invertebrates (see Figure 1). Impacts of ocean acidification on fitness (broadly defined) are highly variable: responses range from severely negative (with implications for species extinction) to neutral to positive (see summary plot below). These appear to be species-specific even in closely related species and unpredictable, with no clear patterns emerging. Field studies have revealed obvious apparent contradictions; for example, calcifiers such as mollusks, crustaceans, and other groups in Kiel fjord are settling when pH is lowest between July and September, but when food supply is highest (Thomsen et al., 2010). Similar observations have been made on the East Coast of

the USA where shellfish larvae in coastal bays and estuaries experience pCO_2 of several thousand µatm (McCorkle, in prep).

At the workshop, several considerations were identified as contributing to the high level of variability and uncertainty regarding specific predictions, beyond the very general prediction that ocean acidification will affect some species and ecosystems. These considerations include the range of calcification mechanisms and $CaCO_3$ minerals employed (calcite, aragonite, Mg-calcite of variable Mg content); the range of non-calcification physiological functions that could be affected including metabolism, food acquisition and processing, and pH regulation; the range of life-history strategies; and the range of natural environmental variability experienced by a given population or species. Invertebrate life cycles can be lengthy and complex, and ocean acidification can affect different life stages or can have latent "carry over" effects. Yet most studies have focused only on adult responses to ocean acidification or on a single life stage, which can lead to underestimation of the potential impact. For example, in sea urchins, Dorey et al. (in prep) find that a pH change from 8.1 to 7.7 had no impact on juvenile survival, but a significant negative impact was observed when both larvae and subsequent juveniles were kept under low pH. Further, the short duration of most experiments can be below the time required for organisms to express plasticity in their response to ocean acidification (as demonstrated by Hernandez and Russell, 2010; Dorey et al., in prep) and/or the generation time needed for selection of potentially resilient phenotypes within populations, thus leading to overestimation of the potential impact. Conversely, short duration experiments can underestimate the real impacts by masking lethal effects that may occur later (e.g., Kurihara et al., 2008; Langenbush and Portner, 2004; Shirayama and Thornton, 2005).

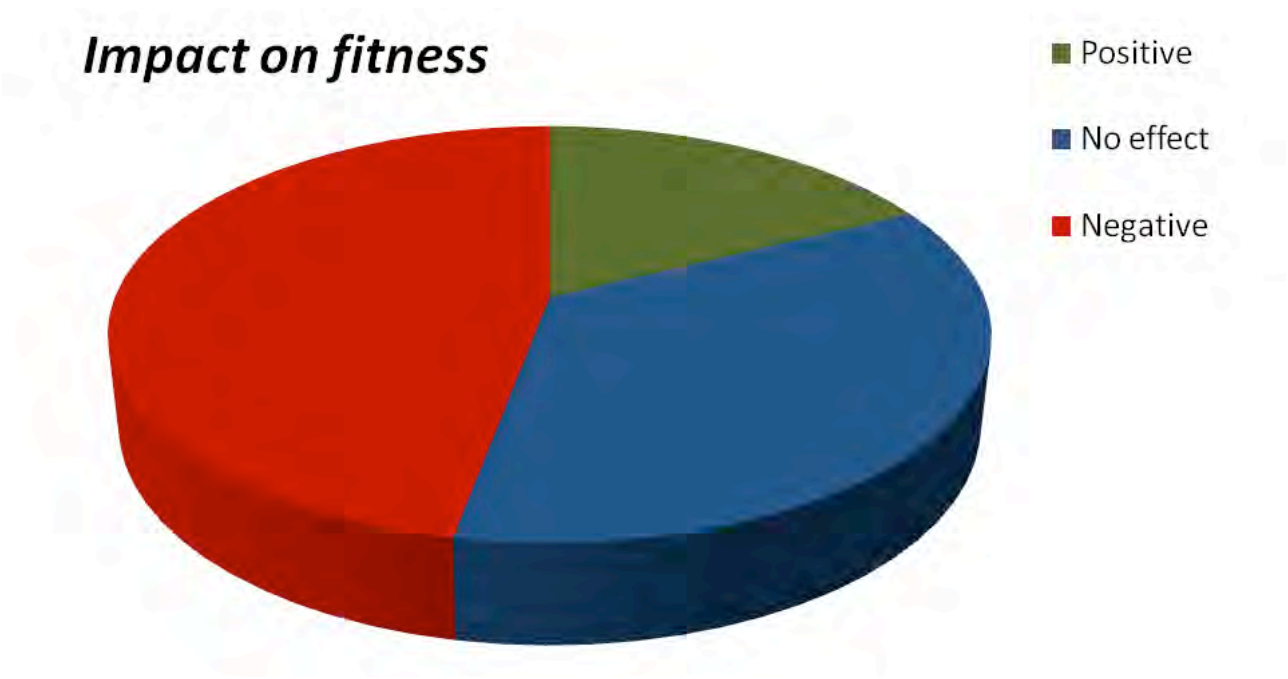

Figure 1. Effect of ocean acidification on fitness broadly defined on 81 invertebrate species. Credit: Sam Dupont.

Remaining uncertainties: While this group is comparatively well-studied, information exists for only 15 of 38 phyla and is robust for only 3 groups: mollusks, echinoderms, and arthropods. Longer term (including multigeneration / all life cycle) studies are needed, as well as studies that include environmental multiple stressors.

1.6 Additional impacts on invertebrates: non-calcification responses, life history effects, and evolutionary considerations

This section of the Synthesis Plenary IV-2 presentation and the corresponding summary here synthesizes the material presented during Plenary Session II, Keynote II-4: Additional impacts on invertebrates: non-calcification responses, life history effects, and evolutionary considerations, by Haruko Kurihara. It also incorporates some points raised during the workshop's breakout group, poster session, and plenary discussions.

There is considerable overlap between this section and Section 1.5. Processes considered here include non-calcification responses amongst invertebrates, life history effects, evolutionary considerations, and "others" including synergistic effects of CO_2 and temperature as well as ocean acidification effects on community level processes. The main perspective expressed at the workshop is that, within a species, sensitivity to ocean acidification depends on life cycle stage, with some stages (often early developmental stages especially juveniles) appearing significantly more vulnerable than others (larval or adult). In addition, ocean acidification affects *different processes* in larval, juvenile, and adult stages (Kurihara, 2008).

Workshop presentations and discussions indicated that, in general, significant variability (positive, negative, neutral) is observed in survival, growth, and physiological responses (e.g., respiration) amongst taxa, and both within and between species. There is evidence that the negative impacts of ocean acidification on growth and survival are enhanced as temperature deviates from optimum for the species (e.g., Metzger et al., 2007; Parker et al., 2009; Findlay et al., 2010). Species interactions, specifically feeding, have been studied, and results are variable. For example, elevated CO_2 and temperature increased feeding rate of *Pisaster* (starfish) on mussel prey (Gooding et al., 2009), but for the sea urchin *Hemicentrotus pulcherrimus*, elevated CO_2 alone decreased feeding rate of adult sea urchins on algae whereas temperature had no effect. Ocean acidification induced disruption of defense mechanisms (increasing mollusk shell thickness in the presence of a predator was diminished under ocean acidification conditions) and behavioral changes (increased avoidance of natural predators) (Bibby et al., 2007). However, opposite effects have also been reported (see Section 1.3, predator avoidance was decreased in tropical fishes under elevated CO_2; Munday et al., 2010). Very few studies have evaluated the effects of elevated CO_2 on reproductive output, and results to date show impacts are highly variable within this group. Some experiments report no impact on gonad development or numbers of laid eggs (e.g., Beesley et al., 2008; McDonald et al., 2009; Kurihara et al., 2007, 2008) but others demonstrated negative impacts (Kurihara et al., 2008). Finally, there is evidence for down/up regulation of genes involved in metabolism, cellular stress, apotosis, and biomineralization, specifically in sea urchin larvae cultured under high CO_2 (Todgham and Hofmann, 2009; O'Donnell et al., 2010).

Remaining uncertainties: Discussions during the workshop noted that few experiments have investigated impacts of ocean acidification on different life stages of the same organism yet there are clear indications that the impacts will probably not be equivalent. The mechanism underlying the high variability of the responses amongst taxa, and amongst and within species, to the ocean acidification (e.g., possible genetic variation for the CO_2 tolerance) is still unknown.

2. Summary of common uncertainties identified at the workshop

This section of the Synthesis Plenary IV-2 presentation and the corresponding summary here summarizes uncertainties identified across presentations in Plenary Session II: Impacts of Ocean Acidification for Individual Organisms, also as considered during the workshop's breakout group, poster session, and plenary discussions.

Key uncertainties: Workshop participants identified two areas of key uncertainties: (i) how to predict future responses of individual organisms and ecosystems based on data generated in mostly short-

term (hours to weeks), small scale, single organism experiments with single parameter manipulations using different methods and (usually) abrupt changes in CO_2 chemistry, whereas actual predicted scenario will be organisms facing gradual, long term exposure to multiple changing parameters at all life cycle stages that will likely affect prey abundance and availability, and possibly predator behaviours, i.e., how to extrapolate laboratory findings to real world situation; and (ii) how to reconcile laboratory data with seemingly contradictory field observations (e.g., organisms living and spawning when and where lab studies suggest they shouldn't). Specifically, participants noted the following:

***Scaling up in time, space and complexity*:** how to predict future responses based on results from abrupt, small-scale, single-organism, single parameter, short term experiments. How to gauge indirect effects, ecosystem engineering role of organisms, representativeness of species/ecological/economical relevance.

How to interpret (and thus better predict) response variability within species: how much variability can be attributed to methodology including methods used to manipulate seawater chemistry, as well as baseline nutrient concentrations and salinity of different aquarium seawaters versus that contributed by environmental history, life stage and gender, genetic variability and plasticity.

Adaptation potential: how to assess potential for acclimation and adaptation in laboratory experiments and field settings. Information contained in the variability of the individual responses versus average responses.

Environmental variability: how to best match spatial and temporal environmental variability to the organism and life stages under study. Also, are the mean, maximum, or minimum values and timing of a given parameter important in the organism response?

Energy: how significant is the role of energetic status in response variability and flexibility and how does climate change impact variability of nutrients (e.g., iron via iron-ligand formation) and food (e.g., pteropods).

Synergistic interactions: ocean acidification will occur in concert with changes in temperature, nutrients, and circulation, yet few experiments have manipulated multiple parameters.

3. Way forward: identification of research gaps discussed at the workshop

This section of the Synthesis Plenary IV-2 presentation and the corresponding summary here summarizes research gaps identified across presentations in Plenary Session II: Impacts of Ocean Acidification for Individual Organisms, also as considered during the workshop's breakout group, poster session, and plenary discussions.

Scaling up in time, space and complexity: There is need for data from single organism, small tank experiments in order to quantify responses, identify thresholds and make a start at identifying mechanisms/pathways. Most helpful would be longer-term experiments that observe different life stages and processes in addition to calcification, and experiments that manipulate multiple parameters simultaneously. These experiments should be linked with larger scale, multi-species community level experiments i.e., increased complexity, using mesocosms, natural high CO_2 environments, and Free Ocean Carbon Enrichment (FOCE). There is need for modelling experiments to predict impact of single organism and multi-level interaction (e.g., predator prey) responses to community and ecosystem level responses, and over longer time periods than is possible with (most) laboratory experiments.

Understanding mechanisms behind responses and response variability: Small-scale experiments are needed to address underlying mechanisms involved in physiological responses to OA as well as

reasons for the observed range of responses, including phenotypic and genotypic variability within and amongst populations. Approaches and tools to estimate adaptation potential within and amongst species are needed.

Environmental variability: Data on natural ranges of carbonate system and other parameters experienced by organisms in their natural environment on diurnal, subseasonal, seasonal, and interannual time scales are sparse and needed. There is also a need for information on spatial variability within habitat ranges.

Energy: There are indications that energetic status is critical to organism responses to ocean acidification but little data exist on energetic cost of most physiological processes under ambient or elevated CO_2. There is a need to assess flexibility in energy partitioning, dynamic energy budget modelling, and considerations of other currency than C, N.

Synergistic interactions: As discussed above, there is a need for multi-factorial experiments, and consideration of additional anthropogenic stressors as well as other population level responses to climate change.

Other: There is a need to understand dissolution and the impact of ocean acidification on dissolution processes, invertebrate acidosis regulation, immune function and health, and the response of pathogens.

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Synthesis Plenary IV-3: Scaling up to ecosystems: the state of knowledge, key uncertainties, and the way forward

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The summary that follows, written by the presenters of the Synthesis Plenary IV-3 presentation, synthesizes perspectives of the IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems, especially as presented during Plenary Session III: Scaling Up to Ecosystems but also as discussed during the workshop's breakout group, poster, and other plenary sessions.

As discussed at the workshop, there are at least two major goals of ocean acidification research related to scaling up to ecosystems: (1) Detection and attribution of observed changes resulting from ocean acidification; and (2) Projections of future changes that would be expected to result from increasing ocean acidification. Both of these goals are important and interdependent.

1. Detection and attribution of observed changes

As discussed extensively at the workshop, there are ecosystem changes occurring today that are clearly attributable to climate change. Temperature change is a key driver, but the situation is usually complex, with several environmental factors and processes changing at the same time. In contrast, clear attribution of ongoing ecosystem change or elements thereof to anthropogenic ocean acidification has not (yet) been made compellingly, but we are still early in the process. Experiments at ecosystem level (mesocosms, free-ocean CO_2 enrichment), studies of natural analogues (e.g., CO_2 seeps), and ecosystem modelling are underway to elaborate the specific effects of ocean acidification at the community level.

2. Projections of future changes

Scientific research into the putative effects of ocean acidification on marine fauna describes a link between rising atmospheric and oceanic CO_2 levels, decreasing ocean pH, carbonate saturation state and carbonate concentrations ($[CO_3^{2-}]$) (Caldeira and Wickett, 2005) and effects on marine organisms. A substantial number of experimental studies have reported significant effects of future ocean acidification on aspects of the physiology, life-history and ecology of individual species and populations. Participant perspectives indicated that uncertainty rises as experimental observations of individual species are used to assess the impact of ocean acidification at higher levels of biological organization (e.g., on community structure, food web dynamics and ecosystem function). This is partly due to the diversity of responses observed, even between closely related species and within families and phyla. Predicting the outcome of interactions among many different species is challenging, especially when species are predicted to respond differently to environmental stressors. Nevertheless, all of these responses integrate into ecosystem change and may affect ecosystem services. Such developments lead to changing benefits for human welfare and imply socioeconomic consequences.

3. Ways forward

Workshop participants noted that strategies are needed to improve skills with respect to both attribution and projection of effects of ocean acidification at ecosystem scale. Several different approaches are likely to be necessary and fruitful, including experiments on and observations of real marine communities, paleo-studies, and modelling studies. However, there will be limited opportunity within the next years or even decades to develop the desired attributional or predictive

capability, unless experiments and observations at the community scale are complemented by a strategy for linking the likely community-scale response to experiments and observations made at lower levels of biological organization. It was posited that such a strategy would need to involve the response of each higher level of organization being constrained by the response at lower levels of organization (e.g., organism level responses must obey the laws of thermodynamics, and ecosystem scale responses must be consistent with truths determined at the organism and lower levels).

Discussions held during the workshop indicated that, across levels of biological organization from the genome via molecular functions to cells, organisms and ecosystems, ocean acidification operates on increasing spatial and temporal scales, with implications for socioeconomic systems and long term evolutionary changes. While short term effects (seconds to days or even weeks) of exposure to elevated CO_2 levels become operative at lower levels, from the genome to whole organism, they may not bear long-term importance for ecosystem level processes as, in many cases, organisms are known to acclimatize and to partly or fully compensate for the respective disturbances. Detection and attribution of ecosystem level processes, therefore, requires long-term investigations of processes involving organisms and ecosystems.

Discussions further indicated that a mechanistic understanding of whole-organism responses is important as it provides a cause and effect understanding and, thereby, identifies the causal links between environmental forcing and the responses of organisms and ecosystems. A mechanistic understanding also builds on knowledge at the tissue, cellular, molecular and genomic levels. Community and ecosystem responses to climate change including ocean acidification as well as evolutionary trends have been extrapolated from the investigation of paleo- and natural analogues. However, paleo-analogues tend to show reduced taxonomic resolution (i.e., they may not show changes at species level). Multiple stressors are involved during ongoing ecosystem change and have also been involved during past evolutionary crises, but possibly to different degrees or in different combinations than during ongoing and future human-induced change. Natural analogues may either be too small in scale (e.g., the seeps) or confounded with atypical patterns of other environmental parameters. Ecosystems in natural analogues are often in exchange with undisturbed neighbouring ecosystems. While being analogues for one specific factor like CO_2, they may otherwise not display the typical influences of climate change. Larvae from unaffected populations, for example, might replenish populations living in natural seeps. Upwelling zones have high CO_2 levels, but may be characterized by low temperatures and high nutrient levels. While there is much to be learned from studying such systems, they are not direct analogues of future ocean conditions. A significant level of uncertainty thus prevails, as to the comparability of these ecosystems to the global impacts of anthropogenic ocean acidification and climate change.

In future analyses, greater consideration of phenotypic variability and the potential for selection of adaptive genetic variation will be important for predicting evolutionary responses to ocean acidification. Many marine species are highly fecund and may spawn many times over their lives. A few tolerant breeding individuals can thereby produce an enormous number of tolerant offspring that may shape the functional properties of future populations. Breeding experiments that estimate the genetic components of variation will be useful for predicting the heritability of individual variation observed in ocean acidification experiments. Experimental studies of evolution over many generations would be suitable to monitor the establishment of new functional traits.

Participants indicated that a cause and effect understanding would help identify the drivers and crucial processes involved and, thereby, reduce the uncertainty in interpreting the respective findings. A cause and effect understanding would also help identifying similarities and differences between paleo- and ongoing change and thereby narrow down the diversity of possible interpretations.

Discussions suggested that a synthesis of present knowledge and the reduction of uncertainty in projecting ecosystem change would benefit from a conceptual framework which places the effects of

ocean acidification into the context of changes induced by other factors involved in climate change. Such a framework should be able to link the levels of biological organization through a mechanistic understanding. Uncertainty will be reduced as analyses at various levels of biological organisation can be shown to be consistent. Higher-level processes do not violate principles operative at lower levels. As a consequence, principles operative at lower levels reduce the number of options followed by processes at higher levels.

As discussed at the workshop, in a climate change context, CO_2 induced ocean acidification occurs due to anthropogenic CO_2 accumulation in warming oceans. In some areas anthropogenic ocean acidification occurs on top of a high natural variability of CO_2 concentrations in the oceans (Pelejero et al., 2010). High dissolved CO_2 concentrations develop, where respiration and the oxidative degradation of organic material exceed the input of oxygen and reduction of CO_2 levels through ventilation and mixing of ocean waters. In so-called oxygen minimum layers, enhanced respiration or enhanced stratification or both cause oxygen deficiency and concomitant CO_2 accumulation. CO_2 induced acidification is also found in systems denominated as natural analogues such as the CO_2 vent systems of the Mediterranean (Hall-Spencer et al., 2008). Changes in ocean currents may also occur with climate change leading to increasing oceanic upwelling and, in consequence, enhanced acidification of surface waters. As a result, effects of ocean warming, acidification, and hypoxia are intertwined in several systems, and these effects would need to be disentangled for an attribution of effects to individual factors. In some cases attribution to individual factors may not be possible, because an effect may manifest itself only in the case of multiple stressors such as might be posed by a combination of warming and acidification. Here again, the question arose whether unifying principles and mechanisms exist of how factors act individually or in combination, from the genomic up to ecosystem level?

4. Developing an integrative perspective

Participant perspectives indicated that CO_2-driven changes in species interactions may become part of this complex picture under future ocean acidification scenarios. Differential CO_2 sensitivities at the species or population level were observed in the Mediterranean around Ischia, an area exposed to volcanic CO_2 emissions and considered a natural analogue (Hall-Spencer et al., 2008). They were also observed in experimental trials under elevated CO_2 levels (Diaz-Pulido et al., 2011). In areas with a mean water pH value below around 7.8, calcareous algae become less competitive for space than non-calcareous algae, such that within a very narrow pH range of further acidification the space occupied by algae overall is fully taken by non-calcareous algae. These findings are in line with a loss in performance capacity of the calcareous algae under elevated CO_2 levels. It remains unclear, however, whether these relative changes in competitiveness also involve a CO_2 dependent shift in the temperature dependent performance curves of the two species.

Building on the general participant consensus of linkages among changes in ocean physicochemistry and those in ocean biology, the application of a consistent conceptual framework known to operate across diverse marine ecosystems would improve the detection and attribution of effects of ocean acidification, as well as projections of future changes. Such a framework would be able to integrate and link results from experimental studies, from paleo- and from natural analogues and from field observations. Establishment of such a framework could substantially reduce the level of uncertainty under which policy decisions relevant to ocean acidification will need to be made.

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Annex 1: Workshop Proposal

ipcc

INTERGOVERNMENTAL PANEL ON climate change

IPCC BUREAU - FORTIETH SESSION
Geneva, 18 September 2009

BUR-XL/Doc. 7
(16.IX.2009)
Agenda Item: 5.5
ENGLISH ONLY

PROGRESS REPORT

Proposal for an IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems

(Submitted by the Government of Japan, Working Group II and Working Group I Co-Chairs)

IPCC Secretariat

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WMO UNEP

Proposed IPCC Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems

Submitted by: Government of Japan
WGII and WGI Co-Chairs

Background

The oceans currently absorb about one-third of fossil fuel CO_2 emitted to the atmosphere and have, as a consequence, been increasing in acidity. Ocean acidification is now recognized as a critical component of global change, potentially responsible for a wide range of impacts on ecosystems, with subsequent consequences on livelihoods and food security. Furthermore, an important aspect is that more CO_2 mitigation may be required to achieve particular stabilization targets because acidification limits the ability of the oceans to continue to absorb CO_2. Previous IPCC assessment reports considered biogeochemical and temperature effects of anthropogenic carbon on the oceans, but the direct impacts of ocean acidification, its combined effects with ocean warming on marine ecosystems and productivity, and potential feedbacks to the climate system, have not been fully assessed.

The Synthesis Report of AR4 concluded: *While the effects of observed ocean acidification on the marine biosphere are as yet undocumented, the progressive acidification of oceans is expected to have negative impacts on marine shell forming organisms and their dependent species* [IPCC 2007 Synthesis report 3.3.4]. The Technical Summary of AR4 WG2 concluded: *Ocean acidification is an emerging issue with potential for major impacts in coastal areas, but there is little understanding of the details. It is an urgent topic for further research, especially programmes of observation and measurement* [IPCC 2007 WG2 Box TS.5].

Since the publication of the AR4, ocean acidification research, especially experimental studies of the impact of increased concentrations of seawater CO_2 on marine biology, and modeling studies of future ocean environments, has been advancing rapidly. With this progress and increasing interest from stakeholders in understanding the implications of ocean acidification, it is extremely valuable to have the IPCC sponsor a meeting of the growing scientific community, which would stimulate communication among the scientists, encourage efficient transfer of information to modelers, and encourage the production of peer-reviewed papers that will be assessed in the AR5. The report of the meeting will focus attention on a specific issue highlighted in the AR4 as requiring additional work

Aim of Workshop

The strategic aim of the Workshop will be to update the rapidly advancing scientific findings on ocean acidification and its impacts since the publication of AR4, and to provide comprehensive, timely scientific information as input to AR5.

The specific aims should include:

- Synthesis of observations and projections of ocean CO_2 and seawater pH;
- Summary of manipulation experiments focused on assessing biological and ecosystem impacts of ocean acidification;
- Discussion of possible ecosystem modeling techniques to study ecological and socioeconomic impacts of future ocean acidification;
- Assembling and assessing emerging scientific findings on ocean acidification to update the AR4 and contribute to the development of the AR5.

Scientific Steering Group

A Scientific Steering Group (SSG) for the planning and execution of the Workshop will be established, taking into account the need for balanced scientific expertise, as well as geographical and developed/developing country representation. The WGII and WGI Co-chairs will jointly lead

the SSG selection process and the meeting planning, with WGII taking the operational lead for the meeting.

Product

A workshop report, based on material presented or discussed at the workshop or in the recent literature, will be produced by mid-2011. The workshop report is expected to organize the results of existing research, highlight key issues, identify major unknowns, and stimulate new research, providing an important starting point for the assessment in the AR5.

Timetable and Location

The Workshop is proposed to be held in the first quarter of 2011 in Japan (exact venue to be decided).

Participants

About 100 participants will be invited, including LAs for relevant chapters of the AR5 from all three WGs. The list of invitees will be developed by the SSG in consultation with the Co-Chairs and Vice-Chairs of WGII and WGI.

Financial Resources

The Ministry of the Environment, Japan is exploring financial resources to host the Workshop (not secured yet). The Ministry would like to obtain authorization for financial support from the IPCC Trust Fund budget to support the participation of developing country experts. It is proposed that 40 Trust Fund journeys should be allocated, including those of WG Vice-Chairs.

Annex 2: Programme

IPCC WGII/WGI Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems

Okinawa, Japan
17-19 January 2011

PROGRAMME

SUNDAY, 16 JANUARY 2011, PRE-WORKSHOP EVENTS

The pre-workshop events were organized and supported by the Ministry of the Environment Japan, in cooperation with National Institute for Environmental Studies and University of the Ryukyus.

13:00 Poster Session (Display and Discussion)

14:30 General Audience Lectures

- How well can we predict the combined impacts of ocean acidification and global warming? *Peter Brewer*
- Potential impacts of ocean acidification on marine biology. *Yoshihisa Shirayama*

16:00 Poster Presentations

18:00 Ice Breaker Welcome

MONDAY, 17 JANUARY 2011

08:30 Registration
09:00 Welcome Address (Local Host)
09:15 Introduction/Background (Field/Barros/Wratt)

PLENARY SESSION I: The Changing Chemistry of the Oceans (Chair: Barros)

9:30 Keynote I-1: Controls on ocean carbon chemistry: a paleo perspective. *Richard Zeebe*
10:00 Keynote I-2: Changes in ocean carbon chemistry since pre-industrial times. *Kitack Lee*

10:30 Break

11:00 Keynote I-3: Future projections of ocean carbon chemistry. *Fortunat Joos*
11:30 Keynote I-4: Ocean acidification in coastal waters and other vulnerable ocean regions. *Rik Wanninkhof*

PLENARY SESSION II: Impacts of Ocean Acidification for Individual Organisms (Chair: Wratt)

12:00 Keynote II-1: Impacts on calcification and dissolution for coral reefs and coral reef organisms. *Jean-Pierre Gattuso*
12:30 Keynote II-2: Impacts on phytoplankton calcification and photosynthesis, with consideration of evolutionary responses. *Debora Iglesias-Rodriguez*

13:00 Lunch

14:00 Keynote II-3: Impacts on non-coral-reef invertebrates. *Sam Dupont*
14:30 Keynote II-4: Additional impacts on invertebrates: non-calcification responses, life history effects, and evolutionary considerations. *Haruko Kurihara*

15:00 Introduction to Break-Out Groups (Field)

BREAK OUT GROUPS I

15:15 BOG I-1: Detection and attribution of ocean acidification and its impacts.
(Chair: Sabine; Rapporteur: Bopp)
BOG I-2: Reconciling apparently contradictory observations.
(Chair: Gattuso; Rapporteur: Riebesell)
BOG I-3: Spatial and temporal scales of variability and rates of change.
(Chair: Munday; Rapporteur: Cohen)

16:30 Break

POSTER SESSION I

17:00 Poster Presentations (2-minute/1-slide)
18:00 Poster Session

19:00-21:00 Reception

TUESDAY, 18 JANUARY 2011

09:00 Introduction to Day 2 (Field/Barros/Ebi)

PLENARY SESSION II, continued: Impacts of Ocean Acidification for Individual Organisms (Chair: Pörtner)

09:15 Keynote II-5: Impacts on fishes, their life histories, and evolutionary responses. *Atsushi Ishimatsu*
09:45 Keynote II-6: Impacts on microbial processes and biogeochemistry. *Nicola Wannicke*

PLENARY SESSION III: Scaling Up to Ecosystems (Chair: Ebi)

10:15 Keynote III-1: What can we learn from the paleo record?: Mass Extinction Events and Recovery. *Ken Caldeira*

10:45 Break

11:15 Keynote III-2: Scaling up from experimental responses. *Ove Hoegh-Guldberg*
11:45 Keynote III-3: Scaling up from natural responses. *Jason Hall-Spencer*
12:15 Keynote III-4: Socioeconomic impacts of ocean acidification: lessons from the past? *Sarah Cooley*

12:45 Lunch

BREAK OUT GROUPS I, continued

13:45 BOG I-1, I-2, and I-3, continued
15:30 Reports from Break-Out Groups I (BOG Rapporteurs and Chairs)

16:30 Break

POSTER SESSION II

17:00 Poster Presentations (2-minute/1-slide)
18:00 Poster Session

19:00 Adjourn

WEDNESDAY, 19 JANUARY 2011

09:00 Introduction to Day 3 (Field/Wratt/Ebi)

BREAK OUT GROUPS II

09:15 BOG II-1: Learning from the past and present to predict the future.
(Chair: Schmidt; Rapporteur: Heinze)
BOG II-2: Understanding the roles of multiple stressors.
(Chair: Haugan; Rapporteur: Hofmann)
BOG II-3: Scaling up to humans: the socioeconomics of ocean acidification.
(Chair: Brewer; Rapporteur: Turley)

10:30 Break

11:00 BOGs II-1 to II-3, continued

12:00 Reports from Break-Out Groups II (BOG Rapporteurs and Chairs)

13:00 Lunch

PLENARY SESSION IV: Synthesis Plenary (Chair: Field)

14:00 Presentation IV-1: The changing chemistry of the oceans: the state of knowledge, key uncertainties, and the way forward. *Richard Feely & James Orr*

14:20 Presentation IV-2: Impacts of ocean acidification for individual organisms: the state of knowledge, key uncertainties, and the way forward. *Andreas Andersson, Anne Cohen, & Yukihiro Nojiri*

14:40 Presentation IV-3: Scaling up to ecosystems: the state of knowledge, key uncertainties, and the way forward. *Ken Caldeira, Philip Munday, & Hans-Otto Pörtner*

15:00 Concluding Discussion

15:45 Break

16:15 Concluding Discussion, continued

16:45 Closing Remarks (Field/Wratt)

17:00 Adjourn

Annex 3: Proposal for Plenary Session Presentations

IPCC WGII/WGI Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems

Okinawa, Japan
17-19 January 2011

PROPOSAL FOR PLENARY SESSION PRESENTATIONS

PLENARY SESSION I: The Changing Chemistry of the Oceans

Keynote Presentation I-1: **Controls on ocean carbon chemistry: a paleo perspective.** *Richard Zeebe*

This presentation will synthesize what is known about the history of ocean chemistry (prior to the Industrial Revolution). Mechanisms and controls on ocean carbonate chemistry will be overviewed. Uncertainties in the estimates of ocean chemistry based on proxy methods should be discussed.

Keynote Presentation I-2: **Changes in ocean carbon chemistry since pre-industrial times.** *Kitack Lee*

This presentation will synthesize what is known about large-scale and long-term changes in global ocean carbon chemistry, pH, and carbonate saturation states. Impacts on aragonite/calcite saturation, on dissolution processes, and on carbonate fluxes in the water column should also be covered.

Keynote Presentation I-3: **Future projections of ocean carbon chemistry.** *Fortunat Joos*

This presentation will synthesize projected changes in ocean carbon chemistry over the 21st century and beyond from coupled climate - carbon cycle models and for a range of carbon dioxide emission scenarios, CO_2 stabilization profiles, etc. The presentation will also consider changes in ocean circulation (vertical mixing, ventilation, stratification, etc.) and biological processes, and their effects on ocean pH, aragonite/calcite saturation states, carbonate dissolution rates, carbonate fluxes, and ballast effect.

Keynote Presentation I-4: **Ocean acidification in coastal waters and other vulnerable ocean regions.** *Rik Wanninkhof*

This presentation will synthesize what is known about changes in ocean carbon chemistry at regional scales from observations and modeling, focusing on the coastal ocean and other vulnerable ocean regions (e.g., the Arctic and Southern Ocean). It will summarize, for example, knowledge on temporal variability of the carbon system in coastal regions and its impacts on carbonate saturation, including effects of primary production and remineralization, hypoxia, upwelling processes, and carbonate dissolution.

PLENARY SESSION II: Impacts of Ocean Acidification for Individual Organisms

Keynote Presentation II-1: **Impacts on calcification and dissolution for coral reefs and coral reef organisms.** *Jean-Pierre Gattuso*

This presentation will synthesize what is known about the impacts of ocean acidification on calcification and dissolution with a focus on coral reefs and coral reef organisms. The presentation will encompass what has been learned through a variety of experimental techniques (e.g., lab and mesocosm studies, observations of natural responses, modeling results, etc.).

Keynote Presentation II-2: **Impacts on phytoplankton calcification and photosynthesis, with consideration of evolutionary responses.** *Debora Iglesias-Rodriguez*

This presentation will synthesize what is known about the impacts of ocean acidification on phytoplankton calcification and photosynthesis, with consideration of evolutionary responses. The presentation will encompass what has been learned through a variety of experimental techniques (e.g., lab and mesocosm studies, observations of natural responses, modeling results, etc.).

Keynote Presentation II-3: **Impacts on non-coral-reef invertebrates.** *Sam Dupont*

This presentation will synthesize what is known about the impacts of ocean acidification on non-coral-reef invertebrate calcifiers, including mollusks, crustacea, and echinoderms. The presentation will encompass what has been learned through a variety of experimental techniques (e.g., lab and mesocosm studies, observations of natural responses, modeling results, etc.).

Keynote Presentation II-4: **Additional impacts on invertebrates: non-calcification responses, life history effects, and evolutionary considerations.** *Haruko Kurihara*

This presentation will synthesize what is known about the other impacts of ocean acidification on invertebrates: non-calcification responses, life history and evolutionary aspects. The presentation will encompass what has been learned through a variety of experimental techniques (e.g., lab and mesocosm studies, observations of natural responses, modeling results, etc.).

Keynote Presentation II-5: **Impacts on fishes, their life histories, and evolutionary responses.** *Atsushi Ishimatsu*

This presentation will synthesize what is known about impacts of ocean acidification on fishes, their life histories, and evolutionary responses. The presentation will encompass what has been learned through a variety of experimental techniques (e.g., lab and mesocosm studies, observations of natural responses, modeling results, etc.).

Keynote Presentation II-6: **Impacts on microbial processes and biogeochemistry.** *Nicola Wannicke*

This presentation will synthesize what is known about impacts of ocean acidification on microbial processes and biogeochemistry. The presentation will encompass what has been learned through a variety of experimental techniques (e.g., lab and mesocosm studies, observations of natural responses, modeling results, etc.).

PLENARY SESSION III: Scaling Up to Ecosystems

Keynote Presentation III-1: **What can we learn from the paleo record?: Mass Extinction Events and Recovery.** *Ken Caldeira*

This presentation will synthesize what is known from the paleo record about past chemistry changes and resulting biological responses, evaluating research on how long it takes ocean ecosystems to recover from mass extinction events. The presentation will evaluate the extent to which past events are analogues for current trends and future acidification scenarios.

Keynote Presentation III-2: **Scaling up from experimental responses.** *Ove Hoegh-Guldberg*

This presentation will synthesize what is known from, and limitations in, scaling up to ecosystems from experimental (e.g., lab and mesocosm studies, modeling results, etc.) responses, making comparisons across a variety of organisms.

Keynote Presentation III-3: **Scaling up from natural responses.** *Jason Hall-Spencer*

This presentation will synthesize what is known from, and limitations in, scaling up to ecosystems from natural (e.g., seep) responses, making comparisons across a variety of organisms and environments.

Keynote Presentation III-4: **Socioeconomic impacts of ocean acidification: lessons from the past?** *Sarah Cooley*

This presentation will synthesize, for various human communities, the effects of failures of ocean ecosystems and corresponding losses of ecosystem services, determining if there are key findings relevant to future ocean acidification impacts. Case studies could be included to provide examples from the past, e.g., from past fisheries collapse or coral-reef losses.

PLENARY SESSION IV: Synthesis Plenary

Keynote Presentation IV-1: **The changing chemistry of the oceans: the state of knowledge, key uncertainties, and the way forward.** *Richard Feely & James Orr*

For the overarching topic of "the changing chemistry of the oceans," this presentation will summarize perspectives of the workshop, as presented and discussed in keynote presentations, break-out group discussions, and plenary discussions. In this final synthesis of the state of knowledge on changing chemistry, the presentation will also identify important open questions and key areas of uncertainty.

Keynote Presentation IV-2: **Impacts of ocean acidification for individual organisms: the state of knowledge, key uncertainties, and the way forward.** *Andreas Andersson, Anne Cohen, & Yukihiro Nojiri*
For the overarching topic of "impacts of ocean acidification for individual organisms," this presentation will summarize perspectives of the workshop, as presented and discussed in keynote presentations, break-out group discussions, and plenary discussions. The presentation will synthesize impacts across organisms discussed at the workshop, identifying general themes. This final discussion of the state of knowledge on impacts on individual organisms will also summarize the important open questions and key areas of uncertainty.

Keynote Presentation IV-3: **Scaling up to ecosystems: the state of knowledge, key uncertainties, and the way forward.** *Ken Caldeira, Philip Munday, & Hans-Otto Pörtner*
For the overarching topic of "scaling up to ecosystems," this presentation will summarize perspectives of the workshop, as presented and discussed in keynote presentations, break-out group discussions, and plenary discussions. This final synthesis of the state of knowledge on scaling up to ecosystems will also identify important open questions and key areas of uncertainty.

CHARGE TO PRESENTERS

-20 minutes will be allocated for each presentation, plus 10 minutes for questions

-Plenary presenters are asked to provide comprehensive syntheses of the body of science related to the assigned topic. Presenters should attempt to synthesize the current state of knowledge and understanding on the topic, delineating as clearly as possible what is known and what key uncertainties remain. Talks should not be descriptions of the presenter's own research. Presenters may want to seek input from colleagues for their presentations in order to represent fully the spectrum of scientific views and discussions.

-As much as possible for statements made, presenters should describe degrees of certainty and the basis of uncertainty estimates. They should provide ranges for variables or outcomes, quantitative uncertainty measures, etc.

-Where relevant, presenters should synthesize and provide the following: 1) an overview of research methods commonly used, and 2) key uncertainties that these research methods fail to address (e.g., multiple stressors and interaction effects, long-term system response, etc.).

Annex 4: Proposal for Breakout Group Discussions

IPCC WGII/WGI Workshop on Impacts of Ocean Acidification on Marine Biology and Ecosystems
Okinawa, Japan
17-19 January 2011

PROPOSAL FOR BREAKOUT GROUP DISCUSSIONS

BREAKOUT GROUP SESSION I:

BOG I-1: Detection and attribution of ocean acidification and its impacts

BOG I-2: Reconciling apparently contradictory observations

BOG I-3: Spatial and temporal scales of variability and rates of change

BREAKOUT GROUP SESSION II:

BOG II-1: Learning from the past and present to predict the future

BOG II-2: Understanding the roles of multiple stressors

BOG II-3: Scaling up to humans: the socioeconomics of ocean acidification

Descriptions of these Breakout Groups follow on the subsequent pages.

BOG I-1: Detection and attribution of ocean acidification and its impacts

Chair: Christopher Sabine
Rapporteur: Laurent Bopp

Ocean acidification is one of a number of stressors affecting the ocean's ecosystems. For present day and projected future changes, this BOG will explore, using data and models, the degree to which ocean acidification and its impacts can be detected and attributed to anthropogenic increases in atmospheric CO_2. The BOG will discuss the ability of the current generation of ocean carbon cycle models to reflect the observed spatio-temporal distribution of carbon system parameters and pH in the global oceans. In addition, the BOG will evaluate when and where changes in carbonate chemistry, along with associated uncertainties, are expected to be quantified in the open ocean, coastal zones, and estuaries. Finally, the BOG will evaluate when and where ocean acidification and its impacts are expected to be identified and understood, independent of other interacting stressors.

Questions to be addressed in this BOG include:

- To what extent can changes in ocean chemistry be directly linked to increases of atmospheric CO_2?
- How do the various components of climate change in the ocean (warming, circulation changes, etc.) affect detection and attribution of direct CO_2-induced changes?
- Are different approaches for determining atmospheric sources of ocean acidification required for coastal zones and estuaries, as compared to the open ocean?
- How well do observations and ocean carbon cycle models agree on the spatial distributions of aragonite and calcite saturation? What are the uncertainties of the present-day estimates of carbonate saturation from these models? How will model-data biases affect future projections of carbonate saturation and of ocean acidification in general?
- What are key considerations in detection and attribution of ocean acidification and its impacts in the context of multiple changes?
- To what degree can impacts expected from ocean acidification be detected and linked to the changing chemistry of the oceans? To what degree can these impacts be formally attributed (e.g., through a formal multi-step attribution approach) to ocean acidification, as well as to anthropogenic increases in atmospheric CO_2?
- How do the interacting processes of calcification, dissolution, and organic matter remineralization impact feedback mechanisms for carbon cycling to the atmosphere?

BOG I-2: Reconciling apparently contradictory observations

Chair: Jean-Pierre Gattuso
Rapporteur: Ulf Riebesell

In the burgeoning fields of study related to ocean acidification, some experimental results (from, for example, oceanic or regional observations, lab and mesocosm studies, observations of natural responses, and modeling) have been apparently contradictory. This BOG will attempt not only to identify the areas of controversy but also to identify ways to reconcile divergent results, in particular as relates to effects of ocean acidification on calcification and other processes.

Because we have limited time, this BOG will discuss three broad areas:

- Coral calcification
- Planktonic calcification (forams, coccolithophorids)
- Effects on processes other than calcification

Questions to be addressed in this BOG include:

- For the three broad areas listed above, what are important contradictory conclusions that different investigators have drawn, and what is the observational basis for those contradictory conclusions?
- For each of those sets of observations:
    - For which can identifiable differences in experimental (or observational) techniques, design, or procedures provide a possible explanation for apparent differences in results?
    - Can the apparent differences among experimental results be clarified already? How much of the variability we have observed reflects real variability in the organism and community calcification response to changing omega (as opposed to differences in experimental protocol or analytical methods)? What additional experiments, if any, are needed to explain observed differences in experimental results?
    - What kinds of feasible experiments would put us in a better position to make reliable predictions about the real ocean later this century?
- For coral and planktonic calcification, is there consensus regarding the magnitude of the impact of ocean acidification on marine calcification, as observed in manipulation experiments and field-based studies? Does large variability in outcome amongst different experiments, the small number of experiments conducted to date, and the lack of replication by different groups preclude a meaningful summary of experimental results? And if so, what do we need to do (experimentally) to close this knowledge gap?
- Is there consensus regarding the magnitude of the impact of ocean acidification on marine biological processes other than calcification?
- For all three areas, what are the major discrepancies amongst results from manipulation experiments and field observations? Can the discrepancies be reconciled?

BOG I-3: Spatial and temporal scales of variability and rates of change

Chair: Philip Munday
Rapporteur: Anne Cohen

The processes associated with and the influences of ocean acidification occur across a wide variety of spatial and temporal scales: from specific ocean regions to whole ocean basins, from molecular and cellular mechanisms to organisms and ecosystems, and from short-term variability to changes over deep evolutionary time. Fully understanding processes and resulting scientific complexities across these scales will take a long time, yet people, including policy-makers, will need to make decisions based on limited information.

In this BOG, we will explore how physical, chemical, and biological processes on different spatial and temporal scales relate to each other, as relevant to changing ocean chemistry and consequences for marine organisms and ecosystems. Overall, we will discuss how we can develop increased mechanistic understanding over spatial and temporal scales, or adopt other strategies, that can improve the ability to project changes in ocean chemistry and resulting biological and ecological impacts over the time scales relevant to decision-makers.

For each question considered, the BOG will identify what is known and outline strategies that could be used to provide better or more certain answers, especially as would inform decision-making over the next few decades.

Questions to be considered in this BOG include:

- How can we predict biological responses at population and ecosystem scales?
    - What insights can we gain from natural and experimental "analogues" (e.g., naturally varying systems, CO_2 seeps, short and long term experimental systems)?
    - What are the advantages as well as pitfalls inherent in scaling up experimental and natural responses to understanding change at the ecosystem level?
    - How can insights gained in physiological studies from the molecular to whole-organism level inform our understanding of ecosystem level impacts of ocean acidification?
    - How do multiple changes and interactions between biological processes (calcification, erosion, photosynthesis, life history, etc.) influence large-scale ecosystem processes? For example, how can we relate changes in survivorship at particular life history stages to consequences at the population level? Is it possible to understand these consequences through modeling?
- Which biological processes are being affected by ocean acidification today and will be affected under future atmospheric levels of CO_2?
    - Does physiological plasticity play a significant role in adaptation to the warmer and more acidic oceans of today, and how will it contribute to ecosystem resilience in the future?
    - How do differences in generation time and genetic variability influence how organisms and ecosystems respond to ocean acidification?
    - How does the rate of change influence whether or not organisms are able to genetically adapt to changes in ocean acidity? Are there circumstances where organisms have adapted to local ('natural') changes in ocean acidity?
- Given this complexity over spatial and temporal scales, what strategies would yield the information needed by decision-makers on the time scales they require?

BOG II-1: Learning from the past and present to predict the future

Chair: Daniela Schmidt
Rapporteur: Christoph Heinze

Ocean chemistry has varied in the past, resulting in conditions that have had consequences for life on Earth. Understanding these changes and their influence on past organisms and ecosystems has the potential to help us understand and project future responses in ocean ecosystems. This BOG will focus on bringing together the present day understanding of ocean acidification and its impacts, with lessons from deep time. In addition to synthesizing the available information, the BOG will explore the advantages and drawbacks of relating present-day mechanistic understanding with information from past periods of high carbon dioxide and ocean acidity. This will include consideration of the short timeframe over which experimental results are often derived, which is fundamentally different from the extremely long periods of time (millions of years) over which most past changes have occurred. This BOG will also consider what we can learn from periods of drastic change such as mass extinction events and will explore some of the issues that arise from ambiguities involved in extrapolating this information for projecting the consequences of current ocean acidification. In exploring the limitations and strengths of each approach, this BOG will determine the ways in which experimental and palaeontological results can be used to understand and project ocean acidification in the present day and in coming centuries.

Questions to be addressed in this BOG include:

- What can be learned from palaeontological perspectives?
    - What were the geological and oceanographic consequences of previous periods of high atmospheric carbon dioxide? What were the rates of the changes in ocean chemistry, and how did life keep up (or not)?
    - What are limitations and strengths of palaeontological studies? Are there ways of overcoming these limitations or capitalizing on these strengths?
    - How relevant are palaeontological findings for understanding current changes in ocean chemistry?
    - How well can experimental and palaeontological results be combined (or reconciled) to understand current and predict future ocean acidification?
- What are the observational uncertainties from the paleo-record?
    - What is the temporal precision of current techniques for exploring past periods of altered ocean chemistry, and how does this relate to understanding the impacts likely to arise from recent rates of change in ocean chemistry?
    - What are the sources of error inherent in the tools (e.g., geochemistry, fossil record) that have provided insight to ocean chemistry over the palaeontological record?
    - Do we have sufficient understanding of the physiological underpinnings of changes in the paleo-world to improve on the certainty of conclusions from paleo-observations?
- Can evolutionary models help inform an understanding of past changes, and help project future changes?
    - What are the pitfalls and advantages of using evolutionary models to understand the consequences of rapid anthropogenic ocean acidification?

For each of these questions, the BOG will address what is already known and what could be done to gain additional understanding and further narrow uncertainties.

BOG II-2: Understanding the roles of multiple stressors

Chair: Peter Haugan
Rapporteur: Gretchen Hofmann

Ocean acidification is one of many stressors relevant to ocean ecosystems. In almost all regions, acidification is occurring in concert with changes in other key parameters such as temperature, circulation patterns, nutrient concentrations, other forms of pollution, invasive species, and trophic alterations associated with fishing. The nature and magnitude of the impacts from ocean acidification on marine organisms and ecosystems may be different (exaggerated or modulated) when coupled with these other changes. Furthermore, questions remain regarding the degree to which unexpected or abrupt changes and regime shifts will occur and the degree to which ocean acidification might affect when these thresholds would be surpassed. This BOG will discuss the role of ocean acidification in the context of other stressors, such as temperature, nutrients, disease, pollution, and fishing pressure, taking into consideration the potential for abrupt changes and the role of complex system feedbacks.

Questions to be addressed in this BOG include:

- What do we know today about the way ocean acidification interacts with other stressors in the marine environment?
    - Under what circumstances or sets of conditions do combinations of stressors enhance or modulate one another? Are interactions between these variables and the carbon chemistry of seawater synergistic, antagonistic or irrelevant?
    - Progressive *versus* threshold responses: Are abrupt changes expected? Can we associate regime shifts with ocean acidification scenarios?
    - Are certain groups of organisms (ecosystem engineers, primary producers, predators) or certain types of ecosystems (e.g. coral reefs, open ocean) more likely to show amplification of ocean-acidification-induced effects through synergistic interactions of multiple stresses?
- How can the roles of multiple stressors be untangled using *in situ* observations of real ecosystems?
- How do we resolve relative importance of multiple co-varying factors—light, water flow, temperature, nutrients, food availability, carbonate saturation, pH, community composition—on organism and ecosystem function in the field?
- What experiments, observations, and modeling are needed to improve our understanding of how ocean acidification will interact with other stressors on marine ecosystems? What parameters not considered "stressors" under ambient conditions could behave as stressors under elevated CO_2?

BOG II-3: Scaling up to humans: the socioeconomics of ocean acidification

Chair: Peter Brewer
Rapporteur: Carol Turley

This BOG will explore the socioeconomic impacts of ocean acidification. It will evaluate the ways in which experimental results from ocean acidification research and socioeconomic knowledge can be combined to project consequences of ocean acidification for ocean ecosystems, for corresponding ecosystem services, and for human communities and economic systems dependent on ocean resources.

Questions to be addressed in this BOG include:

- What ecosystems, and what ecosystems services provided by these ecosystems, are at greater risk from ocean acidification? In what ways are humans dependent on these ecosystems and ecosystem services?
- In order to understand and potentially anticipate possible socioeconomic consequences of ocean acidification, (i) what existing socioeconomic knowledge and (ii) what understanding of past ocean-ecosystem collapse is available and could be used?
- What are consequences of ocean acidification for fisheries and food security? Are there organisms and fisheries/aquaculture systems that are more or less vulnerable to ocean acidification and changing seawater chemistry?
- Do projected impacts of acidification have consequences for shoreline protection by coral reefs and the ability of coral reefs to support coastal tropical fisheries? Do smaller/thinner shells matter for commercially important shellfish, and can we quantify the impacts for these shellfish and their fisheries?
- What are implications for tourism and economic development?
- For decision-making related to the socioeconomic impacts of ocean acidification, what are the most important questions? Which of these questions are scientifically tractable and could be answered in the next one to two decades to inform decision-making?

Annex 5: Keynote Abstracts

PLENARY SESSION I: THE CHANGING CHEMISTRY OF THE OCEANS

Keynote I-1: Controls on ocean carbon chemistry: a paleo perspective.
Richard Zeebe

Keynote I-2: Changes in ocean carbon chemistry since pre-industrial times.
Kitack Lee

Keynote I-3: Future projections of ocean carbon chemistry.
Fortunat Joos

Keynote I-4: Ocean acidification in coastal waters and other vulnerable ocean regions.
Rik Wanninkhof

PLENARY SESSION II: IMPACTS OF OCEAN ACIDIFICATION FOR INDIVIDUAL ORGANISMS

Keynote II-1: Impacts on calcification and dissolution for coral reefs and coral reef organisms.
Jean-Pierre Gattuso

Keynote II-2: Impacts on phytoplankton calcification and photosynthesis, with consideration of evolutionary responses.
M. Debora Iglesias-Rodriguez

Keynote II-3: Impacts on non-coral-reef invertebrates.
Sam Dupont

Keynote II-4: Additional impacts on invertebrates: non-calcification responses, life history effects, and evolutionary considerations.
Haruko Kurihara

Keynote II-5: Impacts on fishes, their life histories, and evolutionary responses.
Atsushi Ishimatsu

Keynote II-6: Impacts on microbial processes and biogeochemistry.
Nicola Wannicke, Hans-Peter Grossart, and Maren Voss*

PLENARY SESSION III: SCALING UP TO ECOSYSTEMS

Keynote III-1: What can we learn from the paleo record?: mass extinction events and recovery.
Ken Caldeira

Keynote III-2: Scaling up from experimental responses.
Ove Hoegh-Guldberg

Keynote III-3: Scaling up from natural responses.
Jason Hall-Spencer

Keynote III-4: Socioeconomic impacts of ocean acidification: lessons from the past?
Sarah Cooley

** Speaker*

Keynote I-1: Controls on ocean carbon chemistry: a paleo perspective.

Richard Zeebe

University of Hawai'i at Manoa, USA

The past may hold important clues to understanding present and future effects of rapid carbon input to the Earth system, including ocean acidification. Studying past changes of ocean chemistry also allows us to evaluate the current anthropogenic perturbation in the context of Earth's history. However, for a meaningful comparison to the future several issues need to be carefully considered, most importantly the magnitude and time scale over which seawater chemistry changes occurred in the past. Over long timescales, the ocean's carbonate chemistry is buffered by processes including sediment carbonate dissolution and rock weathering. Yet, the ability of geologic carbon reservoirs to absorb carbon is slow and currently overwhelmed by the rate of anthropogenic carbon input. Thus the rate of carbon input (amount and time scale) largely controls the extent of ocean acidification and therefore possible effects on marine calcification. In this presentation, I will review the fundamental controls on ocean carbonate chemistry and our knowledge of ocean carbonate chemistry changes in the past. I will discuss past ocean acidification events that may serve as useful analogues for the future. I will emphasize that in addition to the carbon input rate, the ocean's baseline chemistry (steady-state chemistry prior to a perturbation) is critical for the system's sensitivity to carbon perturbations and hence the extent of ocean acidification. Finally, I will discuss uncertainties in the reconstructed carbonate chemistry parameters.

Keynote I-2: Changes in ocean carbon chemistry since pre-industrial times.

Kitack Lee

Pohang University of Science and Technology, Republic of Korea

During the anthropocene, only about half of the total CO_2 released by anthropogenic activities remains in the atmosphere; the remainder has been absorbed by the oceans and the land biosphere. The potential for storage of anthropogenic CO_2 in the global ocean is substantial because of the strong buffering capacity of seawater; the global ocean naturally contains approximately 50 times more carbon than the atmosphere. The major conclusion from analyses of the global carbon data (obtained from surveys in the 1990s) is that as of 1994 the global ocean has stored approximately 48% of the total CO_2 emissions from fossil fuel burning and cement production during the anthropocene (Sabine et al., 2004). The current fraction of total anthropogenic CO_2 emissions stored in the ocean appears to be about one-third of the long-term potential. This oceanic uptake of anthropogenic CO_2 has acidified the upper ocean, making the saturation state of seawater with respect to $CaCO_3$ particles rise by a few hundred meters (Feely et al., 2004). The ocean acidification and the upward movement of the saturation horizon profoundly impact the fate of $CaCO_3$ particles in the ocean (Berelson et al., 2007). A significant fraction of the $CaCO_3$ export production dissolves in the water column before reaching the ocean floor. Key scientific issues that are yet to be fully addressed are how oceanic uptake of anthropogenic CO_2 and its impact on ocean chemistry (e.g., pH, the saturation state of seawater with respect to $CaCO_3$ particles, and water-column dissolution of $CaCO_3$) have evolved over time. Recent findings concerning these key scientific issues since the publication of the IPCC Fourth Assessment Report will be presented.

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Keynote I-3: Future projections of ocean carbon chemistry.

Fortunat Joos

University of Bern, Switzerland

Fossil emissions and the rapid rise in atmospheric CO_2 and other forcing agents cause multifaceted and coupled changes in the chemical and physical state of the ocean. These include increasing ocean temperature, heat content, and sea level, rising pCO_2, carbon concentrations and acidity, decreasing oxygen concentrations as well as changes in ocean circulation, mixing, stratification, and associated spatio-temporal changes in nutrient availability (Bindoff et al., 2007). A focus of this presentation is on the impacts of anthropogenic carbon emissions on the chemical state of the ocean (Caldeira and Wickett, 2003; Feely et al., 2004; Orr et al., 2005). Results from coupled climate-carbon models are presented for the range of recently published multi-gas climate change mitigation and baseline emissions scenarios from the integrated assessment modelling community as well as for idealized emissions and concentration pathways (Van Vuuren et al., 2008; Joos et al., 2011). Mitigation scenarios lead to lower atmospheric CO_2, less climate change, and less ocean acidification than no-climate policy baseline scenarios. Employing some of the most stringent scenarios in the literature allows one to estimate 'minimum warming' and 'minimum ocean acidification' given inertia in both the climate and the socio-economic system. Regionally, surface water in the Arctic is currently changing from over- to undersaturated conditions with respect to aragonite, a mineral form of $CaCO_3$ secreted by marine organisms to build their shells and skeletons (Steinacher et al., 2009). 21st century carbon emissions provide a long-term commitment to future Earth System changes: undersaturation in the Arctic remains widespread for centuries for no-climate policy baseline scenarios, even when carbon emissions are completely and unrealistically stopped in year 2100 (Frölicher and Joos, 2010; see Figure 1). For a high 21st century emissions scenario with subsequent emissions stop, the volume of supersaturated water, providing habitat to aragonite producing organisms, is projected to decrease from 42 to 8%. Minimum extension is reached 200 years after emissions have been stopped. The presentation will also provide information on multi-model projections of the coupled changes in marine oxygen, pCO_2 and in the Respiration Index of (Brewer and Peltzer, 2009) and provide examples on projected biological changes, e.g., in calcification.

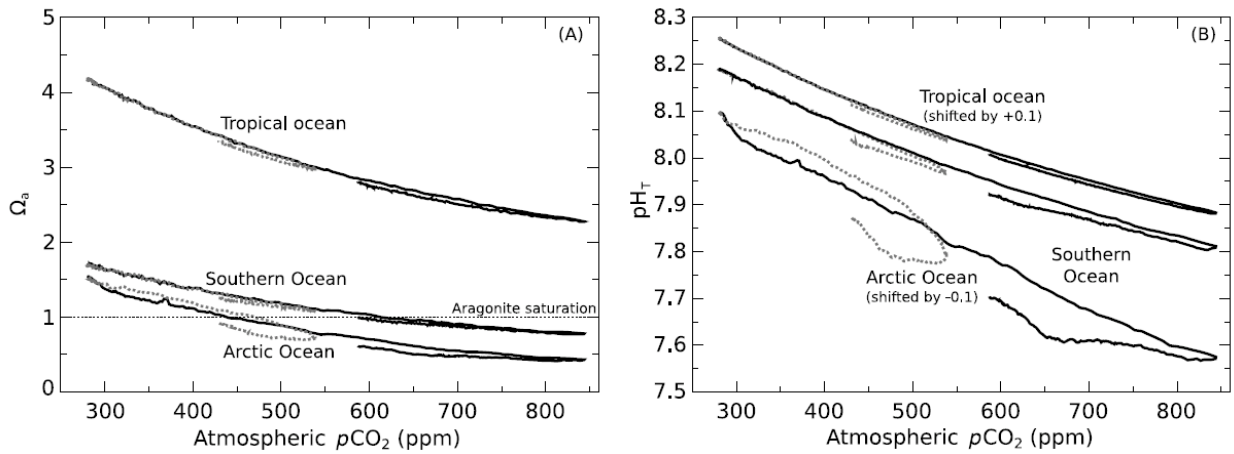

Figure 1: Saturation state with respect to aragonite and pHT in surface water of three regions as a function of atmospheric CO_2. Results are from emission commitment scenarios with high (solid) or medium (dashed) 21st century emissions and no emissions after 2100. The relation between atmospheric CO_2 and saturation state and pHT shows almost no path dependency in the tropical ocean and Southern Ocean. Some path dependency is found in the Arctic Ocean, with lower values in surface saturation and pHT for a given CO_2 concentration simulated after the peak in atmospheric CO_2. Note that the pHT – CO_2 curves are shifted by +0.1 pH units for the tropical region and by –0.1 pH units for the Arctic region for clarity.

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Keynote I-4: Ocean acidification in coastal waters and other vulnerable ocean regions.

Rik Wanninkhof

NOAA/AOML, USA

Increases in ocean acidification occur from largely predictable increases in surface water CO_2 levels due to invasion of anthropogenic CO_2 from the atmosphere. Surface ocean CO_2 levels increase at roughly the same rate as atmospheric increase, which currently is about 2-µatm yr^{-1}. This results in changes in surface water pH and saturation state that differ by 30–50% depending on locale, primarily due to difference in buffering capacity and temperature. For instance, a 2 µatm yr^{-1} change in surface water fugacity of CO_2[1] (fCO_2 levels leads to a pH change pH of –0.0025 for high latitude oceans and –0.0017 in sub-tropical areas along with a decrease in aragonite saturation state of .0084 and .0108, respectively[2]. In coastal and high latitude oceans natural and climate-induced variability, along with regional anthropogenic impacts, can exasperate the ocean acidification impacts. There are several confounding effects on ocean acidification in these areas including high levels of biological productivity and respiration, coastal upwelling, fresh water runoff often with associated high nutrient input and hypoxia, and changes in stratification. Local deposition of sulfate and nitrate bearing aerosols can contribute to coastal ocean acidification as well. Examples of each of these coastal and high-latitude phenomena will be presented.

Many of the coastal and high-latitude regions have naturally elevated fCO_2 levels though the physical and biogeochemical factors listed above. The high latitude regions have low temperatures, and often low total alkalinity to inorganic carbon ratios. These factors decrease the buffering capacity of seawater such that the pH and saturation states are more sensitive to further CO_2 increases. Moreover, at high latitude seawater already is close to aragonite saturation state of 1 that is generally viewed as a critical threshold for creatures with aragonitic shells and skeletons. Most models and empirical estimates suggest that this threshold will be reached for parts of the high latitude oceans in the next few decades.

The high degree and spatial and temporal variability and dearth of high-quality observations of seawater carbon chemistry in the coastal ocean has limited direct quantitative assessment of ocean acidification and saturation states in coastal and high latitude oceans. Global models likely under-predict the local levels of OA because of coarse resolution and lack of incorporation of all relevant coastal process. There have been several powerful interpolation techniques that provide insights of the smaller-scale trends and variability. The techniques take advantage of strong correlations between ocean acidification and other physical and biogeochemical parameters that can be determined at much higher resolution and have successfully applied or upwelling systems along the West Coast of the USA, and in the Caribbean Sea. The often-higher levels of CO_2 and lower saturations states in coastal and high-latitude systems coupled with the ecological, societal, and economic importance of these regions warrant continued investigation and monitoring.

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[1] The fugacity of CO_2 is numerically similar to the more often used term, partial pressure of CO_2 (pCO_2). The fugacity incorporates the non-ideality of the gas.

[2] In this example data from CLIVAR/CO_2 cruises P18 in the South Pacific in 2008 and A16N in the North Atlantic 2003 were used assuming a surface water increase in fCO_2 of 2 µatm:

Cruise	Sta	Lat	Long	S	T	PO4	DIC	TA	fCO_2	OmAr
P18	163	64.8°S	103°W	33.87	2.44	1.5	2136	2284	342	1.65
A16N	71	30°N	23.4°W	37.01	24.08	0	2103	2421	411	3.54

OmAr: saturation state of Aragonite. The full datasets can be found at:
http://cdiac.ornl.gov/oceans/RepeatSections/

Keynote II-1: Impacts on calcification and dissolution for coral reefs and coral reef organisms.

Jean-Pierre Gattuso

Centre National de la Recherche Scientifique, France

Coral reefs are calcium carbonate structures located at or near sea level constructed by zooxanthellate scleractinian corals and coralline algae, whose skeletons are made of the particularly soluble forms of calcium carbonate, aragonite and high-magnesian calcite, respectively. Coral reefs are distributed in waters with a relatively high aragonite saturation state (Ωa; 3.3 on average in 1990). The tropics and subtropics will see the largest absolute changes in surface Ωa with a projected drop from average value of 4.2 in the year 1820 to 2.3 in 2100 under the A2 scenario. Under the same scenario, waters with surface $\Omega a > 3$ will essentially disappear by 2070.

Corals and coralline algae are probably the organisms that have been investigated most actively in the context of ocean acidification. Data have predominantly been collected in perturbation experiments performed on individual organisms and within mesocosms. A decrease of calcification as a function of increasing CO_2 or decreasing Ω is very widespread, indicating a negative impact of ocean acidification, but a few reports suggest that some organisms present a complex response or are unaffected. Whether or not calcification decreases in response to elevated CO_2 and lower Ω, the deposition of $CaCO_3$ is thermodynamically less favorable under such conditions. Some organisms may have the capacity to up-regulate their metabolism and calcification to compensate for lower Ω. However, this would have energetic costs that would divert energy from other essential processes, and thus would not be sustainable in the long term. Full or partial compensation may be possible in certain organisms if the additional energy demand required to calcify under elevated CO_2 can be supplied as food, nutrients, and/or light (for those organisms dependent on photosynthesis).

Although perturbation experiments suggest that coral calcification may have decreased by about 10% since the industrial revolution, the evidence for this is not yet verified in field samples. Some, but not all, retrospective studies show decreasing trends in calcification for the past several decades but whether the decreases are due to ocean acidification, some other environmental factor (e.g., warming), or a combination of factors remains unclear.

Increased dissolution and lower calcification will lead, at some point in the future, to a transition from net calcification and $CaCO_3$ accretion to net dissolution and net loss of $CaCO_3$. Reefs of the Eastern Tropical Pacific are good indicators of what the future of coral reefs could be. They experience naturally high CO_2 and low Ω as a result of upwelling and are poorly developed and subject to high rates of bioerosion. The abundance of cement in intraskeletal pores appears correlated to the seawater aragonite saturation state and inversely related to measured rates of bioerosion. Last but not least, corals lose their endosymbiotic algae at elevated temperature, leading to coral bleaching and high rates of mortality. The combination of ocean acidification and warming undoubtedly makes the coral reef ecosystem one of the most threatened by global environmental change.

Data synthesis, meta-analyses and the assessment of the impacts of ocean acidification on calcification and dissolution for coral reefs and coral reef organisms (as well as other ecosystems and organisms) are hindered by the inadequate experimental set-up and incomplete data reporting of some studies. It is critical that the guidelines provided in the "Guide to best practices on ocean acidification research and data reporting" are followed. It is recommended that Working Group II of the IPCC initiates a compilation of experimental data on all organisms and ecosystems and includes the newly generated data in meta-analyses, which would be run on a yearly basis. Several critical issues specific to coral reefs and coral reef organisms require better investigation: the interaction between ocean acidification and other environmental parameters that will also change in the

decades to come (temperature, ultraviolet radiations, nutrients, food availability...), the molecular and cellular mechanisms that enable a few species to be resistant to ocean acidification, and the response of natural communities through long-term perturbation experiments in the field. The latter is particularly important to our ability to forecast the functioning of coral reefs in terms of biodiversity, fisheries production, shoreline protection, and other ecosystem services.

Keynote II-2: Impacts on phytoplankton calcification and photosynthesis, with consideration of evolutionary responses.

M. Debora Iglesias-Rodriguez

National Oceanography Centre, United Kingdom

The production of calcium carbonate ($CaCO_3$) or 'calcification' is a widespread process in life, which has a pivotal role in the Earth's carbon cycle. Marine organisms use carbonate (CO_3^{2-}) and/or bicarbonate (HCO_3^-) ions in the formation of their shells, tests, coccoliths, and skeletons. A great concern for the future of marine biota is the accelerated rate of increase in anthropogenic carbon dioxide (CO_2) emissions, which increases concentrations of CO_2 and bicarbonate ions and decreases pH and carbonate ions in seawater. Increasing CO_2 levels appear to be advantageous to most photosynthetic organisms. However, among these, the effect is not so clear in a group of calcifying, bloom-forming photosynthetic organisms, the coccolithophores, which utilize CO_2 in photosynthesis but also use either carbonate or bicarbonate ions in the production of calcium carbonate. Calcification shows a complex relationship with climate and atmospheric CO_2 levels, its regulation varies in marine biota, and physiological responses differ when other variables are altered in combination with CO_2. Despite the importance of elucidating the metabolic pathways of calcification in order to make projections of adaptation to ocean acidification, testing experimentally the mechanistic processes involved in calcification remains a challenge. Different experimental and modelling approaches used so far will be discussed as well as emerging ideas to test how the rapid rate of change in marine carbonate chemistry may affect the evolutionary success of calcifiers.

Keynote II-3: Impacts on non-coral-reef invertebrates.

Sam Dupont

Department of Marine Ecology – Kristineberg, University of Gothenburg, Sweden

Invertebrates represent 95% of all animal species and are divided into 36 phyla, 34 having marine representatives and 17 being exclusively marine. It is then of tremendous importance to understand how ocean acidification may impact marine invertebrates and their related ecosystems where they often play key ecological functions.

Study of the impact of ocean acidification on marine species and ecosystems is a relatively new field but the amount of published data is growing exponentially. However, only 10 of the 34 marine invertebrate phyla were investigated to date and within the major studied phyla (crustaceans, mollusks, echinoderms) there is a bias for (i) selected "model" species that may not always be representative of their respective phylum and (ii) calcifying species based on the paradigm that calcifiers will be more at risk in a high CO_2 world. There is then a lack of relevant information on key biologically, ecologically and economically important species.

Most of the published information is based on single-species and single life-history stage (gamete, larvae, juvenile or adult) perturbation experiments and only few studies are dealing with ecological scales (only few studies in mesocosm, CO_2 vents studies or using the modelization approach). However, there is a common trend in all phyla tested so far: the impact of ocean acidification is extremely species-, even in closely related species, and population-specific.

Many factors contribute to this observed variability in responses, some being related to differences in methodology (methods to manipulate the pH, exposure time, etc.), some being linked to biological differences including some ontogenetic and lifestyle traits that lead to differential tolerance towards high environmental pCO_2. For example, active invertebrates such as cephalopods and brachyuran crustaceans possess efficient ion-regulatory machinery that forms the basis for efficient compensation of pH disturbances during exposure to elevated environmental pCO_2.

We are most probably under-estimating and over-estimating the real impact that ocean acidification can/will have in future oceans. Most studies are short term and below the time needed to express plasticity, acclimation potential and potential selection of adapted genotypes. On the other hand, perturbation experiments are over-simplifying the environment, most of them only considering one stressor at the time, only considering one life-history stages (no information on carry-over effects) and ignoring ecological feedbacks.

This makes any extrapolation or large scale prediction very difficult. For example, within the echinoderm phylum, some species are extremely sensitive (e.g., extinction predicted by 2050) when others are resistant or even benefiting from near-future ocean acidification conditions. The lack of standardization (but see EPOCA best practice guide for ocean acidification research) and largely unexplained variability in response are also limiting the power of summarizing the data using a meta-analysis approach (e.g., see the contradictory meta-analysis papers published by Hendriks et al., 2010, Dupont et al., 2010 and Kroeker et al., 2010).

However, some trends for invertebrates can be isolated from available information. Ocean acidification is affecting growth rates and is associated with an increased energy costs that translate into a shrinking of the performance window. Early life history stages are generally more sensitive than adult. Some promising new works tend also to link species-sensitivity to natural environmental variability.

As a consequence, impact of ocean acidification on invertebrates is moving forward as a hypothesis-driven research field. However, it is still in an exploratory phase and some of the original paradigms (e.g., ocean acidification having its main impact on calcification) may not apply to all studied organisms.

In conclusion, we do not have enough data to make any large scale prediction but we have already enough evidence to state that impact of ocean acidification on important invertebrate species is certain with consequences at the ecosystem level.

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Keynote II-4: Additional impacts on invertebrates: non-calcification responses, life history effects, and evolutionary considerations.

Haruko Kurihara

University of Ryukyus, Japan

Acidification is now quickly occurring over the world ocean and its impact on the marine ecosystem is now one of the most urgent issues to be solved. Within these few years, studies evaluating the impacts of ocean acidification to the marine organisms have been considerably increased, and information about biotic responses (growth, calcification, metabolism etc) at individual level is now available for several different groups of organisms. However, there is still a gap of knowledge for our understanding about the effects of ocean acidification at ecological level. In this presentation, I will review the available data for the impacts of ocean acidification on different marine invertebrates including crustaceans (copepods, shrimp, krill, barnacles), echinoderms (sea urchins, sea star, brittle star), and molluscs (bivalves, gastropods, cephalopods, pteropod). Additionally, I will introduce studies that address ecological and evolutionary questions about impact of ocean acidification such as ontogenic impact through different life stages; long-term studies beyond generations; impacts on the interaction between organisms and impacts within and between populations.

Keynote II-5: Impacts on fishes, their life histories, and evolutionary responses.

Atsushi Ishimatsu

Institute for East China Sea Research, Nagasaki University, Japan

In comparison to the majority of marine invertebrates, fishes are characterized by more active lifestyles, requiring high capacities for swimming, metabolism and homeostatic regulation. These traits are supported by efficient systems of locomotion and oxygen transport, high acuity of sensory systems and acid-base regulation of fishes, to list a few.

Fishes in adult stages are generally more robust than invertebrates over the range of CO_2 levels projected in the context of ocean acidification, though data are relatively scarce compared with the amount of data known for invertebrates. Thus, resting metabolism, as measured by oxygen uptake, of adult fishes are unaffected even under CO_2 conditions far higher than predicted for a future high CO_2 ocean, in contrast to metabolic reductions often reported for marine invertebrates in ocean acidification studies (Ishimatsu et al., 2008). Even though oxygen affinity and capacity of fish hemoglobin are usually sensitive to CO_2/pH (but not in cartilaginous fishes), effects may be only marginal, if any, within the range projected for ocean acidification, given the high capacity of acid-base regulation. Fishes can restore extracellular and intracellular pH to control levels even at 10,000 µatm pCO_2 or higher through active transport of ions mainly across the gills. Since this process is energy-demanding, fishes are expected to incur an additional energetic cost when exposed to higher CO_2 levels.

Despite such expected additional cost for living, existing literature demonstrated significant negative effects of CO_2 on fish growth and mortality only under very high levels relevant to aquaculture, but not to ocean acidification (Ishimatsu et al., 2008). However, mortality at high temperatures was recently reported to increase by 1000 µatm pCO_2 exposure in one (*Amphiprion doederleini*), but not another (*A. cyanosoma*) adult clownfish. Aerobic scope (the difference between standard and active metabolic rate) declined in both species (Munday et al., 2009a). The effects on aerobic scope are somewhat variable between temperatures tested, and need further evaluation. Our 5-month exposure experiment of adult Javanese ricefish *Oryzias javanicus* to 1000 µatm pCO_2 demonstrated no significant changes in resting oxygen uptake, growth, egg spawning, or acid excretion rate (Ueoka et al., unpublished). In addition, a recent study demonstrated that adult Atlantic cod *Gadus morhua* can sustain swimming performance, resting and active metabolism even following 4 or 12 month acclimation to elevated CO_2 conditions (Melzner et al., 2009).

Fishes in early developmental stages appear to be often more sensitive to elevated CO_2 conditions than adults, but again these data are obtained under CO_2 conditions far higher than projected in future oceans (Ishimatsu et al., 2008). Many tropical species are known to live near their thermal tolerance, and therefore even a small elevation of temperature could be fatal to them, which might be exacerbated by high CO_2. Our unpublished experiment demonstrated that a temperature elevation of 2°C totally inhibits embryonic development in *A. clarkia* irrespective of pCO_2 (Fukuda et al., unpublished).

An unexpected CO_2 influence includes the disruption of olfactory detection of chemical cues: CO_2 (1000 µatm) was shown to disrupt the olfactory capacity of the larval clownfish *A. percula* to discriminate some of terrestrial plant exudates, which the larvae use as chemical cues for settlement. The experiment also showed that the larvae lost the ability to avoid their own parents (Munday et al., 2009b). Even more dramatically, *A. percula* larvae reared under 1000 µatm pCO_2 until the settlement age were attracted by cues from predator fishes, which were completely avoided by control larvae reared under control (380 µatm pCO_2) conditions (Dixon et al., 2010). These phenomena are presently known for a single species, and need to be tested for other species. Olfactory chemoreception is crucial for fish migration, not only of larvae and juveniles, but also of adults. As a

well-known example, Pacific salmon use olfactory cues in their homing migration to natal rivers (Ueda, 2011). Moreover, fishes rely on olfactory sensation for social interactions, reproductive behaviors and hormone recognition. Thus, CO_2 might affect a wide variety of fish behaviors, and this needs to be urgently investigated.

Effect of CO_2 on sexual maturation and reproduction has not been tested, and needs clarification not only for fishes but also for invertebrates. Even though sperm motility was recently reported to be insensitive to 1400 µatm pCO_2 for the Baltic cod, *Gadus morhua* (Frommel et al., 2010), few data are available on sex differentiation, gonad growth, fecundity or endocrine systems involved in these processes for fish reared under high CO_2 conditions.

Recently, it was suggested that marine fishes contribute 3 to 15% of total carbonate production through precipitation of $CaCO_3$ within the intestine (Wilson et al., 2009). Thus, any effect of ocean acidification on fishes, either directly or indirectly through food-web changes, might have measurable impacts on the marine inorganic carbon cycle.

Even though the importance of conducting multi-generation experiments has been pointed out to predict adaptation potential of a species to ocean acidification, it is unlikely that fishes will adapt to the incoming acidification of their habitats through genetic selection considering the relatively long life span of many fishes (several years or longer).

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Keynote II-6: Impacts on microbial processes and biogeochemistry.

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The process of ocean acidification is rapidly changing the carbonate system of the world´s oceans triggered by an increase in atmospheric CO_2 concentrations from 280 ppm to 385 ppm from pre-industrial times to present days. This has induced already profound consequences for marine ecosystems having its most severe effect on marine calcifiers leading to declines in calcification rate, when net dissolution rates become dominant (e.g., Yates and Halley, 2006; Hoegh-Guldberg et al., 2007). Keynote presentations II-1 and II-2 will give further insight into this topic. However, potential effects of ocean acidification on the vast majority of marine non-calcifying species, e.g., microbial processes and related biogeochemical cycles, are difficult to quantify. Moreover, constrains are put forward when ocean acidification is studied in synergy with additional environmental changes, such as increasing water temperature and anthropogenic nitrogen emissions (Duce et al., 2008). Nevertheless, a growing but still limited number of studies and publications evaluated the role of microbial processes like growth, photosynthesis, nitrogen fixation, bacterial production, respiration, changes in element ratios and subsequent consequences for the microbial processes involved in the cycling of C, N, P in marine ecosystems.

A very recent study by Joint et al. (2010) presented a controversial null hypothesis regarding ocean acidification likely to "have no effect on microbial processes". Liu et al. (2010), however, published a review paper dealing with experimental studies on microbe-driven biogeochemistry and its changes due to ocean acidification. They performed a meta-analysis on published data sets proposing that the null hypothesis of Joint et al. (2010) has to be rejected. Although they ascertained that experimental studies on microbial processes led to contrasting results, largely depending on the methods used and the complexity of the ecosystem being examined. Laboratory studies with only one species can hardly be translated to open sea processes (e.g., Czerny et al., 2009; Kranz et al., 2010), while mesocosm studies with whole food-web manipulations (e.g., Pelagic Ecosystem CO_2 Enrichment Studies: PeECEII+III) may be closer to the natural processes. The overall consensus of a large quantity of publications is that confounding effects will occur, whether positive or negative.

Carbon uptake by phytoplankton is one of the processes identified to change under increasing pCO_2 concentrations, owing to a large part to the cellular carbon-acquisition mechanism and efficiency. Most marine phytoplankton, tested in single-species laboratory experiments or natural community experiments, in fact shows either no or small increases (generally 10%) in photosynthetic rates when grown under high pCO_2 conditions (e.g., Hein and Sand- Jensen, 1997; Giordano et al., 2005; Tortell et al., 2002), but depending on the predominant phytoplankton species, enhancement of primary production can reach up to 39% (Emiliana huxleji, reviewed in Riebesell et al., 2007). Deriving from increased carbon consumption, exudation of carbon compounds (polysaccharides) and formation of TEP increases significantly with pCO_2 (Engel et al., 2004; Mari et al., 2008), although DOC exudation did not show a consistent significant trend (Engel et al., 2004; Rochelle-Newall et al., 2004). A process which has gained little attention so far is the DOC and consequently DOM turnover by bacteria, which might have been too fast in the respective two studies to significantly identify changes within the given time resolution. Enhanced release of carbon compounds, TEP formation and overall increase in the organic carbon pool during mesocosm studies resulted in elevated carbon loss by particles sinking from the upper water column and potentially providing a negative feedback to the increase in pCO_2 concentration (Riebesell et al., 2007; Arrigo, 2007). This rise in efficiency of the carbon pump would lead to pronounced degradation of organic matter in deep water zones leading to a predicted expansion of deep ocean oxygen minimum zones (e.g., Hofmann and Schellnhuber, 2009) with further negative consequences for marine organisms. On the other side, the likely reduction of $CaCO_3$ export flux at increased pCO_2 would weaken the strength of the biological carbon pump, opposite to the above process (e.g., Hofmann and Schellnhuber, 2009). The

interaction of both scenarios in the future ocean cannot yet be fully evaluated, but biogenic calcification can be identified as being a "tipping element" in the climate system.

In contrast to moderate changes in carbon uptake in most of the studies (~10% increase), changes determined for nitrogen fixation were more pronounced with 35 to 100% higher rates for the tropical non-heterocystous cyanobacterium Trichodesmium sp. (e.g., Hutchins et al., 2007; Fu et al., 2008). Contradictory, Czerny et al. *(*2009) published a negative impact of high CO_2 on the heterocystous species *Nodularia spumigena*. This discrepancy could derive from physiological differences between the two species or from differences in the experimental set-ups. Opposite to Czerny´s findings, a recent laboratory study using a *Nodularia spumigena* culture, revealed a significant increase in nitrogen fixation rates by a factor of 3 at the predicted pCO_2 (Isensee et al., 2010). Such an increase in nitrogen fixation rates has far reaching consequences for the marine ecosystem since the dominance of nitrogen fixing cyanobacteria, which occur mainly in nutrient limited ecosystems, leads to a greater draw down of inorganic P, pushing the system further towards P limitation. Species capable of utilizing organic P sources (e.g., phosphonates) will benefit under these conditions. This is in line with findings by Dyhrman et al. *(*2009) demonstrating the capability of cyanobacteria to produce, and metabolize phosphonates, which hence favours their growth in a high CO_2 ocean.

The highest variability exists for the impact of ocean acidification on bacterial abundance and production. Investigated often in mesocosm studies, simulating near-natural conditions, the total abundance of bacteria varied considerably in phytoplankton blooms, but CO_2 had little or no direct effect on bacterial abundance (e.g., Rochelle-Newall et al., 2004; Grossart et al., 2006; Allgaier et al., 2008). On the other hand, bacterial production is stimulated in some studies (Grossart et al., 2006a; Yamada et al., 2008), along with enzyme activity (Grossart et al., 2006) and degradation of e.g., polysaccharides by extracellular enzymes (e.g., Piontek et al., 2010) suggesting a faster turnover of organic carbon in the upper water column. This may weaken the biological carbon pump, in addition to the weakening of $CaCO_3$ export fluxes. To date, bacterial respiration, growth efficiency and bacterial production rates still lack thorough investigation, in particular under natural conditions.

In conclusion, laboratory and mesocosm experiments as well as modelling effort suggest a shift in elemental ratios toward organic matter with higher C:N and C:P ratios for individual phytoplankton species and plankton communities at increasing pCO_2 (e.g., Riebesell et al., 2007). Limitation by P in marine ecosystems might be severely accelerated when including the increase in anthropogenic nitrogen deposition fuelling primary production especially in the oligotrophic regions of the oceans which are depleted in surface nitrate as proposed by e.g., Duce et al. (2008). Enhanced nitrogen deposition will support new production and enhance carbon uptake especially by small phytoplankton species drawing down the inorganic P pool more rapidly counteracting against nitrogen fixation. Thus, in line with management of carbon emission, nitrogen emissions have to be implemented into management strategies in future efforts. Increased C:N ratios would lower the nutritional value of organic matter produced via photosynthesis with potential effects on bacterial degradation efficiency of organic matter and zooplankton growth and reproduction. Thus, changes in microbial processes and biogeochemical cycling identified so far, although in some respects rather contradictory, are likely to change ecosystem processes and function, even more when interacting with other anthropogenic induced climate changes.

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Keynote III-1: What can we learn from the paleo record?: mass extinction events and recovery.

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"Paleo" research efforts, along with related geochemical and geological investigations, have developed several lines of evidence of relevance to the problem of ocean acidification. Different lines of evidence have developed to different levels of scientific maturity, and thus can be expected to lead to predictions that differ in their reliability.

A large body of evidence indicates that over most of geologic time, ocean chemistry is controlled by two main constraints: (1) atmospheric CO_2 adjusts such that the CO_2 consumed in silicate rock weathering and organic carbon production is balanced by CO_2 provided by geologic CO_2 degassing and organic carbon oxidation; (2) ocean carbonate mineral saturation states adjust such that the flux of alkalinity to marine carbonate sediments largely balances the river flux of alkalinity to the oceans. There are a number of lines of evidence regarding how atmospheric CO_2 has changed in the geologic past, but there is little evidence that atmospheric CO_2 was significantly higher than today's value in the past tens of millions of years (Pagani et al., 2005). Today's rate of change in atmospheric CO_2 content is 100 times more rapid than rates typical of glacial-interglacial transitions. On time scales of about 10,000 years or more, flux constraints on the ocean's sedimentary system largely controls the saturation level of carbonate minerals dissolved in seawater. Thus, ocean acidification events (here regarded as events that markedly decrease the saturation state of carbonate minerals in the ocean) only occur when ocean chemistry is perturbed on a time scale significantly shorter than 10,000 years. Observations of the paleo-depth of carbonate accumulation on the sea floor provide a reliable indicator of the saturation state of the deep ocean (Tripati et al., 2005). The scientific community overall has a high degree of confidence in our general understanding of the dominant controls on ocean chemistry over periods of 10,000 years or more, and thus can say with a high degree of confidence that ocean acidification predicted to result this century as a result of "business-as-usual" emission scenarios would be geologically anomalous and that no similar event is known to have occurred for at least the past 50 million years.

We also know from observations of marine carbonate platforms (Kiessling et al., 2003) that, over the past 500 million years or more, carbonate mineral sediments have generally been deposited equatorward of 35 degrees (north and south). This pattern does not appear to expand latitudinally with inferred increases in planetary temperature, which suggest that some combination of carbonate-mineral saturation and light may control the latitudinal distribution of calcifiers in the shallow ocean on geologically relevant time scales. Furthermore, Opdyke and Wilkinson (1993) concluded Holocene rates of carbonate sediment accumulation that the accumulation rates of shallow water carbonates are well-described by a formula of the form $F = k\ (1 - W)^n$. Thus, from the study of the normal function of the paleo record, we understand that the ocean does not normally undergo ocean acidification events and that marine carbonate calcification may be closely related to marine carbonate saturation states.

There have been rapid events in Earth history where ocean chemistry may have changed rapidly. What can be learned from these events? Unfortunately, no event in Earth's geologic past is a perfect analogue of what is projected to occur this century if current CO_2 emission trends continue. In most events in Earth history where ocean acidification may have been present, other factors are known to or are thought to have been at play (Kiessling and Simpson, 2011). Often, the time resolution of the geologic record is insufficient to know how rapidly CO_2 was added to the atmosphere or oceans. Thus, the geologic record of extreme events in Earth history does not at this time yield an unequivocal estimate of the sensitivity of marine calcifiers to ocean acidification.

Past events do not act as direct analogues, but they do present us with important information. For example, model simulations of extreme events such as the end-Cretaceous extinction (Caldeira and Rampino, 1993) and the Paleocene-Eocene Thermal Maximum (55 myr ago; Ridgwell, 2007) provide supporting evidence for the time scales for recovery of the geochemical carbon cycle (hundreds of thousands of years). Observations of biological recovery from mass extinction events indicate that time scales to evolve new ecosystems with comparable geochemical functioning can take hundreds of thousands of years and the recovery of pre-extinction biodiversity can take ten million years or more (Solé et al., 2002). There is no known time in Earth history where ocean chemistry changed as much and as rapidly as projected for this century when there was not a mass extinction event; however, there is no mass extinction for which rapid CO_2 increase seems to be the sole causal factor.

Based on the paleo-record alone, I believe a rational observer would conclude that CO_2 increases predicted to result from a continuation of current CO_2 emission trends pose a significant risk to marine calcifiers. Some of that risk stems from uncertainty: the paleo record alone is not good enough to establish the sensitivity of marine organisms to ocean acidification with a high degree of certainty. Some of that risk stems from what we know: the paleo record tells us we are embarking on an alteration of ocean chemistry that is unprecedented in at least the past tens of millions of years and there is the potential for significant impact on marine organisms; chemical recovery could take tens of thousands of years; biological recovery could take much longer.

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Keynote III-2: Scaling up from experimental responses.

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Our understanding of the impacts of ocean acidification depends heavily on experimental manipulations which have been undertaken with a wide variety of organisms and ecological processes. Information from experimental studies has formed an important cornerstone in how we have shaped our understanding of potential ecosystem responses to perturbations to ocean pH and carbonate chemistry. These studies have included investigations from those on the fine-scale transcriptome responses of cells and organisms in laboratory settings to large-scale mesocosm studies of ecosystem processes such as primary production and pelagic processes. While these studies have provided important insight into the response of marine ecosystems to ocean acidification, a number of key issues need to be carefully considered when applying experimental manipulations, including the experimental design and hypothesis being tested, the methodology for manipulating carbonate chemistry (i.e., bubbling of gas versus the addition of acid), the existence of antagonistic or synergistic variables (e.g., elevated sea temperature), the organisms or process under test (i.e., are they representative?), and the methodology used to measure responses of organisms and processes to the experimental conditions (i.e., enough precision to minimise Type II errors?). Without carefully considering these issues, our ability to scale up to ecosystem processes from experimental responses is likely to be compromised and limited.

This presentation will explore the experimental systems deployed so far, and will review the contribution of different types of experiments in building the direct experimental evidence as well as process knowledge required to project how changes in ocean pH and carbonate chemistry will affect marine ecosystems. In this regard, studies that explore gene expression will provide important information on the response of individual marine organisms to ocean acidification but require combination with other experimental evidence if they are to provide useful perspectives on how marine ecosystems are likely to respond at ecosystem scales. In this regard, studies that span multiple scales and processes are likely to be the most informative. Experimental approaches also need to consider the relevance of the time and spatial scale at which studies have been done. Most experimental systems have involved short incubations over a matter of days or weeks yet ocean acidification is occurring over decades and centuries. In this regard, the combination of these experimental approaches with insights drawn from palaeontological studies and those from 'natural experiments' such as CO_2 seeps may enable inferences to be drawn about how ecosystems are likely to respond over greater temporal and spatial scales.

A range of other considerations will be discussed in this paper, including the need to improve our understanding of the complex behaviour of ecosystems, which may not be tractable under experimental systems which necessarily aim to reduce overall complexity in order to obtain clear and unconfounded answers. Understanding these complex behaviours must be the focus of future studies, along with experiments that strive to manipulate ocean temperatures and acidity on intact ecosystems under as near to 'natural' conditions as possible.

Keynote III-3: Scaling up from natural responses.

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Our understanding of the ecosystem response to ocean acidification is very limited as almost all studies have involved short-term, rapid perturbation experiments on isolated elements of the ecosystem (e.g., single species or small groups of species). This is unsurprising given the difficulty in imitating ocean acidification conditions in situ for sufficient periods to affect whole communities. However, areas with naturally high CO_2 (and/or low pH and low calcium carbonate saturation states) reveal which organisms can tolerate the long-term consequences of OA and reveal how ecosystems respond. Warm-water examples include work by Manzello et al. (2008), who correlated decreasing tropical coral reef strength with naturally decreasing calcium carbonate saturation state, and Marshall et al. (2008) who noted that mollusc shells are weakened along pH gradients in estuaries. Temperate examples include a study by Tyrrell et al. (2008) who reported that coccolithophores were common in the Black Sea, but absent from the Baltic which undergoes seasonal aragonite undersaturation whereas Thomsen et al. (in review) note that sessile calcified invertebrate communities succeed in the naturally CO_2 enriched habitats of the Baltic. Valuable insights can be gained from such studies although effects of confounding factors (e.g., temperature, light regime, nutrient availability and salinity) need to be considered before scaling-up the findings to the global ocean.

Submarine CO_2 vents are proving to be useful 'natural laboratories' for the study of ocean acidification, although many increase the water temperature and emit toxic compounds that can confound the findings (Tunnicliffe et al., 2009). Vents off Ischia (Italy) reveal the long-term effects of OA as they lack toxic compounds but are at ambient temperature, alkalinity and salinity (Figure 1; Hall-Spencer et al., 2008). The pCO_2 gradients reveal tipping points in calcification, recruitment, growth, survival and species interactions. Many species of macroalgae, seagrass, foraminiferans, corals, polychaetes, crustaceans, molluscs and bryozoans are remarkably tolerant of long-term exposures to high and variable carbon dioxide levels at these vents (mean 854 µatm pCO_2). However, a fall in mean pH 8.1 to mean pH 7.8 has detrimental effects on invertebrate recruitment from the plankton (Cigliano et al., 2010) and decreases the biodiversity associated with sedimentary habitats (Dias et al., 2010), rocky shores (Porzio et al., in press) and seagrass beds (Martin et al., 2008) with around 30% fewer species in adult populations at mean pH 7.8 than in adjacent areas at mean pH 8.1. Important groups, such as coralline algae, calcified foraminiferans and sea urchins are absent from areas with mean pH $\leq$7.8, probably due in part to widely variable CO_2 levels, yet invasive species of algae and jellyfish are tolerant of these conditions. Transplant experiments have shown that unusually high sea surface temperatures can act synergistically with ocean acidification at these sites (Rodolfo-Metalpa et al., 2010), strengthening evidence for the CO_2 emissions targets required to avoid declines in coastal marine biodiversity and shifts in ecosystem structure.

Limitations: In situ observations demonstrate which species and communities can tolerate long-term ocean acidification and support concerns, based on model predictions and short-term ($\geq$1 year) laboratory experiments, that ocean acidification will likely combine with other stressors (e.g., temperature rise) to cause a decrease in coastal marine biodiversity and lead to shifts in ecosystem structure including the proliferation of invasive species. However, a comparison of Hall-Spencer et al. (2008) with Thomsen et al. (2010) indicates that the ecosystem response to OA will vary depending on biogeographic region. The Ischia vent work provides data on the effects of OA for around 250 species from shallow water coastal habitats but these data come from one oligotrophic region of the Mediterranean where CO_2 and pH perturbations are highly variable. A further limitation is that fish and plankton continually move in and out of the acidified areas so that extrapolation of the effects of CO_2 at volcanic vents to the effects on a global-scale will require caution (Riebesell, 2008).

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Keynote III-4: Socioeconomic impacts of ocean acidification: lessons from the past?

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Anthropogenic emissions of carbon dioxide to the atmosphere are altering ocean chemistry worldwide. The resultant ocean acidification, which decreases pH, increases carbon dioxide concentrations, and alters the availability of carbonate and bicarbonate ions in seawater, also affects physiological processes in many marine species. The processes known to change include calcification, respiration, olfaction, photosynthesis, reproduction, and nitrogen fixation (NRC, 2010). Just as rising temperature's effects on physiological function can alter the biogeography of both marine and terrestrial organisms (reviewed in IPCC, 2007), it is expected that any effects of ocean acidification on physiological functions that could alter the survival, growth, or reproduction of individuals could thus alter overall population size or location of species.

Shifting abundance or distribution of species because of ocean acidification could also transform the composition of entire ecosystems by affecting trophic relationships or habitat availability. Once perturbed from their original ecosystem state, marine communities may adopt new stable configurations composed of a different range of species and trophic or habitat relationships. For example, coral reefs damaged by ocean acidification could be overtaken by macroalgae, leading to loss of resilience and diversity and inability to recover to original states (Hoegh-Guldberg et al., 2007). Ocean acidification is not the only stressor likely to cause this reaction in coral reefs; rather, it is one of several environmental stressors that could elicit the same outcome. Similarly, overfishing or repeated recruitment failure due to an environmental stressor could both decrease populations of key marine species over time.

Coral reefs or other marine ecosystems altered by ocean acidification will likely provide a different array of ecosystem services to human communities (Hoegh-Guldeberg et al., 2007; NRC, 2010). Benefits such as harvests of shellfish, coastal protection by coral reefs, tourism of coastal zones, cultural identity, or ecosystem support via biogeochemical cycling could decrease if ocean acidification directly harms calcifying organisms. If ocean acidification also indirectly affects broad sectors of marine communities via trophic relationships or physiological effects other than changes in calcification, these and other ecosystem services could be even more profoundly altered.

At present, it is not possible to thoroughly evaluate the likely direct and indirect effects of ocean acidification on marine ecosystems and ecosystem services that support human communities. In addition to needing more information about the responses of individual species to ocean acidification, we lack a detailed mechanistic understanding of species' relationships and roles in the marine ecosystem, which prevents us from predicting how whole communities will respond to change. We also have difficulty quantifying and valuing ecosystem services that marine communities provide. Losses of these benefits, and the socioeconomic consequences of those disruptions, can be most clearly quantified in cases where short-term perturbations decrease revenues in a commercial industry. For example, the effects of harmful algal blooms on shellfish harvests and recreational spending have been tracked through local economies (Jin et al., 2008; Dyson et al., 2010). As a long-term, chronic stressor, ocean acidification is not likely to provide similar clear-cut opportunities for assessing losses after discrete catastrophic events, unless ocean acidification drives marine ecosystems past thresholds or tipping points.

For insight into the socioeconomic effects of how ocean acidification will affect marine ecosystem services as it progresses gradually worldwide, we should consider basin-scale and global-scale assessments of other long-term changes. Basin-scale assessments have been completed for the Baltic sea fishery regime shifts (Daskalov et al., 2007) and for the North Atlantic cod fishery collapse (Lindegren et al., 2009, 2010), showing that these ecosystem failures were driven by decades of

overfishing, environmental stressors, and other human decisions. Understanding the socioeconomic implications of these ecosystem failures is only possible by assessing both environmental and human stressors. To determine the global socioeconomic impacts of ocean acidification, we may find useful precedents within global-scale socioeconomic analyses of climate change, similar to those of Stern (2007). In all, quantifying the total consequences of ecosystem failures associated with ocean acidification will require incorporating environmental and ecosystem information as well as considering the effects of human decisionmaking.

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Annex 6: Poster Abstracts

POSTER 1: BEACON: Bermuda Ocean Acidification and Coral Reef Investigation
A. J. Andersson, N. R. Bates, S. J. de Putron, and A. Collins*

POSTER 2: Heterogeneity, uncertainty and predictions of the carbonate system on the NW European shelf
Jeremy Blackford and Yuri Artioli*

POSTER 3: Potential impacts of rising atmospheric CO_2 on the biogeography of planktonic Foraminifera
Tilla Roy, Fabien Lombard, Marion Gehlen, and Laurent Bopp**

POSTER 4: The effect of ocean iron fertilization on ocean acidification
Long Cao and Ken Caldeira*

POSTER 5: Competition limits adaptation and productivity in a photosynthetic alga at elevated CO_2
Sinéad Collins

POSTER 6: An eco-physiological model of the impact of ocean acidification on invertebrate larvae - energy budget flexibility as a unifying principle
S. Dupont, M. Stumpp, F. Melzner, and M. Thorndyke*

POSTER 7: Predictive relationships for pH and carbonate saturation in the Southern California Current System using oxygen and temperature data
Simone R. Alin, Richard A. Feely, Andrew Dickson, Martin Hernandez, Lauren W. Juranek, Mark Ohman, and Ralf Goericke*

POSTER 8: Effects of ocean acidification on calcifying algae, diatom and phytoplankton assemblages, with special references to interactive impacts with UV
Kunshan Gao, Z. Ruan, Y.P. Wu, G. Gao, K. Xu, G.Y. Yang, G. Li, W. Li, P. Jin, Y.H. Li, S.W. Chen, X.J. Wu, and Y. Zheng*

POSTER 9: European Project on Ocean Acidification (EPOCA)
J.-P. Gattuso, L. Hansson, and the EPOCA Consortium*

POSTER 10: Volcanic CO_2 vents reveal the ecosystem effects of ocean acidification
Jason Hall-Spencer

POSTER 11: Potential of radionuclides to detect large scale impacts of ocean acidification
Christoph Heinze and Tatjana Ilyina*

POSTER 12: Influence of the OMZ in the ocean acidification in the Pacific Mexican Coast
J.M. Hernández-Ayón, Gilberto Gaxiola, R. Lara-Lara, Francisco Chavez, Richard A. Feely, Simone R. Alin, C. L. Sabine, Katty Barbeau, and R. Durazo*

POSTER 13: Understanding ocean acidification on coral reefs: two next generation experimental systems for simulating future conditions.
*David I. Kline, Sophie Dove, and Ove Hoegh-Guldberg**

POSTER 14: Ocean acidification in the tropical to subtropical western North Pacific: Results from time-series observations of carbonate chemistry along 137°E
M. Ishii, N. Kosugi, D. Sasano, S. Saito, T. Midorikawa, and H. Y. Inoue*

POSTER 15: Complete inhibition of spawning by CO_2 and temperature increases in the sea urchin *Hemicentrotus pulcherrimus*
*Rui Yin, Kyoung-Seon Lee, Haruko Kurihara, and Atsushi Ishimatsu**

POSTER 16: High-CO_2 impact on the coral-reef ecosystem
Haruko Kurihara, Yuji Hiratsuka, Asami Takahashi, Tomoki Watanabe, Atsuko Fukuda, Akino Aoyama, Hiroyuki Fujimura, Saki Harii, Shihori Inoue, and Hajime Kayanne*

POSTER 17: Response of the Chinese seas to the increase in anthropogenic carbon dioxide — a preliminary result
Su Mei Liu

POSTER 18: Ocean acidification and evidence of systemic seasonal aragonite undersaturation in the high latitude seas
Jeremy T. Mathis

POSTER 19: Effects of ocean acidification on tropical marine fishes
Philip L. Munday

POSTER 20: Design and use of a precise pCO_2 control system for ocean acidification manipulation experiments
Yukihiro Nojiri, Yoshihisa Shirayama, Hideshi Kimoto, Takeshi Egashira, and Katsumoto Kinoshita*

POSTER 21: Response of coral reefs to ocean acidification over multiple temporal scales
John M. Pandolfi

POSTER 22: Has been observing the acidification of the Black Sea waters in XX century?
Alexander Polonsky

POSTER 23: Unifying principles in ocean acidification effects on marine ectotherms?
*F.C. Mark, A. Stark, K. Walther, A. Strobel, A. Hüning, C.E. Schaum, C. Kreiss, L. Harms, M. Lucassen, C. Held, D. Storch, and H.O. Pörtner**

POSTER 24: Robust prediction of pH and carbonate mineral saturation state in the North Pacific Ocean using empirical relationships with hydrographic data
*L.W. Juranek, R.A. Feely, S.R. Alin, and C.L. Sabine**

POSTER 25: Effects of CO_2-driven acidified seawater on early life stages of scleractinian reef corals (Genus *Acropora*)
Kazuhiko Sakai

POSTER 26: The Palaeocene-Eocene Thermal Maximum (PETM): ocean acidification in the geological record
Daniela N. Schmidt, Laura C. Foster, Andy J. Ridgwell, and Ellen Thomas*

POSTER 27: Animal performance in a changing ocean: synergistic effects of climate-related variables
Brad A. Seibel

POSTER 28: Effects of low pCO_2 conditions on sea urchin larvae
Yoshihisa Shirayama and Ryota Suwa

POSTER 29: Ocean acidification impact on calcification of algal symbiont-bearing benthic foraminifers
*Mana Hikami, Kazuhiko Fujita, Azumi Kuroyanagi, Takahiro Irie, Yukihiro Nojiri, and Atsushi Suzuki**

POSTER 30: Integrated assessment of ocean acidification within coral reef ecosystems
*Dwight Gledhill, Kevin Helmle, Ruben van Hooidonk, Jim Hendee, Derek Manzello, and Rik Wanninkhof**

POSTER 31: Studying the impacts of ocean acidification on key benthic ecosystems: A UKOARP funded consortium
Steve Widdicombe and the UKOARP Benthic Consortium*

POSTER 32: Interannual and interdecadal variability of pH in the seas of Russia
*P.N. Makkaveev and P.O. Zavialov**

* *Presenter*

POSTER 1 **Presenter: A.J. Andersson**

BEACON: Bermuda Ocean Acidification and Coral Reef Investigation

A. J. Andersson, N. R. Bates, S. J. de Putron, and A. Collins

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The potential response of coral reef ecosystems to ocean acidification is of great concern as the existence of these ecosystems is dependent on the deposition of $CaCO_3$ and construction of reef framework structure. The majority of experimental investigations have demonstrated that the ability of many important coral reef calcifiers to build their skeletons is reduced in seawater conditions expected to occur within the next several decades as a result of uptake of anthropogenic CO_2 and ocean acidification (e.g., Kleypas et al., 2006). It has also been proposed that coral reefs may transition from a condition of net accumulation to net dissolution of $CaCO_3$ as a result of these changes (e.g., Andersson et al., 2009; Silverman et al., 2009). Nevertheless, relatively few field studies have been undertaken to elucidate and examine the interactions among the major environmental parameters (e.g., temperature, light, nutrients, food, and seawater CO_2 chemistry) that control coral reef calcification in a natural environment.

The Bermuda ocean acidification and coral reef investigation (BEACON) aims to investigate the major parameters controlling calcification in the natural environment at the scale of individual coral colonies, coral communities, and the regional ecosystem of the Bermuda coral reef in the context of ocean acidification. The Bermuda coral reef serves as a unique and highly suitable site to address these aims. Firstly, Bermuda's high latitude location (32°N) predisposes this reef to naturally lower annual mean seawater $[CO_3^{2-}]$ values compared to reefs located at lower latitudes. Consequently, as $[CO_3^{2-}]$ continues to decrease in response to ocean acidification over the next century, Bermuda's reef may be especially vulnerable as reef waters transition through critical threshold values of $[CO_3^{2-}]$ to chemical conditions unconducive to calcification earlier than coral reefs located at lower latitudes. Secondly, the Bermuda platform serves as a natural laboratory to study the responses of coral communities to the changes in environmental parameters and seawater carbonate chemistry that occur over diurnal to seasonal timescales, as well as across reef spatial scales.

Preliminary results from the Bermuda coral reef platform show that the rate of calcification of colonies of *Diploria labyrinthiformis* is most strongly related to the $[CO_3^{2-}]$ and less so to other environmental parameters such as light and temperature (Bates et al., 2010). Ongoing experiments that continuously measure *in situ* seawater temperature, salinity, dissolved oxygen, light, turbidity, chlorophyll, pCO_2 and pH_{sws} concurrent with frequent measurements of calcification and growth rates of *D. labyrinthiformis* and *Porites astreoides* at two contrasting sites that vary in seawater carbonate chemistry will allow us to solidify our understanding in terms of the parameters controlling calcification. Based on temporal and spatial surveys of total alkalinity anomalies across the Bermuda coral reef platform, this system is currently depositing significant amounts of $CaCO_3$ during most of the year as inferred from large depletions in salinity normalized total alkalinity relative to the Sargasso Sea source water. In contrast, during wintertime, little or no depletion in total alkalinity is observed suggesting that the opposing processes of calcification and $CaCO_3$ dissolution are balanced and the net ecosystem calcification (*NEC* or *G*) is close to zero at this time.

As the oceans continue to become less alkaline as a result of uptake of anthropogenic CO_2, it is anticipated that the Bermuda coral reef ecosystem will undergo a gradual transition from net accumulation to net loss of $CaCO_3$ because of decreasing calcification and increasing dissolution. Based on the current observed relationships between coral calcification and seawater carbonate chemistry and the current increase in the rate of anthropogenic CO_2 emission, this transition could occur within the next few decades.

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POSTER 2 **Presenter: Jeremy Blackford**

Heterogeneity, uncertainty and predictions of the carbonate system on the NW European shelf

Jeremy Blackford and Yuri Artioli

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Predicting the impacts of Ocean Acidification is a science and societal priority for which modelling approaches provide an important methodology. Marine system responses to ocean acidification are complex and involve several mechanisms which impact a variety of marine processes and trophic interactions. Ecosystem evolution over the next decades will be driven by many factors including ocean acidification, climate change and modification to fishing pressures, pollution and eutrophication. It is proposed that a policy relevant ecosystem approach to ocean acidification requires a synergistic consideration of both the complexity of drivers and the complexity of responses, posing a significant challenge to existing model systems. Whilst current modelling approaches can make valuable contributions to predictive science, it is argued that developing methodologies including a hierarchy of simple and complex models and novel model paradigms, including optimal allocation concepts, provides the optimal strategy for improving understanding and predictive capability.

Shelf seas are the region where the majority of the social and economic interactions with the marine system occur. However they tend to be highly variable environments both in space and time and are not characterised by global modelling approaches. Quantifying this heterogeneity is a challenge: the carbonate system, being strongly non linear and with high uncertainty, is not an exception. Strong annual and spatial signals exist driven by dynamic biological (including benthic) processes, hydrodynamics and highly variable riverine and other boundary conditions.

Here we demonstrate a holistic approach to predicting the evolution of carbonate chemistry on the North-West European shelf using the coupled carbonate-ecosystem-hydrodynamic model POLCOMS-ERSEM. We include explicit riverine alkalinity amongst other improvements to the parameterization of total alkalinity. The model has been validated against observed data from the North Sea and the results show that the model is reasonably able to reproduce the values of the variables we use to drive the carbonate system calculations (DIC and TA). However worse results are obtained for the derived variables (pH and pCO_2). We used standard algorithms to solve the carbonate system (CO_2sys), estimate a standard reference error for the derived variables and assess their sensitivity to errors in the driving variables.

Despite the uncertainties we present predictions of carbonate system and associated variables for future atmospheric pCO_2 levels, illustrating the seasonal and spatial variability that will influence organism productivity and survival. In particular we show that at around a pCO_2 (atmosphere) of 1000 ppm the system oscillates between under and over- saturation (aragonite) during an annual cycle.

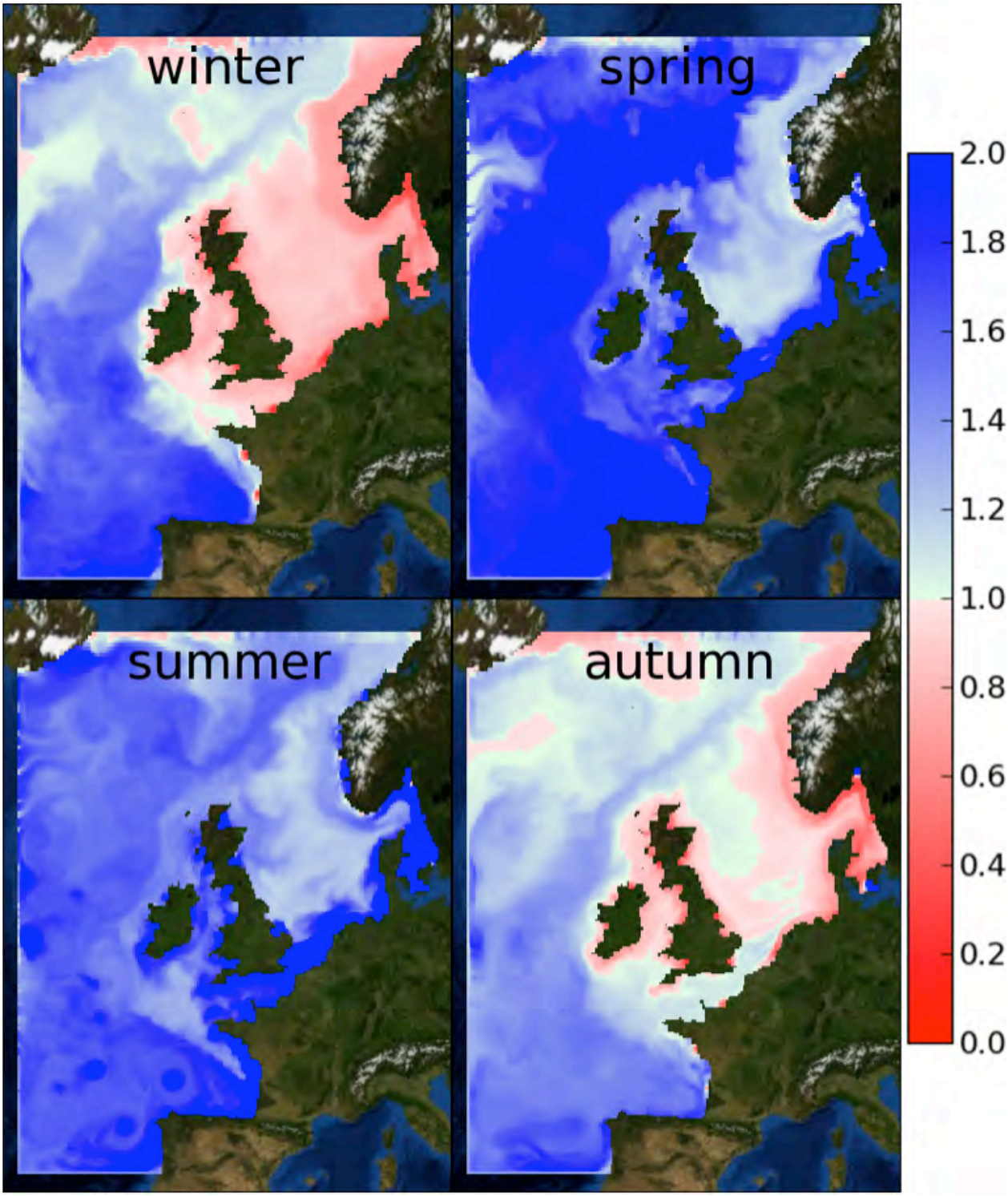

Figure 1: Seasonal snapshots of aragonite saturation state for the surface layer of the NW European shelf seas at pCO_2 atmosphere = 1000 ppm. Apart from pCO_2a, all other forcing fields are as for the year 2000.

POSTER 3 **Presenter: Laurent Bopp / Marion Gehlen**

Potential impacts of rising atmospheric CO_2 on the biogeography of planktonic Foraminifera

Tilla Roy[1], Fabien Lombard[2], Marion Gehlen[1], and Laurent Bopp[1]

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[2]*National Institute for Aquatic Resources, Oceanography Section, Technical University of Denmark, Denmark*

Planktonic foraminifera (forams) are responsible for between 30% and 80% of the global carbonate flux. The global distribution of each planktonic foraminifera species is largely driven by temperature, food availability, and light (i.e., for species with algal symbionts). Present (2000–2010) and future (2090–2100) 3D distributions of the growth-rates and abundances of eight well-studied foraminifera species are simulated using an ecophysiological foram model. The empirical model is driven with temperature, food, and light from a coupled climate-carbon cycle Earth System model that has been forced with historical CO_2 emissions and future emissions from the IPCC A2 scenario. A key strength of the foram model is that it is observation-based: the growth-rate relationships are derived from laboratory experiments and the abundance relationships are calibrated using data from multi-depth plankton tows. The simulated foram distributions agree well with the dominant species observed in surface waters and the relative foram species abundances in top-core samples from deep-ocean sediments. In response to climate change i) foram species diversity decreases in the tropics and increases towards the poles, and ii) tropical species shift both from surface to deeper layers and towards the subtropics as thermocline waters become to warm to sustain high growth rates. High-latitude species are most vulnerable to climate change: both their abundance and their potential available habitat decreases in response to warming and decreased food availability. We examine how ocean acidification further modifies the potential available habitat for foraminifera by the end of the century.

POSTER 4 **Presenter: Long Cao**

The effect of ocean iron fertilization on ocean acidification

Long Cao and Ken Caldeira

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Ocean iron fertilization has been proposed as a method to mitigate anthropogenic climate change, and there is continued commercial interest in using iron fertilization to generate carbon credits. It has been speculated that ocean iron fertilization could help mitigate ocean acidification, but there is no quantitative studies investigating this issue. In this study we provide for the first time a quantitative assessment of the effect of ocean iron fertilization on ocean acidification. Using a global ocean carbon cycle model, we performed idealized ocean iron fertilization simulations by depleting the surface macro-nutrient concentrations over the global ocean all year round. The idealized ocean iron fertilization simulation is used to place an upper bound on the effect of iron fertilization on atmospheric CO_2 and ocean acidification.

Under the IPCC A2 CO_2 emission scenario, at year 2100 the model simulates an atmospheric CO_2 concentration of 965 ppm with a mean surface ocean pH 0.44 units less than its pre-industrial value of 8.18. A globally sustained ocean iron fertilization diminishes atmospheric CO_2 concentrations by 132 ppm and reduce the mean surface ocean pH change by 0.06 units (A pH reduction of 0.38 units relative to the pre-industrial value with the implementation of ocean iron fertilization, compared to a reduction of 0.44 units without iron fertilization). The 0.06 unit mitigation in surface pH change by the end of this century is achieved at the cost of storing more anthropogenic CO_2 in the ocean interior, furthering acidifying the deep ocean.

Our study demonstrates that ocean iron fertilization, even implemented at the global scale and all year round, can only slightly mitigate surface ocean acidification caused by anthropogenic CO_2 emissions, and at the expense of accelerated acidification in the deep ocean. In the context of a carbon-emission offset scheme, ocean iron fertilization could lead to further acidification of the deep ocean without mitigating surface ocean chemistry change.

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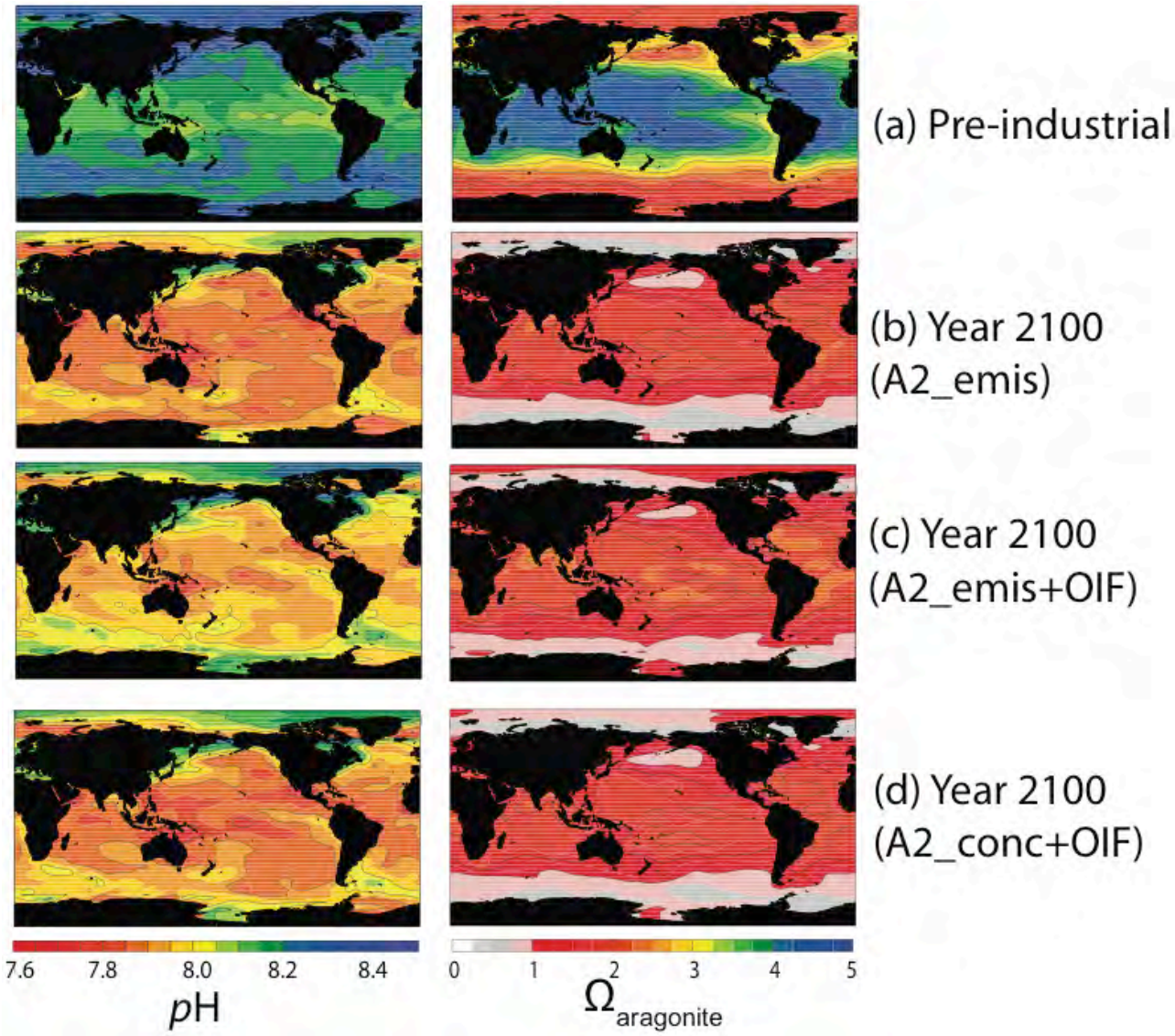
(a) Pre-industrial
(b) Year 2100
(A2_emis)
(c) Year 2100
(A2_emis+OIF)
(d) Year 2100
(A2_conc+OIF)
7.6
7.8
8.0
8.2
8.4
pH
0
1
2
3
4
5
Ω aragonite

Figure 1

POSTER 5 **Presenter: Sinéad Collins**

Competition limits adaptation and productivity in a photosynthetic alga at elevated CO_2

Sinéad Collins

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When competitive exclusion between lineages and genetic adaptation within lineages occur on the same timescale, the two processes have the potential to interact. I use experimental microbial evolution where strains of a photosynthetic microbe that differ in their physiological response to CO_2 enrichment are grown either alone or in communities for hundreds of generations under CO_2 enrichment. After about 300 generations of growth, strains that experienced competition while adapting to environmental change are both less productive and less fit than corresponding strains that adapted to that same environmental change in the absence of competitors. In addition, I find that excluding competitors not only limits that strain's adaptive response to abiotic change, but also decreases community productivity. I present a method to quantify this effect using the Price equation. The Price equation partition demonstrates that competition always makes a large and negative contribution to community productivity in this system, while the contribution from adaptive genetic change varies and can be positive, negative, or near-zero.

These data allow me to empirically test the common hypothesis that phytoplankton that are most able to take advantage of carbon enrichment in single-strain populations over the short term will increase in frequency within multi-strain communities over longer timescales. My experimental data do not support this hypothesis, and instead suggest that lineages that respond poorly to abiotic change (but can still avoid extinction) evolve into superior competitors and increase in frequency.

More generally, this work demonstrates how experimental microbial evolution can be used to test basic assumptions used for predicting how phytoplankton populations may respond to ocean acidification on the timescale of decades, where we expect communities to respond by changes in the physiology of individual organisms, changes in community composition, and evolution (genetic change) within lineages.

POSTER 6 **Presenter: S. Dupont**

An eco-physiological model of the impact of ocean acidification on invertebrate larvae - energy budget flexibility as a unifying principle

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The impact of ocean acidification on marine species appears to be extremely species- and even population-specific within a single species. It also depends on life-history stages and the processes studied. This impact also needs to be considered in the context of additional relevant factors such as temperature and other anthropogenic stressors such as pollution. The current paradigms (e.g., that ocean acidification will negatively impact calcifiers) are now being revisited making any large scale prediction impossible or over-simplistic.

To understand the distribution and potential resilience of a given species in response to today's and to future environmental variability, it is crucial to understand that species physiological ability to buffer and/or regulate when exposed to these changes. For example, it is claimed in the literature that early life history stages are generally more sensitive to environmental variation, including pH, and that invertebrates such as echinoderms demonstrate a poor ability to compensate acid-base disturbance. As a consequence, invertebrate larvae are predicted to be highly sensitive to ocean acidification with little or no buffering / pH regulation capabilities.

This poster will summarize our data on the impact of ocean acidification and energetic balance in invertebrate larvae and presents new evidence challenging these paradigms.

There is a growing body of evidence indicating that the major impact of ocean acidification on larvae is a developmental delay rather than the previously postulated reductions in size at comparable developmental stage. In sea urchin larvae, we found an up to 2 × increase in respiration rate under elevated pCO_2 expected by the end of this century (DpH = 0.4 units), while feeding rates did not differ between larvae from either control or experimental treatments. Calculating scope for growth illustrates that larvae raised under high pCO_2 spent an average of 60% of the available energy for maintenance, while control larvae only allocate 40% of available energy for maintenance (Stumpp et al., submitted).

We also found evidence of unexpected pH regulatory potential in sea urchin larvae. Combining internal pH mapping techniques using confocal microscopy and a newly developed physiological assay to study skeletal calcification/dissolution, we demonstrated that sea urchin larvae possess an unexpectedly high resilience to low pH conditions. Under moderate ocean acidification conditions, sea urchin larvae are able quickly to compensate for environmental pH changes by using H+/K+-ATP pumps (or v-ATPases) and can maintain a stable pH in the extracellular matrix. This very efficient pH regulatory system allows sea urchin larvae to maintain their skeleton under extremely low pH conditions (down to pH5.6). However, complete skeleton dissolution occurs within 1h when H+/K+-ATP pumps are specifically inhibited. This regulation is associated with an energy cost and changes in energy budget that translate into the well-described decreased growth rate under low pH conditions.

Using a method to decalcify larvae and follow the re-calcification process both under control and high pCO_2 conditions, we were able to estimate the cost of calcification as less than 10% of the larval energy budget in control conditions. Under high pCO_2, an additional 10% energy cost is needed to regulate extracellular matrix pH.

Based on these data, we postulate that calcification may not be a major indicator component to predict the impact of ocean acidification on a given taxa but rather the additional costs, direct (e.g. pH regulation) or indirect (e.g., through food availability and/or acquisition) and how they are able to switch their energy budget.

For example, a given species may benefit from ocean acidification through increased metabolism if not energy limited (e.g., the seastar *Crossaster papposus*, Dupont et al., 2010) or be totally unable to survive if insufficient energy is available to service the additional costs (e.g., the brittlestar *Ophiothrix fragilis*, Dupont et al., 2008). We further hypothesize that the ability or inability to cope with this additional cost (the physiological window) will be related to the natural variability currently experienced by a given species in its native ecosystem.

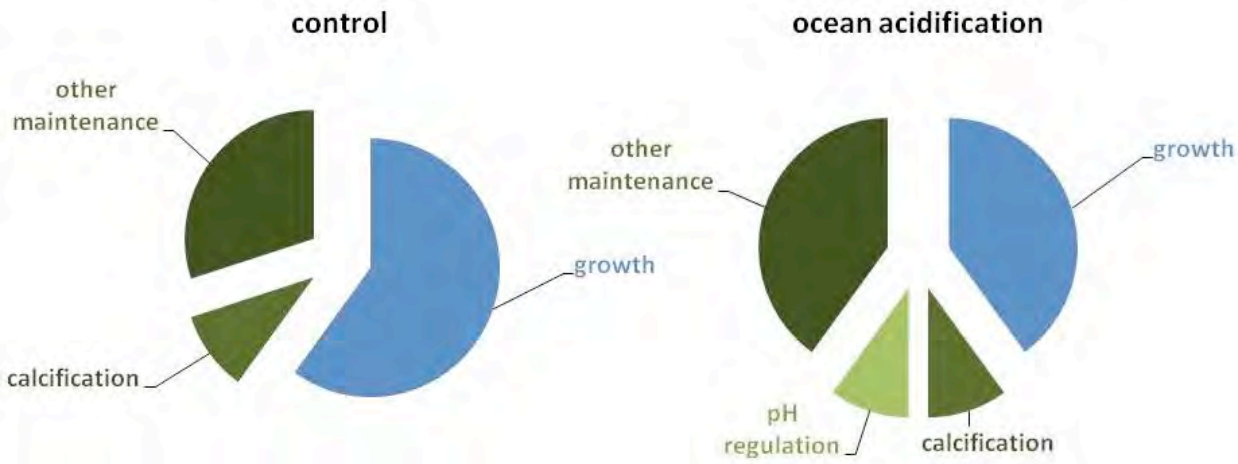

Figure 1: Sea urchin *Strongylocentrotus purpuratus* energy budget under control and near-future ocean acidification conditions

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POSTER 7 **Presenter: Richard A. Feely**

Predictive relationships for pH and carbonate saturation in the Southern California Current System using oxygen and temperature data

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The California Current System is expected to experience the ecological impacts of ocean acidification earlier than most other ocean regions because marine waters in the North Pacific are among the oldest in the global oceans and natural upwelling processes in this eastern boundary current system bring CO_2-rich water masses to the surface in coastal oceans during late spring-early fall months. We used a multiple linear regression (MLR) approach to generate predictive models using oxygen and temperature as proxy variables to reconstruct pH and carbonate saturation states in the Southern California Bight. The calibration data set included high-quality measurements of dissolved inorganic carbon, alkalinity, oxygen, temperature, salinity, and nutrients and was collected during a cruise from British Columbia to Baja California in May–June 2007. The resulting relationships predicting pH and aragonite and calcite saturation states (Ω) from oxygen and temperature data were robust, with r^2 values >0.98 and root mean square errors of 0.020 (pH), 0.048 (Ω_{arag}), and 0.075 (Ω_{calc}). Predicted vs. measured ocean acidification conditions (i.e., pH, Ω_{arag}, and Ω_{calc}) matched very well for seven verification data sets collected between 2008 and 2010 during quarterly CalCOFI cruises in the Southern California Bight and during several sampling dates on an Ensenada transect occupied numerous times between 2006 and 2010. Over sub-decadal time scales, these predictive models provide a valuable tool for reconstructing time-series of ocean acidification conditions in the California Current Ecosystem where historical inorganic carbon measurements are scarce. Reconstructed pH and saturation state values based on CalCOFI oxygen and temperature data for all cruises between 2005 and 2010 reveal a seasonal cycle in the upper water column, with higher pH and Ω values present during the winter cruises, and stronger gradients including much lower pH and Ω values during spring through fall cruises. Deeper in the water column (~300 m), conditions are more stable throughout the annual cycle, with consistently low pH, undersaturation with respect to aragonite, and calcite saturation values <1.5. These predictive relationships can also be used to improve the performance of models used to "nowcast" and forecast ocean acidification in eastern boundary current systems like the California Current System.

POSTER 8 **Presenter: Kunshan Gao**

Effects of ocean acidification on calcifying algae, diatom and phytoplankton assemblages, with special references to interactive impacts with UV

Kunshan Gao, Z. Ruan, Y.P. Wu, G. Gao, K. Xu, G.Y. Yang, G. Li, W. Li, P. Jin, Y.H. Li, S.W. Chen, X.J. Wu, and Y. Zheng

State Key Laboratory of Marine Environmental Science, China

Calcifying Algae

Previous studies showed that increased CO_2 concentration and associated seawater acidification decrease calcification in some macroalgal (Gao et al., 1993) and planktonic (e.g., Riebesell et al., 2000) calcifiers. However, little is known on how calcifying algae respond to solar UV radiation (UVR, 280–400 nm). UVR may act synergistically, antagonistically or independently with ocean acidification to affect their calcification processes. Recently, we showed (Gao et al., 2009) that when the coccolithophore *Emiliania huxleyi* calcified less under lowered pH levels (pH_{NBS} of 7.9 and 7.6; pCO_2 of 804 and 1759 ppmv) (leading to thinned coccolith layers), the cells became more sensitive to UVR. Exposure to UVR resulted significant inhibition of both photosynthesis and calcification. The combined effects of UVR and seawater acidification resulted in inhibition of calcification rates by 96% and 99% and that of photosynthesis by 6% and 15%, at pH 7.9 and 7.6, respectively. This differential inhibition of calcification (C) and photosynthesis (P) leads to significant reduction of the C/P ratio. Seawater acidification enhances the transmission of harmful UVR by about 26% through a reduction of the coccolith layer by 32%. Our data indicate that the impact of a high CO_2/low pH ocean on *E. huxleyi* enhances the detrimental effects of UVR on the major phytoplanktonic calcifier.

We also showed (Gao and Zheng, 2010) that the articulated coralline alga *Corallina sessilis* Yendo grown at elevated CO_2 (1000 ppmv) for more than a month under solar radiation calcified less and even lesser in the presence of UVR. PAR+UVR, in contrast to PAR alone treatment, inhibited the growth, photosynthetic O_2 evolution and calcification rates by 13%, 6% and 3% at the low (380 ppmv) and by 47%, 20% and 8% at the high CO_2 concentrations, respectively, reflecting a synergistic effect of CO_2 enrichment with UVR. UVR induced significant decline of pH in the CO_2-enriched cultures due to its harmful impact on the photosynthetic carbon removal. The contents of key photosynthetic pigments, Chl.a and phycobiliproteins decreased, while UV-absorbing compounds and carotenoids increased under the high pCO_2/low pH condition. Nevertheless, UV-induced inhibition on photosynthesis increased when the ratio of PIC/POC decreased under the high CO_2-acidified seawater, reflecting a UV-protective role played by the calcified layer. Both UVA and UVB negatively impacted the photosynthesis and calcification, however, the inhibition caused by UVB was about 250–260% higher than that by UVA. The results imply that coralline algae may suffer from more damages caused by UVB when they calcify less and less with progressing ocean acidification.

Diatoms

The ongoing OA due to increased CO_2 is likely to have an impact on non-calcifying phytoplankton via its effects on inorganic carbon speciation and consequent down regulation of CO_2 concentrating mechanisms (CCMs), and on the overall energetics of the cell through its impact on electrochemical potentials.

We showed (Wu et al., 2010) that, in *Phaeodactylum tricornutum* (CCMA 106), after acclimation (>20 generations) to ambient (LC, 390 ppmv) and elevated CO_2 (HC, 1000 ppmv) conditions (with corresponding pH values of 8.15 and 7.80, respectively), growth and photosynthetic carbon fixation rates of the HC-grown cells were enhanced by 5% and 12%, respectively, and dark respiration stimulated by 34% compared to the LC-grown cells. The half saturation constant (K_m) for carbon fixation (dissolved inorganic carbon, DIC) increased by 20% under the low pH and high CO_2 condition, reflecting a decreased affinity for HCO_3^- or/and CO_2 and down-regulated carbon concentrating mechanism (CCM). When grown under N-limited conditions, its growth rate decreased

by 38% and 30% in HC and LC condition, respectively; at the same time, organic carbon to nitrogen ratio (C/N) increased by 53% and 21% in the HC and LC-grown cells, respectively, with the C/N ratio increased from 5.7 to 6.9. In *Cylindrotheca closterium f. minutissima, the CCM was also down-regulated, but growth was not stimulated at the elevated* CO_2 *(Gao* et al., *in preparation). In Thalassiosira pseudonana* (CCMP1335) grown at 1000 ppmv CO_2, the activity of both extracellular and intracellular carbonic anhydrace (CA) was decreased by about 50% with decreased growth rate by about 4% (significant) (Wu, 2010, doctoral thesis); and its CCM was also down-regulated. In the HC-grown diatom cells, the electron transport rate from photosystem II (PSII) was photoinhibited to a greater extent at high levels of PAR, and it took longer time for them to acclimate to solar radiation in the presence or in the absence of UVR.

Phytoplankton Assemblages (based on data from the *grow outs* during 3 cruises)

CO_2 perturbation experiments during the cruises (summer and winter, 2009–2010), using a CO_2 enrichlor (Ruihua, Wuhan) and 30 L water-jacketed tanks, showed that, short-term (12 h) CO_2 enrichment enhanced by 9–50% (different stations) the daily photosynthetic carbon fixation by the surface phytoplankton assemblages in the Southern and Eastern China Seas; however, long-term (>7 days) grow-out experiments led to decreased daily photosynthetic carbon fixation by up to 21%. Solar UV radiation reduced the daily photosynthetic carbon fixation by 11–18%. On the other hand, the production of particulate inorganic carbon (PIC) decreased under the high CO_2 level in both the short and long term grow-out experiments, the CO_2-induced acidification reduced the daily PIC production by 43–74% (different stations). Phytoplankton dominant species shifted from cyanobacteria to diatoms.

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POSTER 9 **Presenter: J.-P. Gattuso**

European Project on Ocean Acidification (EPOCA)

J.-P. Gattuso, L. Hansson, and the EPOCA Consortium

EPOCA Project Office, France

The *European Project on Ocean Acidification* (EPOCA) was launched in May 2008 with the overall goal to advance our understanding of the biological, ecological, biogeochemical, and societal implications of ocean acidification. Its consortium includes more than a hundred principal investigators from 31 institutes and 10 European countries. The budget of this four year long project is 15.9 M€, including 6.5 M€ from the European Union. The research efforts of EPOCA are distributed into four themes (see Figure 1).

Theme 1 focuses on past and present spatiotemporal changes in ocean chemistry and biogeography of key marine organisms. Archives of foraminifera and deep-sea corals help determine past variability in ocean chemistry (carbonate, nutrients and trace metals), which are linked to present-day chemical and biological observations.

Theme 2 quantifies impacts of ocean acidification on marine organisms and ecosystems. Molecular, physiological and ecological approaches are used to study climate-relevant biogeochemical processes, including calcification, primary production and nitrogen fixation. Laboratory and field perturbation experiments focus on key organisms in terms of their ecological, biogeochemical or socioeconomic importance.

Theme 3 seeks to improve biogeochemical, sediment and coupled ocean-climate models to better account for how ocean acidification will affect ocean biogeochemistry and ecosystems. Special attention is paid to feedbacks of physiological changes on the carbon, nitrogen, iron and sulfur cycles and how these changes will affect and be affected by future climate change.

Theme 4 evaluates uncertainties, risks and thresholds (tipping points) related to ocean acidification at molecular, cellular and organismal levels from local to global scales. The project assesses the decrease in CO_2 emissions required to avoid these thresholds and describes the change to the marine environment and Earth system, should these emissions be exceeded.

EPOCA research is performed in close collaboration with EU (CARBOOCEAN, MESOAQUA, EUROSITES, ATP, CALMARO and MEECE) and national projects (BIOACID, UK Ocean Acidification Programme, CHOICE-C and US initiatives as part of the FOARAM Act). EPOCA has generated a large number of critical data: 68 papers were published in the first two years and 267 presentations were given at meetings.

Overarching activities include data management, training and outreach. A coherent database of past ocean acidification experiments has been developed and made accessible to the community. Students and young scientists were trained in several courses organised or co-organized by EPOCA in Bergen, Cambridge, Bremerhaven and Woods Hole. Outreach is performed through the project web site (http://epoca-project.eu), the EPOCA ocean acidification information blog (http://ocean acidification.wordpress.com/) and newsletter articles, press releases, media articles. Last but not least, the EPOCA Reference User Group (RUG) is a key tool to disseminate scientific research to various stakeholders, including policymakers. The RUG has produced, in 5 languages, two guides presenting key facts on and key answers to ocean acidification questions.

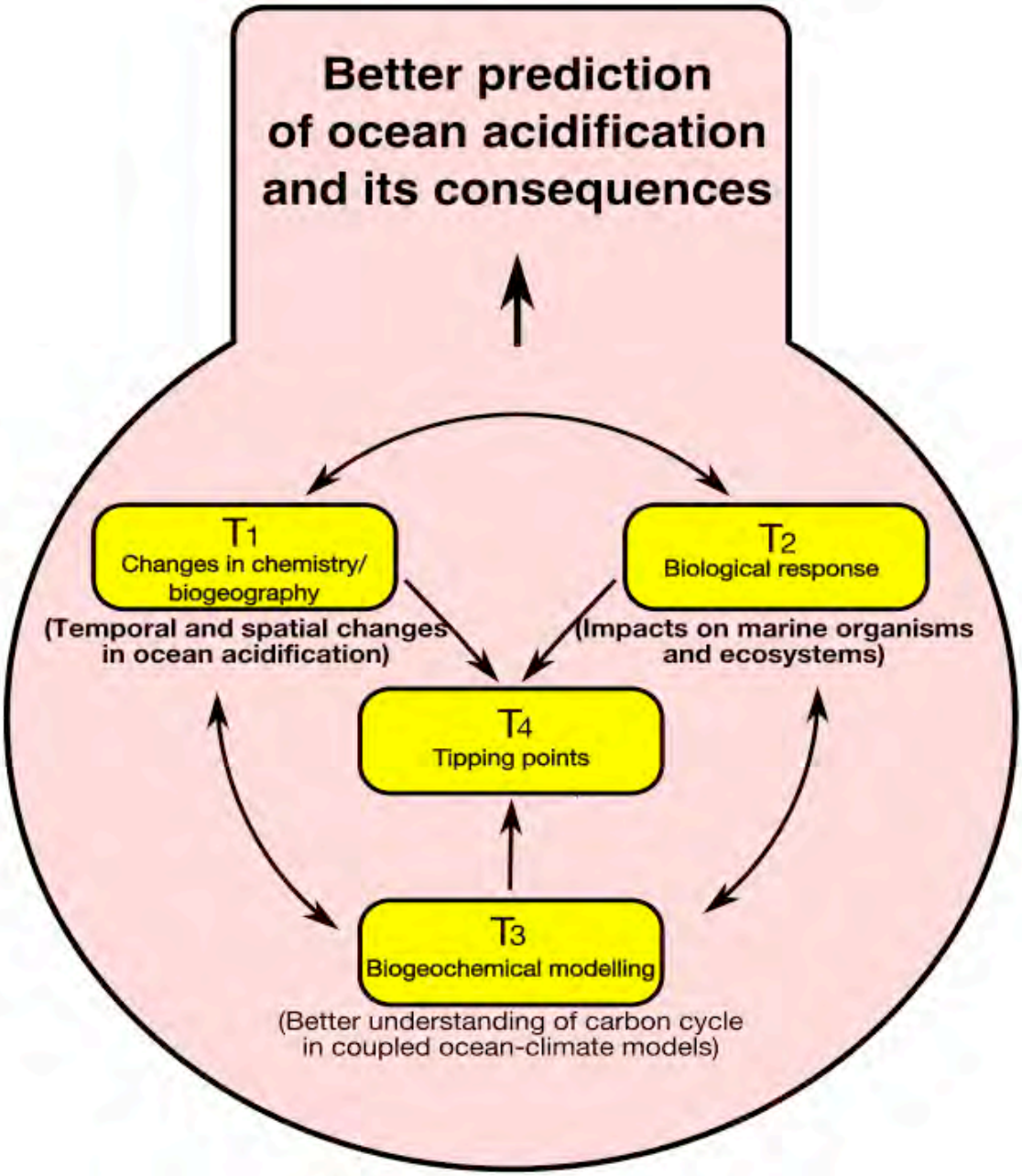
Better prediction of ocean acidification and its consequences
T1
Changes in chemistry/ biogeography
(Temporal and spatial changes in ocean acidification)
T2
Biological response
(Impacts on marine organisms and ecosystems)
T4
Tipping points
T3
Biogeochemical modelling
(Better understanding of carbon cycle in coupled ocean-climate models)

Figure 1

POSTER 10 **Presenter: Jason Hall-Spencer**

Volcanic CO_2 vents reveal the ecosystem effects of ocean acidification

Jason Hall-Spencer

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The global oceans currently absorb over 25 million tons of human-made CO_2 every day causing unprecedented changes to ocean chemistry. As well as lowering pH, increased CO_2 levels are altering surface water chemistry, causing a decline in carbonate ions, an increase in bicarbonate ions and lowering calcium carbonate saturation states. Current research into ocean acidification is mainly being carried out using short-term experiments whereby CO_2 levels are manipulated in aquaria and enclosures. We have adopted a new approach using volcanic carbon dioxide vent systems as 'natural laboratories' as they cause long-term changes in seawater carbonate chemistry. A wide range of organisms, including macroalgae, seagrasses, motile invertebrates and sessile invertebrates have now been investigated in shallow areas located off the island of Ischia (Castello Aragonese, Tyrrhenian Sea, Italy). The gradients in CO_2 levels reveal winners and losers within the benthic community. All calcifiers (coralline algae, molluscs, polychaete spirorbids, foraminiferans) are strongly reduced in abundance or are absent from acidified areas (pH <7.8) and the overall benthic biodiversity is around 30% lower than in normal conditions. However, 67% of the species observed, including macroalgae, seagrass, polychaetes and peracarid crustaceans are resilient to long-term exposures to CO_2 levels predicted for the end of this century and beyond. Long-term transplantation experiments using scleractinian corals and bryozoans show that the combined effects of abnormally high summer temperatures and ocean acidification are detrimental to these key organisms.

Our *in situ* observations give support to concerns, based on model predictions and short-term laboratory experiments, that ocean acidification will likely combine with other stressors (e.g., temperature rise) to cause a decrease in coastal marine biodiversity and lead to shifts in ecosystem structure.

POSTER 11 **Presenter: Christoph Heinze**

Potential of radionuclides to detect large scale impacts of ocean acidification

Christoph Heinze[1] and Tatjana Ilyina[2]

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[2]*Max Planck Institute for Meteorology, Germany*

Progressing ocean acidification due to oceanic uptake of human produced CO_2 from the atmosphere is clearly documented by in-situ carbon measurements from the ocean surface and the deeper water column. Future climate projections with coupled Earth system models indicate a considerable acceleration of ocean acidification during the coming decades depending on the respective CO_2 emission scenario. The related effects on marine ecosystems and biota species are currently under investigation but in many aspects are still inconclusive. Among potential key changes is a reduction in $CaCO_3$ shell producing organisms which contribute to the marine vertical particle flux through the water column. Respective (not yet fully conclusive) results on the mechanisms and extent of changes in $CaCO_3$ particle production come from local experiments under idealised conditions (laboratory, mesocosm). Ilyina et al. (2009) show that respective large scale effects would become measurable through changes in surface ocean alkalinity only after 20-40 years from now under realistic conditions. It is, therefore, challenging to find alternative indicators for changes in large scale $CaCO_3$ production and $CaCO_3$ particle abundances in the ocean water column.

^{230}Th is a long-lived radionuclide from the uranium decay series. Its half life is ca. 75,200 yr, but its residence time in the ocean is much shorter because it is removed quite quickly from the ocean water column through scavenging by sinking particles. Its delivery function is easy to simulate as it is quasi-homogeneous (uranium is very well mixed throughout the ocean). The preferential carrier phase for ^{230}Th is still under debate; however, in any case $CaCO_3$ is one of the key particle species to which ^{230}Th attaches to. Equilibrium between particle attached and dissolved concentrations can be approximated through an equilibrium reaction, where – like in the mass action law for chemical reactions – an equilibrium constant determines the partitioning between the phases. ^{230}Th was implemented in the latest version of the HAMOCC2s biogeochemical ocean general circulation model. We show results from model simulations on the sensitivity of the concentration of ^{230}Th in the ocean water column to changes in large scale $CaCO_3$ production. Indeed simulated water column ^{230}Th activities change with saturation dependant $CaCO_3$ particle export (see also an earlier study by Heinze et al., 2006, where the principle effect of declining $CaCO_3$ production on dissolved ^{230}Th had been tested in a basic sensitivity experiment). However, the detection thresholds for large scale ocean acidification impacts using state-of-the-art ^{230}Th measurements would be approximately of the same order as for alkalinity measurements. Therefore, ^{230}Th can be used as an additional constraint for detection of large scale ocean acidification impacts but probably cannot lead to earlier detection thresholds. ^{230}Th is nevertheless very attractive as its concentration – and the effect on its concentration due to ocean acidification – increase with depth and due to horizontal mixing serves as an integrator over larger horizontal areas. A limited measurement network of regularly re-occupied observational stations could potentially provide a powerful monitoring system for large scale ocean acidification impacts which otherwise may be difficult to detect from direct observations.

Acknowledgment: This work was supported through the ''European Project on Ocean Acidification'' which received funding from the European Community's Seventh Framework Programme (FP7/2007-2013) under grant agreement 211384, through EU FP6 Integrated Project CARBOOCEAN funded by the European Commission under contract 511176 (GOCE), and through funding from the Bjerknes Centre for Climate Research (national centre of excellence, Norwegian Research Council). Travel support for IPCC activities was provided through KLIF (Norway).

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POSTER 12 **Presenter: J.M. Hernández-Ayón**

Influence of the OMZ in the ocean acidification in the Pacific Mexican Coast

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In the Mexican Coast, spatial variability can be as short as several kilometers. Significant differences exist between the subregions in the Mexican Coast of the Central American Isthmus, and southern California Current. For example the open ocean Pacific waters south of 30°N are, on the annual average, a CO_2 source to the atmosphere, whereas the area north of 40°N is a sink, and the zone between 30° and 40°N is neutral. In the Mexican Pacific coast off Baja however, seasonal CO_2 fluxes were identified using CO_2 measurement from 1993 to 2001. From December to May (winter and early spring), the oceanic and shelf surface water was a sink for atmospheric CO_2; however the rest of the year it was a strong source of CO_2. The strong sink area started in the coast north of Punta Eugenia (up to latitude 27º), while the coastal system become a source from June through November. Seasonal data from 1994 show a variation of pCO_2 from February to August with the dominance of the low-CO_2 early in the year in the waters over the shelf area making the region a net sink during upwelling season but changing to a source of CO_2 during August in all the area with higher fluxes south of latitude 28. However, the annual flux positive average suggests this zone as a source of CO_2 to the atmosphere. The Ω aragonite in the oceanic transect in the region from Baja was located ~170 m as was reported in 2008. However, in the subtropical coast it was observed in ~70 m without upwelling transport. Good relationship was observed between Equatorial Subsuface water and the undersaturated Ω aragonite depth, but also with low oxygen waters. This water mass in the subtropical area as part of the OMZ is shallower in comparison with Baja. This water mass had rich DIC waters with Ω aragonite values of 0.90 ± 0.08. During a cruise in 2007 it was found a gradual shallower subsaturated Ω aragonite horizon for the last two transect in Baja coast. Results from several cruises from the Imecocal program (Investigaciones Mexicanas de la Corriente de California), some opportunity cruises and measurements from two buoys support the roll of subtropical waters influence in the carbon chemistry from north Mexican coastal waters.

POSTER 13 **Presenter: Ove Hoegh-Guldberg**

Understanding ocean acidification on coral reefs: two next generation experimental systems for simulating future conditions.

David I. Kline, Sophie Dove, and Ove Hoegh-Guldberg

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Global warming and ocean acidification pose major threats to the future of coral reef ecosystems. However, there are still significant limitations to better understanding these impacts on corals reefs. We have designed two custom experimental systems to get around many of these experimental limitations at Heron Island on the southern Great Barrier Reef. The Coral Proto – Free Ocean Carbon Enrichment (CP-FOCE) system is the world's first *in-situ* coral reef acidification system. It uses an integrated network of instruments to monitor and control the pH in four experimental chambers on the Heron Island reef flat. The data is transmitted via radio link, real time to a computer in the laboratory where the data is logged and used for real-time control of the pH as an offset from the environment. This experimental system avoids many of the artifacts of tank or mesocosm experiments such as unnatural light, currents, food, microbial populations, currents, sediment communities, and associated animal communities. We have also established a computer controlled mesocosm system on Heron Island in which four four climate scenarios of pCO_2 levels and temperature (preindustrial, present day, B2, and A1FI) are simulated using a custom designed pCO_2-stat system. Four, 8000 L insulated sumps are used to create the pCO_2 and temperature conditions and create ample residence time for high precision pCO_2 and temperature control. The water from these sumps is then pumped to 3 experimental tables that can hold up to 72 experimental aquaria that uses LEE filters to mimic the light levels from where the organisms were collected. The water is also pumped to twelve, 300 L mini-reefs where ecosystem interactions and changes can be studied under the different climate scenarios. The pCO_2 control system achieves precision of better than 20 ppm to the desired level, a level unachievable with a pH-stat system. Furthermore the large, insulated sumps insure that the carbonate chemistry and temperature treatments are stable. The system allows a high level of replication and avoids studying just the CO_2 or temperature effect associated with rising carbon dioxide levels in the atmosphere. The combination of the in situ CP-FOCE and the climate scenario producing CRCCE experimental systems will allow for a much more in depth understanding of the challenges facing coral reef ecosystems in the future. Early results from these systems will be presented along with discussions of future challenges and limitations arising from these types of experimental systems.

Figure 1: Coral reef climate change experimental systems on Heron Island, Great Barrier Reef, Australia. In A) the Coral Proto – Free Ocean Carbon Enrichment System (CP-FOCE), an in-situ ocean acidification system currently deployed on the reef flat at Heron Island. The system uses a system of integrated instruments connected to four experimental chambers to control the pH in the chambers as an offset from the environmental pH using a float that has a series of computer pods that determines the rate and direction of dosing. The doors in the chambers are closed regulary B) for calcification and respirometry measurements. In C) the $pCO_{2\text{-stat}}$ and temperature climate change system is shown. Each of the 4 large white boxes are 8,000 L insulated sumps that are each controlled to a different environmental scenario of pCO_2 stat system and large heater-chillers. The manipulated water from each of these sumps is then pumped to three replicate, 300 L mini-reefs (12 total) with Lee filters stimulating the 5 m water depth where the reef organisms were collected. The treatment water is also pumped to 3 experimental tables D) which can hold a total of 72, 30 L glass aquaria fitted with LEE filters to stimulate the light environment where the organisms were collected.

POSTER 14 **Presenter: M. Ishii**

Ocean acidification in the tropical to subtropical western North Pacific: Results from time-series observations of carbonate chemistry along 137°E

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1. Introduction

Repeated observations of atmospheric and oceanic CO_2 levels have been conducted since 1983 in the western North Pacific along 137ºE onboard the Japan Meteorological Agency's research vessels *Ryofu Maru* and *Keifu Maru*. We report the trend of increase in CO_2 and acidification in surface waters of coastal zone off of Japan and of open ocean zone from tropical through subtropical zones. We also present the results from repeat water-column CO_2 observations in 137ºE section since 1994 that indicates accumulation of anthropogenic CO_2 and acidification in the interior of the subtropical gyre.

2. Observations of CO_2 at repeat line 137ºE

Measurements of partial pressure of CO_2 in surface seawater (pCO_2sw) and in the atmosphere have been made since 1983 using a shower-head equilibrator–NDIR analyzer. Concentration of total inorganic carbon (TCO_2) has been measured since 1994 using a CO_2 extraction–coulometry method, and pH has been measured in total hydrogen ion concentration scale at 25ºC since 2006 using an indicator dye–spectrophotometry method. The measured pH values in surface seawater and pH calculated from pCO_2sw, TCO_2, temperature (T) and salinity (S) using dissociation constants given by Lueker et al. (2000) agree well. The mean ± standard deviation of their differences is –0.003 ± 0.005. The frequency of observations has changed from annually each winter in the 1980s, to biannually each winter and summer in the 1990s and early 2000s (although TCO_2 measurements were made at irregular intervals), to each season since 2003.

3. Acidification in coastal zone off of Japan

The coastal zone between the south coast of Honshu, Japan, and the Kuroshio (32°N to 34°N, 137°E) is characterized by higher primary productivity (>200 gC m^{-2} yr^{-1}). It is an important spawing region for many species of pelagic fish, and is also known as a northern limit of hermatypic coral's habitat in the North Pacific.

In this zone, pH is lower (7.90 to 7.94) in winter and higher (8.08 to 8.16) in summer (Figure 1). This seasonality is opposite that of TCO_2 normalized at S = 35 ($NTCO_2$) that is higher (2050 to 2090 mmol kg^{-1}) in winter and lower (1970 to 1980 mmol kg^{-1}) in summer. In contrast, salinity-normalized total alkalinity (NTA) calculated from TCO_2 and pH, and from pCO_2sw and TCO_2, show no distinct seasonal variation. These results indicate that changes in pH are tightly coupled to changes in $NTCO_2$ resulting from net air-sea CO_2 exchange, net biological CO_2 uptake, and vertical mixing that are not associated with large changes in NTA. Multilinear regression of $NTCO_2$ as a function of T, S, and timing of observations shows that $NTCO_2$ is increasing at a rate of +1.1 ± 0.2 μmol kg^{-1} yr^{-1} for 1994 to 2008, while no long-term change has been determined for NTA. These results indicate that pH and the index of aragonite saturation (Ω_{arag}) are decreasing at a rate of –0.018 ± 0.004 $decade^{-1}$ and –0.11 ± 0.02 $decade^{-1}$, respectively (Ishii et al., submitted).

If future CO_2 emissions keep increasing as the IPCC SRES A1FI, a further reduction of –0.8 to –1.0 in Ω_{arag} is likely in the next 50 years. Laboratory experiments have shown that, for a variety of calcareous organisms, the rate of calcification decreases as Ω decreases. Such a rapid reduction of Ω_{arag} could have negative impacts on these organisms.

4. Acidification in surface water of the open ocean

In the open ocean zone (30°N to 3°N) where there are many islands with coral reefs, the trends of $NTCO_2$ increase and no long-term change in NTA have also been determined for 1994 to 2008. The rate of increase in $NTCO_2$ in each latitudinal zone is also compatible to the rate of increase in CO_2 concentration in the atmosphere.

On the assumption that surface NTA has not changed for the past longer period, Midorikawa et al (2010) evaluated the trend of acidification using the long record of pCO_2sw observations in the extensive tropical to subtropical zones. The computed pH time series at in-situ temperature exhibited significant trends of decrease from –0.0015 to –0.0021 yr^{-1} in winter for 1983 to 2007 and from -0.0008 to –0.0019 yr^{-1} in summer for 1987 to 2007. The thermodynamic effects of rising sea surface temperature (SST) accounted 15%, on the average, of the trend of pH decrease in the subtropical zone in winter, whereas a trend of decreasing SST slowed the pH decrease in summer in the northern subtropical zone.

Increases in pCO_2sw and surface $NTCO_2$ have also been observed in the warm pool of the western equatorial Pacific (5°S to 5°N, 144°E to 160°W) (Ishii et al., 2009). The mean rate of increase in pCO_2sw was +1.5 ± 0.2 μatm yr^{-1} for 1985 to 2004 and that for surface $NTCO_2$ was +1.3 ± 0.3 μmol kg^{-1} yr^{-1} for 1992 to 2004. These trends indicate that acidification is also in progress in this region.

5. Acidification in the interior of the ocean

The trend of increase in TCO_2 has also been firmly determined for 1994–2008 in the interior of subtropical gyre at each of isopycnal surfaces from s_q = 25.0 below winter mixed layer (~200 m) to around s_q = 27.0 in lower layer of the North Pacific Intermediate Water (NPIW). Along 137°E section at 30°N for example, significant temporal variabilities and long-term trends have been observed for both $NTCO_2$ and dissolved oxygen in particular in the upper layers. It is likely that the observed changes in apparent oxygen utilization (AOU) for isopcynals reflects change in the region of formation and/or subsequent interior ventilation pathways, in addition to changes in ocean biology.

Salinity-normalized TCO_2 shows a significant trend towards increased concentrations of +0.8 ± 0.3 to +1.4 ± 0.3 μmol kg^{-1} yr^{-1} on s_q = 25.0 to 25.8, and +0.4 ± 0.2 to +0.9 ± 0.3 μmol kg^{-1} yr^{-1} on s_q = 26.1 to 27.0. In order to correct for the changes reflected in AOU, we have calculated what we will refer to as preformed TCO_2 by subtracting (117/170)*AOU from the measured TCO_2. This reveals the TCO_2 of a watermass parcel when it was last in contact with the atmosphere. The trend in preformed $NTCO_2$ shows a significant trend towards increased concentrations of +1.0 ± 0.1 to +1.1 ± 0.1 μmol kg^{-1} yr^{-1} on s_q = 25.0 to 25.8, and +0.1 ± 0.2 to +0.7 ± 0.3 μmol kg^{-1} yr^{-1} on s_q = 26.1 to 27.0. These results suggest that increases in $NTCO_2$ are controlled by the uptake of anthropogenic carbon into the interior of the ocean. The role of changes in ocean circulation for $NTCO_2$ change is also significant.

These changes in $NTCO_2$ corresponds to the change in pH of –0.014 ± 0.006 to –0.028 ± 0.003 $decade^{-1}$ on s_q = 25.0 to 25.8, and of –0.019 ± 0.006 to –0.025 ± 0.003 $decade^{-1}$ on s_q = 26.1 to 27.0. They also corresponds to the change in Ω_{arag} of –0.06 ± 0.04 to –0.13 ± 0.01 $decade^{-1}$ on s_q = 25.0 to 25.8, and –0.08 ± 0.01 to –0.04 ± 0.01 $decade^{-1}$ on s_q = 26.1 to 27.0. The isopycnal surfaces around s_q = 26.8 in the NPIW changed from supersaturation to undersaturation with respect to aragonite during the past 20 years.

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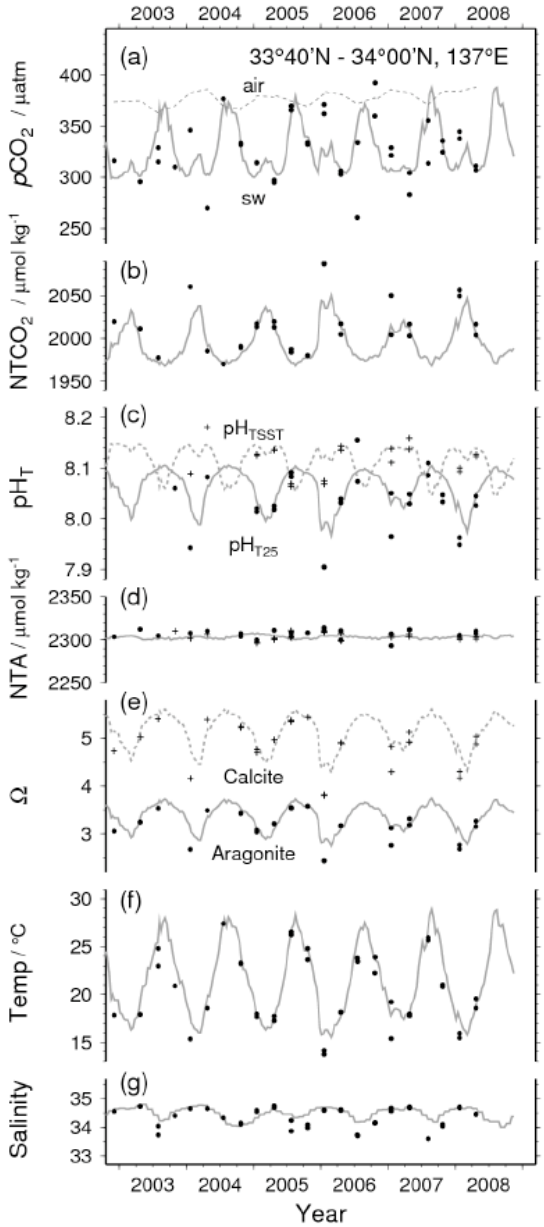

Figure 1: Time-series data for seawater CO_2 and hydrographic parameters in surface water of the coastal zone south of Honshu, Japan, for December 2002 through April 2008.

POSTER 15 **Presenter: Atsushi Ishimatsu**

Complete inhibition of spawning by CO_2 and temperature increases in the sea urchin *Hemicentrotus pulcherrimus*

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Future oceanic environmental changes such as acidification and warming are projected to alter marine ecosystems, which could have far-reaching implication for both global ecosystem per se and food security for humanity (Caldeira and Wickett, 2003; Orr et al., 2005). Recent models predict the buildup of atmospheric CO_2 (max. 1000 µatm) will result in a decrease of seawater pH by 0.1~0.4 units and an increase of temperature by 1.8~4°C by the end of this century (Cao and Caldeira, 2008; IPCC, 2007). Of the two sensitive life stages to environmental perturbations, increasingly more attention has been paid to effects of ocean acidification and warming on early development, but there have been hardly any data on reproduction. In this paper, we report separate and combined effects of elevated CO_2 and temperature on reproduction of the sea urchin *Hemicentrotus pulcherrimus*, and some physiological and behavioral changes observed during 9 month continuous exposure to increased CO_2 and temperature conditions.

Twenty individuals of adult *H. pulcherrimus* were reared in each of the following four treatments; control (at ambient pCO_2 and temperature), high CO_2 alone (at pCO_2 1,000 µatm and ambient temperature), high temperature alone (at ambient pCO_2 and temperature 2°C above ambient) and combined (at pCO_2 1,000 µatm and temperature 2°C above ambient), for 9 months. Spawning was checked daily. Oxygen consumption and feed intake were determined monthly. The behavior tests (light avoidance and chemoreception) were performed at the end of the exposure.

Spawning occurred only in the control (February, 2010) and high temperature alone (January, 2010) treatments: ca. 10^6 eggs were spawned per female, and fertilization rates were >95% for both treatments. However, spawning never occurred in the other two treatments (high CO_2 alone and combined) by the end of the exposure (August, 2010). Feed intake became significantly suppressed in the two high CO_2 treatments (high CO_2 alone, and combined), with an earlier onset of the suppression in the combined treatment (after two months). High CO_2 exposure, regardless of temperature, initially stimulated oxygen consumption but then resulted in a significant average 45% suppression in oxygen consumption (40% and 50% in high CO_2 and combined treatments, respectively) at the end of the exposure. Concomitantly, moving speed as determined by light avoidance was slowed by 20% and 30% in the high CO_2 alone and combined treatments, respectively. Moreover, the time for sea urchins to reach feed items (algal pellets) was prolonged by 80% and 120% in the high CO_2 alone and combined treatments, respectively.

The complete inhibition of the spawning observed under the high CO_2 and temperature conditions implies that the species will incur possible extinction unless they can adapt to the expected ocean environmental changes, which will occur on a more extended time scale than we tested in our laboratory experiment. The significant reduction in feed intake may be responsible for an 80% reduction in ovarian mature egg number as found in our earlier study on the same species (Kurihara et al., in revision). In that study, sea urchins of the high CO_2 alone and combined treatments did spawn, though the number of spawned eggs was not quantified. The reason for this apparent discrepancy may be higher seawater temperatures recorded during this study than during the earlier one (by ca. 1.2°C during winter months). The depressed mobility as shown by the light avoidance and feed search protocols may be a consequence of the metabolic suppression. We must untangle

cause-and-effect relationships of these CO_2 impacts, which may have manifested as the total inhibition of spawning.

It is crucially important to evaluate long-term impacts of combined CO_2 and temperature increases on sexual maturation and reproduction for different taxa of marine organisms with different reproductive strategies. Together with knowledge on larval responses to CO_2 and warming, such information would provide a basis for implementing adaptive strategies to protect sensitive species from future ocean environmental changes, and thereby maintain the health of entire coastal ecosystems and sustain marine ecological services. We are now analyzing histology/morphology of the alimentary canal, feeding apparatus, and several physiological and molecular parameters to gain insights into underlying mechanisms that led to the observed inhibition of spawning in our sea urchins.

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POSTER 16 **Presenter: Haruko Kurihara**

High-CO_2 impact on the coral-reef ecosystem

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Coral reef ecosystem is widely accepted to be particularly at a risk in the high CO_2 world. However, most of the available information is mainly restricted to the effects of high CO_2 on the calcification rate of corals. Considering the high coral reef biodiversity, we urgently need to comprehensively examine how does the changing CO_2 will affect the diverse coral-reef organisms and its potential impact at a community level.

In this presentation, I will present our new project based on laboratory and field studies evaluating the long-term carbonate chemistry change in the Okinawa coral reef and the biological and ecological effects of high CO_2 on different ecological functioning species including coral, soft-coral, sea grass, sea urchins, sea star and coral reef fishes.

POSTER 17 **Presenter: Su Mei Liu**

Response of the Chinese seas to the increase in anthropogenic carbon dioxide—a preliminary result

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Enrichment of the ocean with anthropogenic carbon dioxide is reducing ocean pH and carbonate ion concentrations, and thus the oceanic saturation states of carbonate minerals and the calcification rates of some marine organisms (Feely et al., 2004; Orr et al., 2005). These changes in turn decrease calcifying organisms or modify marine food webs (Cooley et al., 2009). The coastal ocean plays a disproportionate role in comparison with its surface area (Borges, 2005). A three-dimensional physical-biogeochemical model was constructed to evaluate seasonal and interannual variation of air-sea CO_2 flux in the Yellow, East China and South China Seas. From 1990 to 2004, the surface pCO_2 increases in the Chinese Seas, indicating that the Yellow and East China Seas are sources of CO_2 to the atmosphere and the South China Sea is a weak source of CO_2 to the atmosphere (Liu and Chai, in revision). Changes of CO_2 may affect the phytoplankton species composition and marine nutrient biogeochemistry in the Chinese Seas.

Rainwater samples were collected at Qianliyan Island within the Yellow Sea and upon the Shengsi Archipelago in the East China Sea during 2000 to present. Considering pH ~ 5 as the threshold for recognizing acid rain, the two stations were both affected by frequent acid rains, with a frequency of 70% at Shengsi and 47% at Qianliyan. The pH values at both stations show slight decrease trends. The frequency and acidity of rainfall is more intense at Shengsi than at Qianliyan. Hence, at Qianliyan, non-sea-salt (nss-) sulfate is the dominating factor influencing precipitation acidity. At Shengsi, nss-sulfate and nitrate are comparable in terms of their contribution to the acidity of precipitation. While nss-Ca is the major contribution to H^+ neutralization at Qianliyan it is less important in terms of neutralization at Shengsi (Zhang et al., 2007; unpublished data). Qianliyan has an annual rainfall of 600–700 mm and low rainfall frequency (i.e., 20–30 events yr^{-1}); Shengsi has an annual rainfall of 1000–1200 mm distributed relatively evenly throughout the year and has 60–70 rain events per year. And the surface area of the Yellow Sea is 38×10^4 km^2; the surface area of the East China Sea Shelf is 55×10^4 km^2. Acid rain may be a serious environmental problem for coastal regions. More studies need to concern with the impact of acid rain on coastal waters of the Chinese Seas.

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POSTER 18 **Presenter: Jeremy T. Mathis**

Ocean acidification and evidence of systemic seasonal aragonite undersaturation in the high latitude seas

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Rising CO_2 levels in the atmosphere and ocean have lead to an anthropogenically induced acidification phenomenon in the surface waters of high latitudes seas. These areas are projected to become persistently undersaturated with respect to important carbonate minerals as early as mid-century and seasonal aragonite undersaturation in surface and shallow subsurface waters over the continental shelves has already been observed in the Chukchi and Bering Seas. Calcifying marine organisms, including pteropods, foraminifers, cold-water corals, sea urchins, mollusks, and coralline algae that could be susceptible to reduced calcification rates under increasing ocean acidity make up significant components of the diverse ecosystems in polar and sub-polar regions. Over the next decades, trends of rising temperatures and species invasions coupled with progressive ocean acidification are expected to increasingly influence both planktonic and benthic marine communities of the arctic and sub-arctic. In commercially important regions, like the benthic fisheries of the Bering Sea this trend could have dramatic consequences. Here, data and synthesis products will be presented from a number of cruises in the region during the past decade to demonstrate the extent and controls on ocean acidification processes in these environments. The rate and magnitude of changes in pH and carbonate mineral saturation states illustrate the urgent need for expanded efforts in ocean acidification research and monitoring in these sensitive regions.

POSTER 19 **Presenter: Philip L. Munday**

Effects of ocean acidification on tropical marine fishes

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In general, fishes are thought to be relatively tolerant to increased CO_2 and reduced pH because they have well developed physiological mechanisms for acid-base compensation (Pörtner et al., 2004). Adults of some marine fishes can tolerate CO_2 concentrations several orders of magnitude greater than predicted to occur under climate change scenarios (Ishimatsu et al., 2008). However, one recent study found that the scope for aerobic activity in two species of tropical cardinalfishes decreased by up to 30% when they were exposed to ~1000 ppm CO_2 (Munday et al., 2009a). This is consistent with hypotheses about the physiological mechanisms by which ocean acidification will affect water-breathing animals (Pörtner and Farrell, 2008). The extent to which changes in aerobic function will affect the ecology of marine fishes is currently unknown, but reproductive success could be especially sensitive (Pankhurst and Munday, 2011).

The few studies that have investigated the effects of ocean acidification on the early life history of marine fishes have found no evidence for negative impacts on development, growth and survival. Elevated CO_2 and reduced pH did not have a negative effect on embryonic duration, size at hatching, survival, and growth of larvae and juveniles of two common reef species, *Amphiprion percula* and *Acanthochromis polyacanthus* (Munday et al., 2009b, submitted). Similarly, skeletal and otolith development were not affected by exposure of larvae and juveniles to water acidified with up to 1000ppm CO_2 (Munday et al., 2011). In contrast, dramatic changes were observed in the behaviour of larvae and newly-settled juveniles exposed to seawater simulating ocean acidification scenarios that could occur in the next 50–100 years. Larval fish reared in control seawater discriminated between a range of cues that could help them locate suitable settlement habitat and avoid predators. This discriminatory ability was impaired in larvae reared in conditions simulating ocean acidification (Munday et al., 2009c; Dixson et al., 2010). Larvae exposed to elevated CO_2 were more active and exhibited riskier behavior (Munday et al., 2010). As a result, they had markedly higher mortality from predation in natural habitat compared with current-day controls (Figure 1; Munday et al., 2010). These results indicate that larval growth and development might not be adversely affected by ocean acidification, but that changes to larval behaviour and impairment of their sensory systems could have significant effects on population replenishment and connectivity patterns of many species. Significant variation in individual responses was observed among larvae at intermediate CO_2 levels (~700 ppm CO_2), but not at higher levels (~850 ppm CO_2), indicating some potential capacity for selection of tolerant phenotypes if more extreme atmospheric CO_2 scenarios are avoided.

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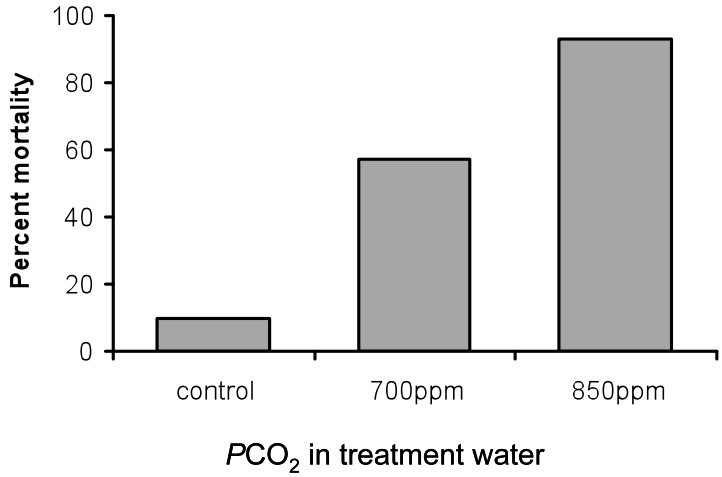

Figure 1: Mortality rate from predation increased markedly in juvenile reef fish that had been exposed to elevated CO_2 during their larval phase. Larvae exposed to elevated CO_2 become attracted to the smell of predators and exhibit riskier behaviour in their natural reef habitat (Munday et al., 2010). Figure shows percent mortality after 30 hours for larval damselfish exposed to elevated PCO_2 and then transplanted to coral reef habitat.

POSTER 20 **Presenter: Yukihiro Nojiri**

Design and use of a precise pCO_2 control system for ocean acidification manipulation experiments

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Ocean acidification impact should be critically examined for probable future levels in atmospheric CO_2 and the RCP scenarios have been identified for common future conditions in the drafting of IPCC AR5 assessment. Typical future atmospheric CO_2 concentrations in these scenario group are >1370, 850, 650, 490 ppm for RCP 8.0, 6.5, 4.0 and 2.6, respectively, however these concentrations are not at the same future time period. Even CO_2 exposure is a basic experiment to examine the biological response of marine organisms, however, the exposure concentration has been typically higher than the lower zone of the new scenario concentrations. Especially, RCP 8.0 may give a serious climate (temperature) impact upon both terrestrial and marine ecosystems and then much concern should be given for low CO_2 level exposure impact. Japan started a research program entitled as 'Experimental study of ocean acidification impact on benthic calcifiers (AICAL)' funded for 2008–2010 by Ministry of Environment. In this program, precise CO_2 controlling system for overflow tank culture has been commonly used and we are trying to examine low level CO_2 exposure impact for various species of benthic calcifiers.

Preliminary study and numerical consideration demonstrate difficulties in controlling seawater pCO_2 using a regular aquarium tank with CO_2/air mixed gas bubbling. It is because of insufficient equilibration efficiency with several tens of centimeters of bubbling height in the tanks. Insufficient equilibration is especially enhanced when aquarium is maintained by overflowing water, because CO_2 away by the overflowing water gives insufficient equilibration and then it needs very high equilibration efficiency of bubbling air. In case the experiment is done without monitoring pCO_2 of the aquarium tank may give an artifact. We developed a new type of air-seawater equilibrator by combination of a 'counter current dissolution water tower (CCDWT)' and a 'measurement water tower (MWT)'. Figure 1 is the schematic of the CO_2 control system. The system can produce seawater with target pCO_2 and record its pCO_2 by a LICOR840 gas analyzer. Seawater having target pCO_2 can be supplied to an aquarium tank at around 20L/hour flow rate, which enables the turnover time of several hours for regular size of tanks. The system can simulate diurnal cycle of pCO_2, generally occurs in coastal area.

Our culture experiment has been stared to research long term and low level exposure of CO_2 for benthic animal species in Japanese coastal environment. We examined growth rates of post-larvae of Ezo abalone with varying pCO_2 and erosion on shell surface in the case of higher exposure of CO_2 was observed (Kimura et al., submitted). An experimental results of adult branch of polyp showed that the calcification rate was higher at the pre-industrial pCO_2 than at the present-day level, and it did not significantly change between present-day and near-future ocean acidification levels, suggesting that the past increase in pCO_2 more seriously decreased the adult coral calcification than future increases are likely to do (Ohki et al., in preparation). An experiment of examining impact of diurnal change on growth of sea urchin is ongoing.

The AICAL project targets to improve quality of CO_2 exposure experiment by developing dip-in type pCO_2 system to ensure the *in situ* pCO_2 of culture tank. An experimental proof has already been done comparing with precise ship board type pCO_2 system.

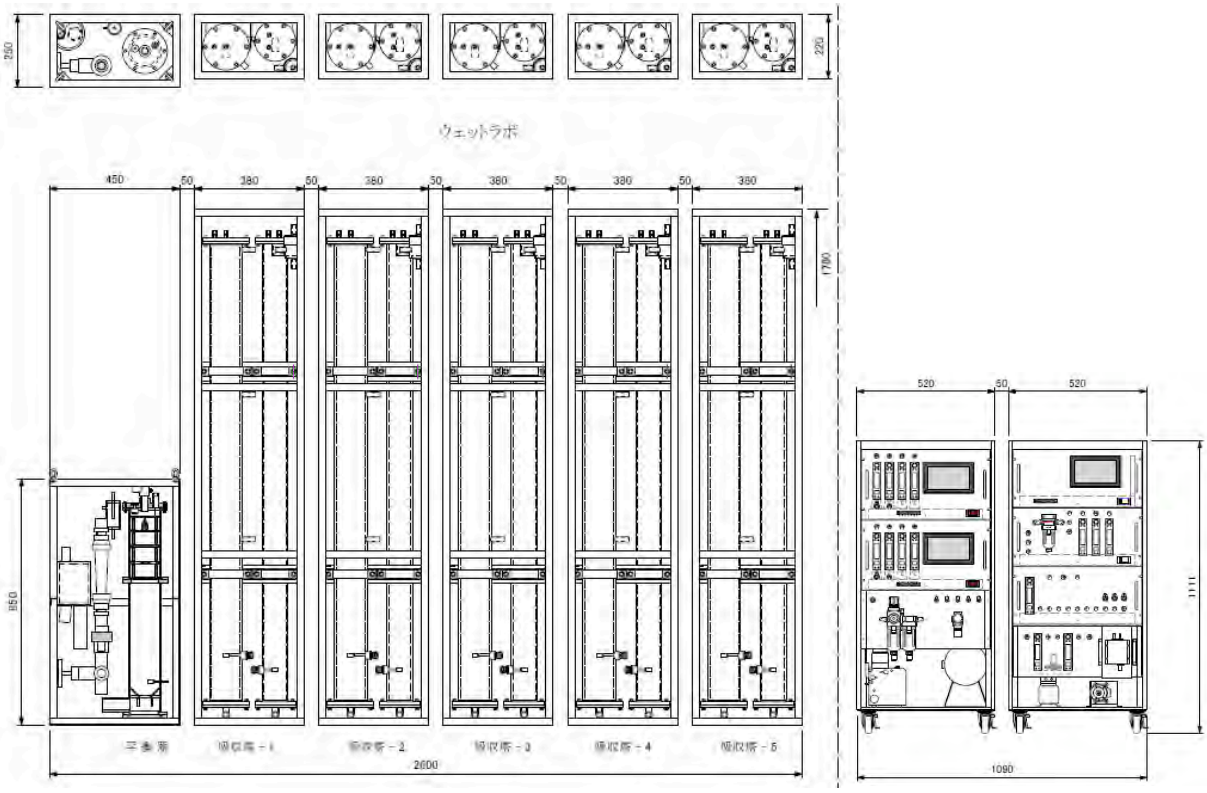

Figure 1: Schematic view of pCO_2 controlled seawater preparation system (AICAL system).

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POSTER 21 **Presenter: John M. Pandolfi**

Response of coral reefs to ocean acidification over multiple temporal scales

John M. Pandolfi

Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, University of Queensland, Australia

The fossil record represents an important archive for understanding the long-term effects of global climate change on Earth's ecosystems. Marine ecosystems, in particular, have an extensive fossil record, heavily biased towards invertebrates that secrete a calcium carbonate exoskeleton. This bias falls favorably in studies attempting to understand the effects of ocean chemistry on the secretion of skeletons, a process commonly referred to as calcification. Calcification has also been studied in long-lived corals living today. Skeletal growth records of long-lived corals are variable across coral species on the Great Barrier Reef.

The effects of ocean acidification in the geological history of the earth's tropical biota can be viewed at a number of scales with varying degrees of resolution, from the mass extinction events occurring over the past hundreds of millions of years to the latest records of coral calcification in living coral colonies. There have been five exceptionally rapid and devastating extinctions during the past 500 my or so of earth history and these are generally referred to as the 'Big Five' mass extinctions (Raup & Sepkoski 1982). Moreover, there have been 5 biotic reef crises during this time, but only 3 of the Big 5 mass extinctions qualify as biotic crises for reefs (Kiessling and Simpson, 2010). The four most recent reef crises coincided with OA and rapid global warming, including two of the 'Big 5' Phanerozoic mass extinctions at the end-Permian (251 MA) and end-Triassic (200 MA). However, the role of OA in these crises is not clear, as they co-occur with significant temperature changes. Moreover, the geological record contains additional episodes of likely OA with which there were no associated reef biotic crises. On balance, the deep time record of reef perturbations shows that OA played a significant role in ecological decline, and the combination of rapid warming and acidification appears to be a major cause of reef crises in the geological past.

One of the major, as well as the most recent, reef crisis events in which OA has been implicated as a primary cause of biotic decline is the Paleocene-Eocene Thermal Maximum or PETM event (55.8 Ma). While far from a perfect analogue for modern increases in CO_2 (Kump et al., 2009), the PETM was characterized by rapid SST rise and a similar order of magnitude of CO_2 increase as present, probably consisting of CO_2 release in multiple pulses over 1–10 ky time scale. During this time there was a marked shift from coral-algal reefs to reefs dominated by large benthic foraminifera, a state that persisted into the early Eocene (Scheibner and Speijer, 2008).

A number of recent studies show declines in coral growth rates associated with recent climate change. However, these changes are generally ascribed more easily to SST anomalies than changes in aragonite saturation state (Ω_{arag}) (De'ath et al,. 2009; Cantin et al., 2010). We gathered data on linear extension rates from a ~900-year composite record of coral growth from multiple colonies of a dominant genus of reef coral (*Goniopora*) from sediment cores derived from two inshore reefs (Pandora and Havannah) of the central Great Barrier Reef. Linear extension rates decreased by 38% over a 900-year interval, with most of the decline occurring after 1580 (Figure 1A). The decline in linear extension predated European settlement in the region, and is strongly predicted by sea surface temperature and river discharge. Surprisingly, *Goniopora* growth rates *increased* by 28% from 1980–2005, during increasing intensity of anthropogenic influence on the adjacent Burdekin River catchment during this time (Figure 1A). This increase in extension rate contrasts markedly with previous studies of linear extension in *Porites* spp. (Figure 1B) from 69 reefs of the Great Barrier Reef (De'ath et al., 2009). In *Porites*, linear extension *decreased* by 13.3% since 1990. Thus, different responses to global warming and ocean acidification characterize linear extension rates in large massive corals from the Great Barrier Reef.

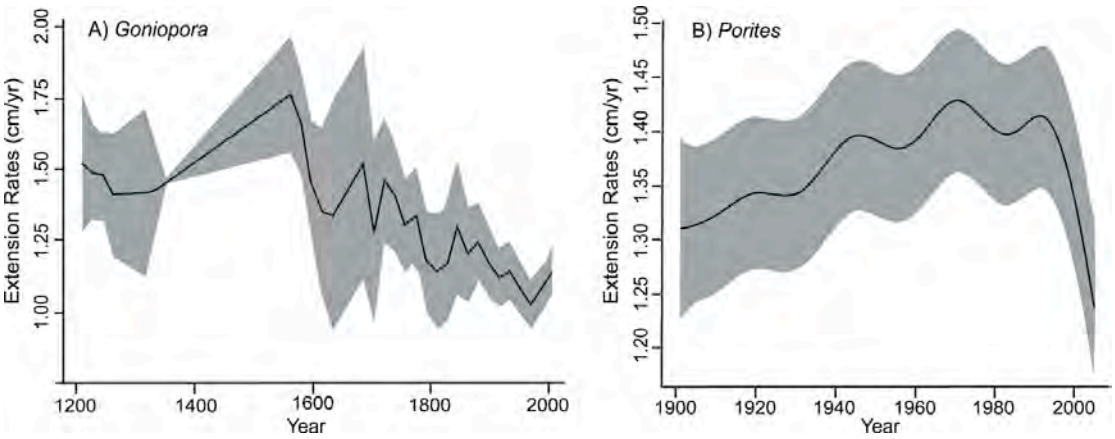

Figure 1: Contradictory patterns of linear extension rates between A) *Goniopora* corals from the Palm Islands, Great Barrier Reef, Australia (Pandolfi, unpublished data) and B) *Porites* corals from 69 sites from the Great Barrier Reef, Australia (De'ath et al., 2009). Shaded areas are 95% confidence intervals. Note scale differences for both *x*- and *y*-axes.

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POSTER 22 **Presenter: Alexander Polonsky**

Has been observing the acidification of the Black Sea waters in XX century?

Alexander Polonsky

Marine Hydrophysical Institute, Ukraine

The goal of presentation is to assess the rate of acidification (if it does exist) of the Black Sea waters in XX century using historical data since 1924. It is shown that acidification has been observed between 1980 and 2000 in spite of high level of the noise and intense interannual variability. The rate of acidification for the last decade of XX century exceeded 0.2 pH units per decade in the upper sea layer. Note at the same time that such high level of the acidification of the Black Sea upper layers is mostly due not to the rise of carbon dioxide concentration in the atmosphere but to intensification of the upward motion in the subsurface layer of the Black Sea because of increasing of $circ_z\boldsymbol{\tau}$ in that time (Polonsky and Shokurova, 2009). In fact, this leads to pH decreasing in the upper layers because pH is decreasing to the depth (Figure 3).

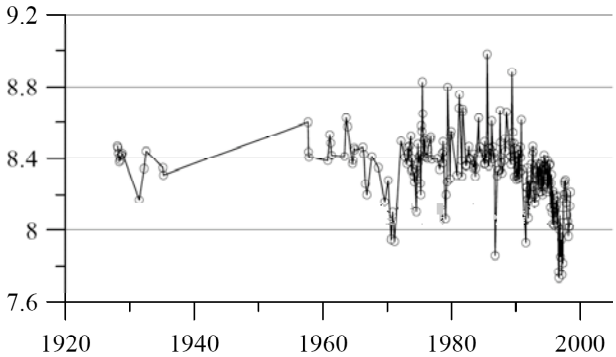

Figure 1: Time series of monthly pH at the surface.

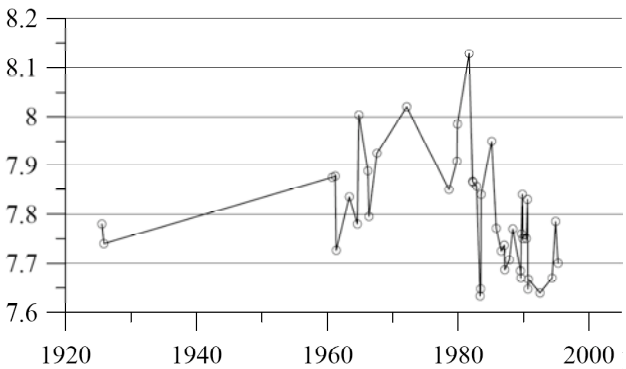

Figure 2: The same as in Figure 1 but for 1000 m.

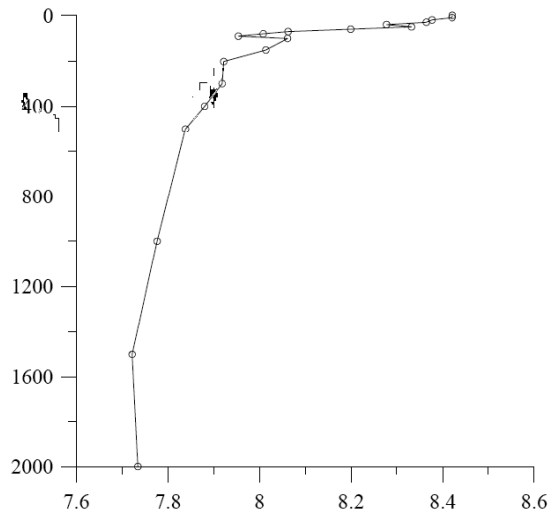

Figure 3: Vertical profile of the average pH in the Black sea.

POSTER 23 **Presenter: H.O. Pörtner**

Unifying principles in ocean acidification effects on marine ectotherms?

F.C. Mark, A. Stark, K. Walther, A. Strobel, A. Hüning, C.E. Schaum, C. Kreiss, L. Harms, M. Lucassen, C. Held, D. Storch, and H.O. Pörtner

Integrative Ecophysiology, Alfred Wegener Institute for Polar and Marine Research, Germany

The apparently specific effects of ocean warming and acidification on the physiology of individual species of marine ectotherms may be based on some "common denominators", i.e., physiological responses that can be assumed to reflect unifying principles, common to all marine animal phyla. To contribute to an accurate understanding of ongoing ecosystem change as well as to a mechanism-based projection of future scenarios, efforts thus have to reach beyond studies of the species specific physiological response, for example to temperature or CO_2 or extreme hypoxia. Also, while comparative physiology has traditionally looked at each factor in isolation, studying the interaction of factors is required for the development of realistic scenarios. For a cause and effect understanding and the prediction of ecosystem-level effects, unifying physiological concepts thus need to be identified, which integrate all relevant factors into the picture. We are in the process of addressing processes relevant for physiological performance on various levels, from transcriptome analysis to patterns of acid-base regulation and whole animal thermal tolerance windows in bivalves (temperate *Mytilus edulis,* Arctic *Serripes groenlandicus*), crustaceans (temperate and Arctic *Hyas araneus*) and fish (temperate and Arctic *Gadus morhua,* Antarctic *Notothenia rossii*).

The first line of defense in aquatic organisms to counter hypercapnia-induced disturbances of the extracellular acid-base status is situated in the gills, the prime organ of interchange between the outside medium and the body fluids. Upregulation of genes related to ion transport in the gills (as found in fish, crustaceans and bivalves) are often the first step in a cascade of mechanisms improving compensation of the extracellular acid-base status, the degree of which is dependent on a particular species' regulatory capacity to compensate for the passive flux of ions. Marine fishes can fully compensate for the acidosis by increasing extracellular bicarbonate levels, while some bivalves only display passive shifts in acid-base status along the non-bicarbonate buffer lines. However, even if the extracellular acidosis is fully compensated for as in higher vertebrates, chronic exposure to elevated PCO_2 may cause unfavourable shifts in energy budget and beyond that, hamper cellular and mitochondrial metabolism, reflected in lower efficiencies of mitochondrial coupling, especially during warming, as observed in the example of Antarctic fish. These findings directly connect to an earlier onset of cardio-vascular energy limitation and failure under elevated temperatures, causing a narrowing of whole animal thermal tolerance windows by exacerbation of the heat or cold induced oxygen and capacity limitation of thermal tolerance (OCLT). In the spider crab *Hyas araneus*, such narrowing of the thermal window was found under moderate increases in CO_2 levels. Furthermore, the decrease in efficiency in energy production under enhanced CO_2 levels may contribute to the extended duration of larval development observed in the spider crab, associated with reduced larval growth and fitness, much more so in cold adapted Arctic larvae than in those from temperate populations. The higher sensitivity of megalopae larvae to temperature and hypercapnia than those of later and adult life stages suggests that the megalopa stage is one physiologically sensitive bottleneck within the life cycle of *H. araneus*.

Available evidence suggests that the OCLT concept provides access to the physiological mechanisms closely defining the sensitivity and response of individuals to climate change at ecosystem level. Using this concept as a matrix allows to link the various mechanistic insights discussed herein and to integrate the effects of various stressors. In providing causality and in quantifying levels and changes of performance and resistance, these approaches and results provide a link between physiology and ecology and support an understanding of ecosystem-level processes as needed to achieve more realistic estimates of species and ecosystem sensitivities to environmental change.

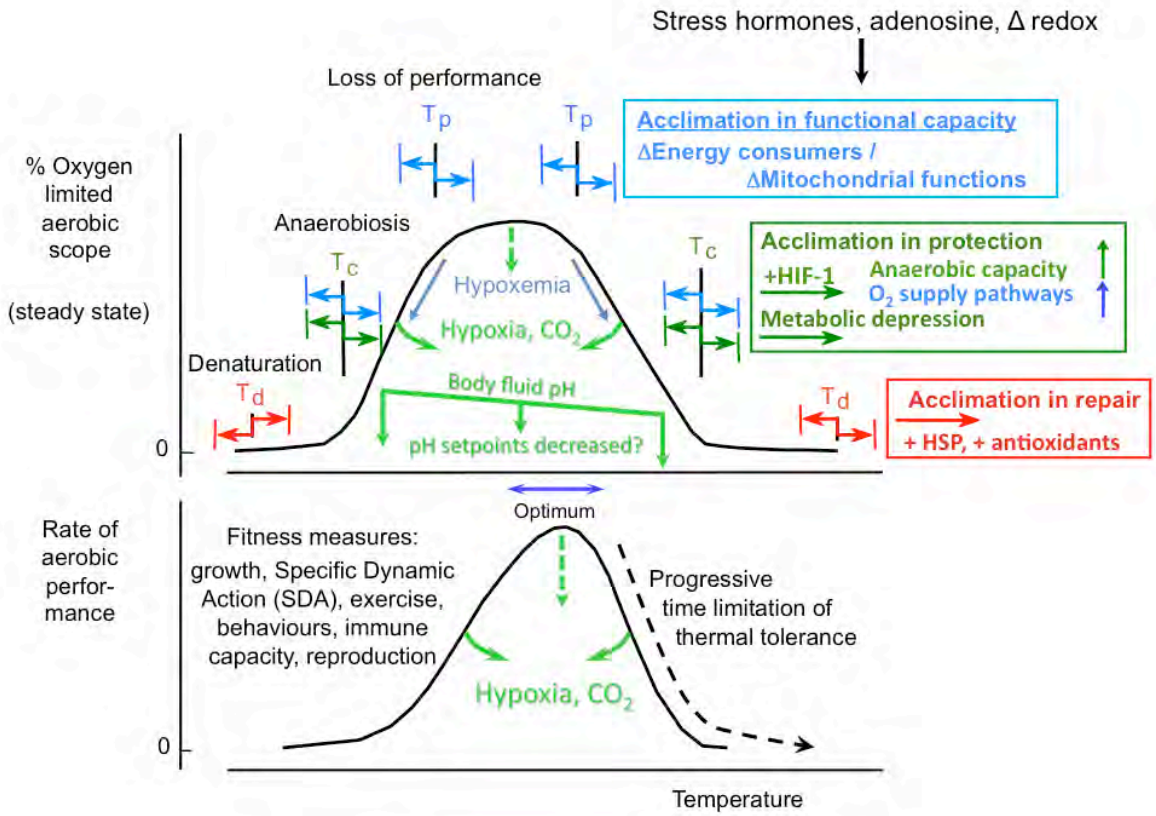

Figure 1: Conceptual model integrating the effects of ocean acidification, warming and hypoxia on marine animals, using the model of oxygen- and capacity-limited thermal tolerance (OCLT) as a matrix. The resulting acute thermal window of performance of a species, of one of its lifestages or its population shifts within the low and high limits of thermal acclimatization (vertical lines), thereby delineating the thermal niche of a species, seen in long-term processes like growth and development and their response to change. Through specific mechanisms affecting performance, CO_2 accumulation or ambient hypoxia cause a narrowing of thermal windows and, possibly, lower performance optima through lower functional capacities and/or reduced systemic oxygen tensions (green arrows). Effects may be mediated through acidotic shifts in acid-base status and in defended setpoints of pH (green arrows).

POSTER 24 **Presenter: C.L. Sabine**

Robust prediction of pH and carbonate mineral saturation state in the North Pacific Ocean using empirical relationships with hydrographic data

L.W. Juranek[1,2], R.A. Feely[2], S.R. Alin[2], and C.L. Sabine[2]

[1]*Joint Institute for the Study of the Atmosphere and Ocean, USA*
[2] *NOAA Pacific Marine Environmental Laboratory, USA*

The subarctic North Pacific has recently attracted attention as a region particularly sensitive to ocean acidification, warranting ongoing observing and monitoring efforts. Here, cold surface waters drive an enhanced solubility pump which aids surface ocean uptake of anthropogenic CO_2, while intermediate-depth waters bearing the signature of the biological pump (CO_2-rich, O_2-poor) accumulated over basin-transit timescales penetrate upwards to depths of 200–300 m. Thus, the surface pelagic community is subject to acidification from above and below, arising from both natural and anthropogenic causes. Unfortunately, detailed time-series of water-column carbon measurements are not available for this region, hindering efforts to understand scales of natural variability and vulnerability to future change. In order to parlay available carbon data toward this end, we developed empirical relationships between commonly available hydrographic parameters (i.e., temperature, O_2) and pH, aragonite saturation state (Ω_{arag}), and calcite saturation state (Ω_{calc}) using high-quality data from two recent cruises along 152ºW: CLIVAR P16N (March, 2006) and STUD08 (September, 2008). For the subarctic region (40ºN –55ºN), R^2 values of >0.98 and root mean square errors of 0.016 (pH), 0.049 (Ω_{arag}), and 0.078 (Ω_{calc}) were attained for data between 50–500 m, with O_2 explaining the majority (>95%) of the variability. Comparable statistics are achieved for subtropical data, although temperature plays an increasingly prominent role in explaining observed variability compared to the subarctic region. Although the errors of this approach prohibit it from being used to resolve secular trends in carbon system parameters, the relationships will provide insight into seasonal controls on pH, (Ω_{arag}), and (Ω_{calc}), and could be used to predict these variables from autonomous platforms.

POSTER 25 **Presenter: Kazuhiko Sakai**

Effects of CO_2-driven acidified seawater on early life stages of scleractinian reef corals (Genus *Acropora*)

Kazuhiko Sakai

Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, Japan

Ocean acidification and global warming, which would be caused by increased atmospheric carbon dioxide (CO_2) through human activities, are important environmental problems at present. It is reported that acidified seawater may reduce the calcification rates of marine calcifiers including reef corals. However, few studies have concerned about the effects of increased CO_2 on coral early life stages which are expected to be vulnerable to environmental stresses. In this study, AICAL (Acidification Impact on CALcifiers) research group at Sesoko Station, Univ. Ryukyus, evaluated the effects of increased CO_2 on early life stages of corals (*Acropora* spp.) by focusing on the following main early life stages: (1) fertilization and embryogenesis, (2) planula, (3) primary polyps and symbiosis establishment by using several acidified seawater conditions (pH 8.0–6.6).

Our results showed that the progress of embryogenesis and larval survival rate were not significantly different among pH conditions. By contrast, fertilization rate at pH 6.6, and polyp growth and algal infection at pH 7.6 were significantly decreased from the values of control condition. In particular, sperm flagellar motility was most vulnerable to acidified seawater. These results suggest that ocean acidification caused by increasing CO_2 would have negative impacts on not only calcification but also early life stages of corals. As a next step, using precise CO_2 control system which was set up in Sesoko station, we will re-evaluate the effects of increased CO_2 on several coral life stages which were found to be vulnerable to acidified seawater in our experiments above, and clarify the effects of near-future ocean acidification on coral survival.

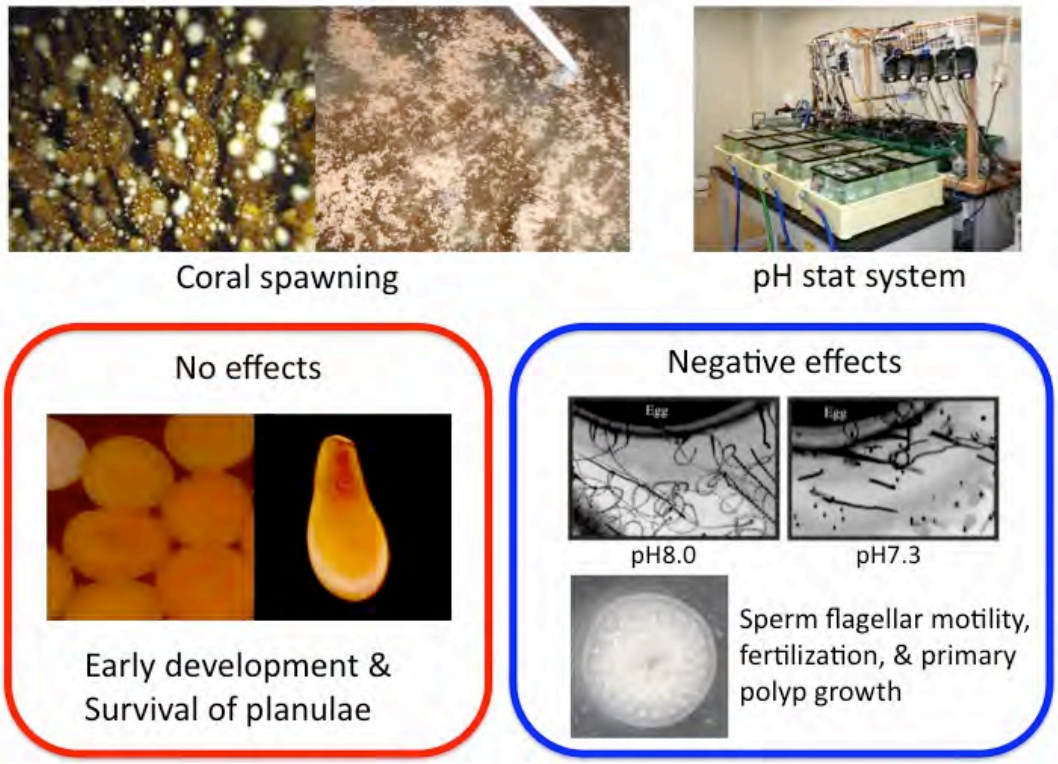

Figure 1

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POSTER 26 **Presenter: Daniela N. Schmidt**

The Palaeocene-Eocene Thermal Maximum (PETM): ocean acidification in the geological record

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The Palaeocene-Eocene Thermal Maximum (PETM) provides possibly the closest geological analogue for understanding ocean acidification impacts, as it was a period of rapid global warming (5–9°C) (Sluijs et al., 2007) ~55.5 Ma and associated with a pronounced negative $\delta^{13}C$ excursion (Carbon Isotope Excursion, CIE) of >3.0% (McCarren et al., 2008), indicating a massive input of isotopically light carbon and hence greenhouse gases into the atmosphere. The input of carbon mass is estimated to be ~3000–7000 PgC in Panchuk et al. (2008) and Zeebe et al. (2009) and is hence comparable to estimates of current fossil fuel reserves. The rate of carbon input is likely to have been sufficiently fast (<<10 kyr) to drive future-relevant changes in ocean chemistry, characterized by a coupled decline in both pH and carbonate saturation and indeed, a pronounced shoaling of the carbonate compensation depth (Zachos et al., 2005) is observed during the PETM. The reduction of saturation is important because it may increase the metabolic demand on organisms as the energy required to calcify under lower saturation states may increase. In contrast, slow (>>10 kyr) greenhouse gas releases enable weathering to approximately balance carbonate burial keeping ocean carbonate saturation (Ω) well regulated.

Laboratory experiments aim to replicate future carbon levels, but such experiments are typically brief (often on the order of days), with limited number of generations and organisms studied, and hence provide restricted information on the adaptation potential of marine biota. The geological record can help by providing information about responses to environmental change taking place on much longer time-scale than is possible in the laboratory. While the rate of carbon release during the PETM may have been an order of magnitude slower than modern-day anthropogenic carbon input (Ridgwell and Schmidt, 2010; Zeebe et al., 2009), its associated environmental changes led to a significant perturbation of deep sea benthic habitats (Thomas, 2007). The interest in the geological record is hence in potentially allowing a minimum threshold of response of organisms and ecosystems to the consequences of carbon release to be identified. We present data from sites from around the world: deep sea Sites on Maud Rise (ODP 690 Southern Ocean), Walvis Ridge (ODP 1262 and 1263 South East Atlantic) and shelf site Bass River (New Jersey, USA) to give a current overview on the state of understanding the PETM and the biological response to the carbon perturbation.

Foraminiferal tests are a key component of marine carbonate and their boron isotope composition is a widely used proxy to reconstruct oceanic pH and hence past atmospheric CO_2 concentrations. Measurements of boron isotopes ($\delta^{11}B$) in the shallow infaunal benthic foraminifer *Oridorsalis umbonatus* indicate significant ocean acidification in the deep sea and on the shelf. Reconstructions of bottom water temperature using Mg/Ca ratios of the same benthic foraminifer show an increase in temperature of >4°C at Walvis Ridge, consistent with Maud Rise and Bass River (neritic,New Jersey, 100-140 m).

During the PETM, benthic foraminiferal species extinction was on the order of 35–50% (Thomas, 2007), and combined with significant changes in the faunal composition. Synchrotron Radiation X-ray tomographic microscopy of *O. umbonatus* shows that this species increased its wall thickness during the PETM and hence a potential increased calcification. This is counterintuitive and in stark contrast to the few studies of planktic foraminiferal calcification response in cultures (Bijma et al., 1999) and sediment traps (de Moel et al., 2009; Moy et al., 2009). Such changes would require

energy to be reallocated to calcification at this low saturation state and hence reallocation of metabolic costs. Additionally, synchrotron data suggest changes in life strategy in these benthic foraminifers.

In contrast, the calcifying surface dwellers during the PETM did not suffer significant extinction (Gibbs et al., 2006; Kelly, 2002; Raffi et al., 2009). While there was significant evolutionary turnover, and changes in the composition of the fauna and flora, there is no indicating of selective extinction at higher than background extinction rates, although there was evolution of several short-lived species. Coastal ecosystems record a marked community change as coralgal reefs disappeared and were replaced by banks of larger foraminifera as a response to warming, eutrophication or acidification or some combination of these factors (Scheibner and Speijer, 2008). In contrast, the open ocean atoll community of corals, bivalves and gastropods at Limalok Guyot in the Pacific does not show any significant changes in composition or any indication of reduced growth of the atoll (Robinson, 2011) suggesting a difference in response between open ocean and coastal ecosystems.

To provide spatial estimates of environmental changes, an Earth system model of intermediate complexity ('GENIE') was used to make projections of the PETM rates of change in the surface and deep ocean and compare to expected future changes (Ridgwell and Schmidt, 2010) (see Figure 1), hence providing context for ecological and evolutionary changes. The model predicts first, that the future oceans will likely experience a higher degree of undersaturation in the deep ocean than during the PETM and second, that future rates of environmental change at the surface will be significantly higher than during the PETM, thereby posing a potential risk for marine calcifying plankton (Ridgwell and Schmidt, 2010).

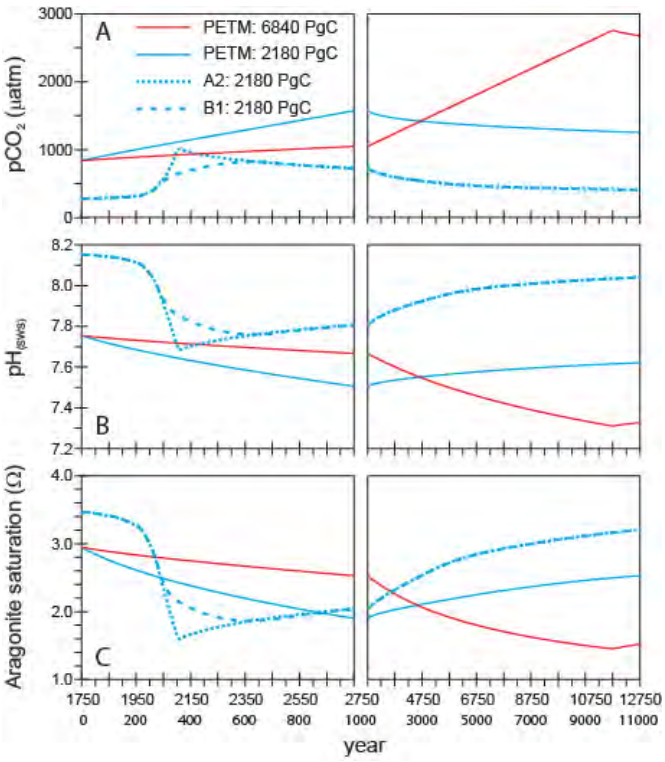

Figure 1: The predicted evolution of global average surface ocean environmental conditions to massive CO_2 release are shown for future (dashed line) and PETM (solid line) configurations of GENIE (Ridgwell and Schmidt, 2010). CO_2 releases of 6840 PgC (red) and 2180 PgC (blue) and different time scales of release (1 kyr and 10 kyr) are tested for the PETM. For the future, 2180 PgC total fossil fuel CO_2 are released but with two different scenarios for possible future socio-economic development, hence energy usage and fossil fuel dependence based on the IPCC Special Report on Emissions Scenarios (IPCC, 2000).

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POSTER 27 **Presenter: Brad A. Seibel**

Animal performance in a changing ocean: synergistic effects of climate-related variables

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Unlike air-breathing animals, aquatic organisms generally maintain extracellular CO_2-concentrations in equilibrium with the respired medium. Thus, as seawater PCO_2 increases, the PCO_2 of extra-, and to a lesser extent, intracellular fluids in animals increases. High internal PCO_2 may affect numerous processes, but a common response is the suppression of total energy consumption (i.e., metabolic suppression). The extent to which elevated PCO_2 affects animal physiology depends, in part, on their capacity to buffer pH changes, transport proton-equivalent ions out of the cell and on the pH-sensitivity of oxygen transport systems (Seibel and Fabry, 2003; Seibel and Walsh, 2001). Most species studied to date show no detectable effect on metabolism of the increases in CO_2 expected under climate-change scenarios. However, CO_2 is not changing in isolation and animal metabolism is strongly dependent on a variety of environmental variables and on the animal's own nutritional state. Climate change alters temperature and oxygen levels as well as CO_2 and may influence feeding dynamics via effects on primary productivity and ecological interactions with less tolerant species. Here I present two examples of important metabolic effects of ocean acidification, detectable only under specific experimental conditions. Importantly, these conditions do occur in nature but are rarely mimicked in the lab.

The jumbo squid, *Dosidicus gigas*, is a large, extremely active oceanic predator. Its oxygen demand is higher than any other animal's at a common temperature and body size (Seibel, 2007). The oxygen transport system is working at capacity to meet this demand. A highly pH-sensitive respiratory protein facilitates off-loading of oxygen at the sites of demand where respiratory CO_2 production reduces local pH (Seibel, 2011). However, at the gills, high pH-sensitivity of oxygen binding reduces oxygen uptake under ocean acidification scenarios. The effect is subtle, reducing the oxygen saturation of the blood by only a few percent. However, squids are known to use almost all of the oxygen carried in the blood on each pass through the body (Pörtner, et al., 2011). This is especially true under conditions that maximize oxygen demand (high temperature or activity levels). Thus, as surface waters warm and become more acidic, the oxygen demand of the squid will increase and the capacity to transport oxygen will be reduced. Under acute experimental conditions the squid's metabolic rate and scope for activity was significantly reduced at high temperature and 1000 ppmv CO_2 (Rosa and Seibel, 2008). Metabolic suppression is an evolved response to low oxygen in this species that facilitates daytime forays into the oxygen minimum zone (OMZ; Rosa and Seibel, 2010). The squid's must return to shallower waters at night to burn off an accumulated oxygen debt. The OMZ is expanding, raising the floor below which the squid's cannot dive without metabolic consequences. High CO_2 exacerbates this phenomenon. Simultaneously, global warming and ocean acidification are lowering the ceiling above which they cannot rise without impaired oxygen transport. Thus the habitable night-time depth range of the squids is compressed in a future ocean.

Recent evidence suggests that energy limitation also plays a large role in the response of animals to elevated CO_2 and that enhanced nutrition can ameliorate the effects in some cases (Cohen and Holcomb, 2009). The shelled pteropod, *Limacina helicina,* is an ecologically important grazer, widely viewed as an indicator of ecosystem health in polar oceans (e.g., Seibel and Dierssen, 2003). We examined the metabolic rate of *L. helicina antarctica*, over 6 seasons, and determined the effect of feeding history, body size, temperature and carbon dioxide. In seasons with low regional productivity, metabolism was suppressed and CO_2 had no further effect. However, during seasons with elevated productivity, metabolism was high but strongly and negatively (~30%) impacted by elevated CO_2 (~600 ppm) relative to controls (~300 ppm). The CO_2-induced metabolic suppression is equivalent to that caused food deprivation, which has been linked to delayed spawning (Bernard and Froneman, 2009) and local extinction (Seibel and Dierssen, 2003). Thus, food deprivation and CO_2

act independently, not additively, to limit metabolism with likely fitness consequences for the species and its predators. Without the context provided by our long-term observations, the effects of ocean acidification would have been overlooked or confounded by feeding effects. The reported inconsistency in the short-term response of marine organisms to CO_2 alone is, thus, not surprising (Hendriks et al., 2010). We emphasize the need for long-term physiological monitoring and the inclusion of multiple stressors into analyses for accurate assessment of the impacts of ocean acidification (Seibel et al., in preparation).

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POSTER 28 **Presenter: Yoshihisa Shirayama**

Effects of low pCO_2 conditions on sea urchin larvae

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Ocean acidification, which is caused by increased atmospheric carbon dioxide (CO_2) concentrations, is predicted to occur in the future. Atmospheric pCO_2 level (ca. 400 ppm) will be doubled by 2100 (IPCC, 2007) and has already increased from that in the pre-industrial era (280 ppm; IPCC, 2001). Many studies have examined the impact of increased pCO_2 levels on marine organisms and have warned its impact on the marine ecological services. Sea urchins play an important ecological role as grazers of marine algae in the coastal zones, and their larval size is reduced under increased pCO_2 conditions (Kurihara and Shirayama, 2004). However, the effect of the low pCO_2 conditions on sea urchins, which is predicted to occur earlier than year 2100, remains largely unexamined. In the present study, the effects of low-level pCO_2 conditions on sea urchin larval morphology were examined using a high-accuracy pCO_2 control system. In this system, optimal levels of pCO_2 gas were generated by blending pure CO_2 gas with CO_2-reduced air (pCO_2: <200 ppm) in the pCO_2-regulation system (CGM-07 and DGG-07, Kimoto Electric, Japan). The regulated pCO_2 gas of 5.5 L/min was bubbled from the bottom of a plastic tower (WAT-07, Kimoto Electron, Japan) for CO_2 dissolution. Seawater was continuously pumped from the sea in front of the Seto Marine Biological Laboratory, Kyoto University. The pCO_2 of the seawater in the tower was equilibrated with the pCO_2 of the bubbled gas, and then the pCO_2-regulated seawater at 300 ml/min was pumped from the tower into 4 replicate exposure chambers during each experimental condition. The levels of pCO_2 were monitored every hour by using the pCO_2 monitoring system (CO_2-07, Kimoto Electric, Japan) with a non-dispersive infrared analyzer (LI-840, LI-COR, NE) just before seawater was pumped into the chambers. In Experiment 1, fertilized eggs of the sea urchin *Hemicentrotus pulcherrimus* were exposed to 230 ppm and 400 ppm (control) of pCO_2 for 3 days after fertilization. In Experiment 2, the sea urchin *Anthocidaris crassispina* was exposed to 300, 400, 500, and 600 ppm of pCO_2. These pCO_2 conditions simulated the atmospheric pCO_2 levels of the pre-industrial-era and the pCO_2 level predicted to occur in the near future (in the years before 2100). For evaluating the effects of these pCO_2 conditions on the sea urchins, larval sizes such as overall length, postoral arm length, and body length were measured from the photographed images.

The results showed that all the larval sizes of *H. pulcherrimus* showed significant increase at low pCO_2 levels (230 ppm) (Nested-ANOVA, $F_{1, 159} = 38.1$ for overall length, $F_{1, 159} = 13.9$ for postoral-arm length, and $F_{1, 159} = 21.5$ for body length, $p < 0.001$). The results of the experiment 2 showed that the overall length (Figure 1) and the postoral arm length of *A. crassispina* larvae under high pCO_2 conditions (500 and 600 ppm) were significantly shorter than those of *A. crassispina* larvae under low pCO_2 conditions (300 ppm). The body length of *A. crassispina* in the control condition (400 ppm) was significantly shorter than that at high pCO_2 condition (600 ppm) (Nested ANOVA, post hoc Tukey-Kramer HSD test, $p < 0.05$). In the present study, we found that the larval sizes of both species were significantly larger at the pre-industrial levels of pCO_2 than those at the present level or those at the levels predicted in the near future. It is also reported that chemically increased pH of pH_{NBS} 8.2 increased the shell weights of young benthic foraminifera *Marginopora kudakajimensis* (Kuroyanagi et al., 2009). There is a possibility that predicted impacts of ocean acidification on the calcifiers in the future are already appearing in the present.

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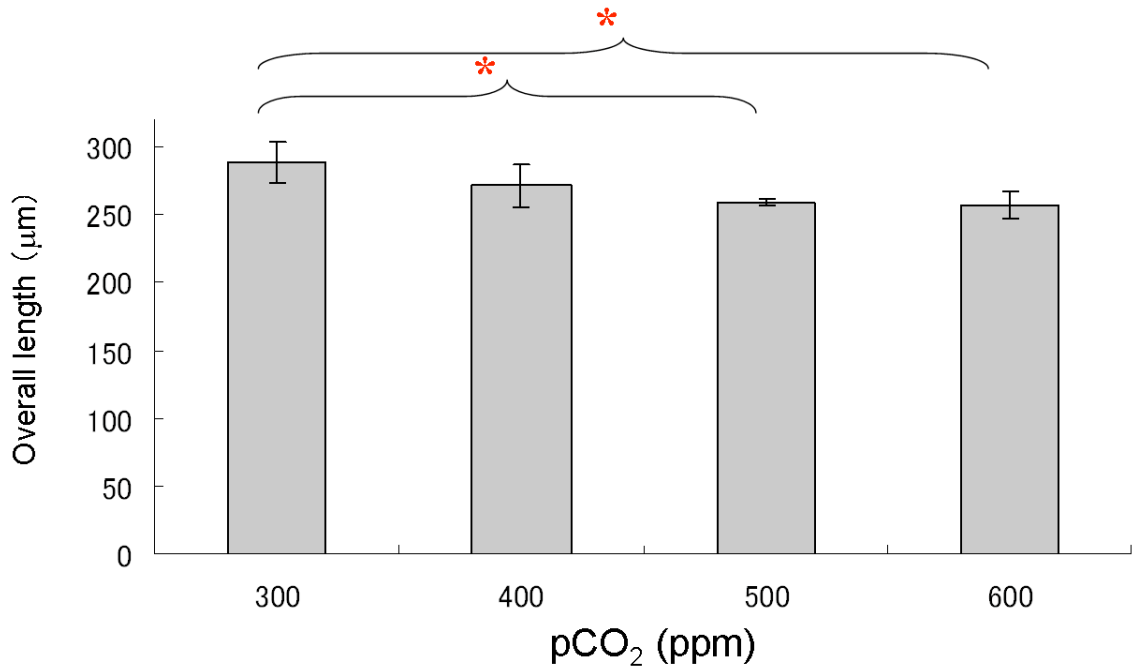

Figure 1: Overall length of *Anthocidaris crassispina* larvae exposed to pCO_2 conditions of 300, 400, 500, and 600 ppm for 3 days after fertilization. Asterisk indicates the statistical significant difference among the 4 different conditions.

POSTER 29 **Presenter: Atsushi Suzuki**

Ocean acidification impact on calcification of algal symbiont-bearing benthic foraminifers

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Ocean acidification has become recognized recently to be a major threat to calcifying organisms. Previous studies have reported that calcification rates of calcareous marine organisms (e.g., corals, coccolithophores, pteropods, mussels, and oysters) change in response to lowering pH levels even in waters oversaturated with respect to calcium carbonate. However, the impact of ocean acidification on large benthic foraminifers, which are major contributors to organic and inorganic carbon production in coral reefs, is still unclear. First, we cultured asexually produced individuals of *Marginopora kudakajimensis* under four different pH conditions prepared by acid addition for about 10 weeks in order to examine the effects of lowering pH on their growth rates (Kuroyanagi et al., 2009). The species secretes a porcelaneous shell and hosts dinoflagellate symbionts, Growth rate, measured by shell diameter, shell weight, and the number of chambers added, generally decreased with lowering pH. Shell weight was most closely dependent upon pH. Second, we conducted culture experiments using a high-precision pCO_2 control system. Asexually produced individuals of the species were subjected to seawater at five pCO_2 levels from approximately 300 to 1000 µatm. Cultured individuals were maintained for about 8 weeks in an indoor flow-through system under constant water temperature, light intensity, and photoperiod. After the experiments, the shell diameter and weight of each cultured specimen were measured. Net calcification tended to decrease at elevated pCO_2. Our findings suggest that ocean acidification might be unfavorable to calcification of the species.

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POSTER 30 **Presenter: Rik Wanninkhof**

Integrated assessment of ocean acidification within coral reef ecosystems

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Ocean acidification (OA) describes the secular global-scale changes in surface ocean carbonate chemistry in response to oceanic uptake of rising concentrations of atmospheric CO_2. Increasing rates of OA in coming decades could alter coral reef communities in a number of ways including changes in carbonate budgets, community structure and function. Most of these concerns have emerged solely from laboratory investigations under simplified carbonate chemistry regimes. Relatively few field studies have been conducted to adequately characterize the spatiotemporal dynamics of carbonate chemistry within reef waters which nor investigated how this variability interacts with the fundamental processes of reef construction and breakdown. The National Oceanic and Atmospheric Administration's (NOAA) Atlantic Oceanographic and Meteorological Laboratory (AOML) is actively engaged in monitoring the progression of OA from regional to local-scales and evaluating the effects on coral reef growth and persistence within select coral reefs of Puerto Rico and the Florida Reef Tract. AOML researchers are utilizing an integrated and holistic approach that includes *in situ* synoptic near-real-time monitoring of reef carbonate chemistry, historical and recent measurements of coral calcification, and investigation of the processes that control the persistence of reef framework structures, such as inorganic cementation, bioerosion, and the community feedbacks to local carbonate chemistry. These studies will help elucidate the potential vulnerability of coral reef ecosystems in a high-CO_2 world by documenting rates of OA, its effects, and the local feedback processes within the real-world.

POSTER 31 **Presenter: Steve Widdicombe**

Studying the impacts of ocean acidification on key benthic ecosystems: A UKOARP funded consortium.

Steve Widdicombe[1] and the UKOARP Benthic Consortium

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In coastal seas, seafloor habitats, and the organisms they contain, play a crucial role in maintaining a healthy and productive marine ecosystem; providing food, economic prosperity and social well-being. Given that these coastal habitats also harbour incredibly high levels of biodiversity, any environmental change that affects these important ecosystems could have substantial environmental and economical impacts. In order to predict the nature and scale of these potential impacts new research is urgently needed. In particular we need long-term studies that determine: which organisms are likely to be tolerant to high CO_2 and which are vulnerable; whether organisms will have time to adapt or acclimatise to this rapid environmental change; and how the interactions between individuals that determine ecosystem structure will be affected. The current lack of understanding is a major problem as ocean acidification is a rapidly evolving management issue and, with an insufficient knowledge base, policy makers and managers are struggling to formulate effective strategies to sustain and protect the marine environment in the face of ocean acidification.

Funded by the United Kingdom Ocean Acidification Research Programme (UKOARP), a consortium of 25 key researchers from 12 UK organisations are aiming to provide the knowledge and understanding so desperately needed (www.benthic-acidification.org). Their overarching aim is to quantify and predict the impact of ocean acidification on biodiversity and ecosystem functioning in three key UK coastal habitats; soft sediments, calcareous biogenic habitats (such as cold water coral reefs and maerl beds) and the rocky intertidal. The consortium has six science objectives:

- Quantify the impact of ocean acidification and warming on the health and activity of key benthic organisms
- Assess the potential for organism adaptation to ocean acidification and warming
- Quantify the impact of ocean acidification and warming on the biogeochemistry of marine benthic habitats
- Quantify the impact of ocean acidification and warming on benthic microbial communities
- Predict the impact of future CO_2 scenarios on the population dynamics of benthic marine organisms
- Predict the impact of future CO_2 scenarios on the biodiversity and functioning of coastal habitats

The approach will be to use laboratory experiments to determine the ways in which ocean acidification will change key physiological processes, organism behaviour, animal interactions, biodiversity and ecosystem functioning. The understanding gained will be used to build and run conceptual, statistical and numerical models which will predict the impact of future ocean pH scenarios on the biodiversity and function of coastal ecosystems. The consortium also hopes to act as a focal point for benthic ocean acidification research in the UK, promoting communication between many different interested parties; UK and international scientists, policy makers, environmental managers, fisherman, conservationists, the media, students and the general public.

POSTER 32 **Presenter: P.O. Zavialov**

Interannual and interdecadal variability of pH in the seas of Russia

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Regional data sets have been assembled at Shirshov Institute of Oceanology, Russian Academy of Sciences (SIO RAS), encompassing the principal chemical indicators for the seas of Russia, more specifically, the Black Sea, the White Sea, the Baltic Sea, and the Caspian Sea. These data sets include the original data obtained in several expeditions of SIO RAS since the 1940s, as well as other historical data. Basing on these records, we analyze the long-term (interannual to multi-decadal) variability of pH and alkalinity in these seas. At most of the locations, the temporal dynamics of pH proved to be complex, involving cyclic variability superimposed on a linear trend. We describe the variability patterns for each of the seas and some of their specific parts.

In addition, we present reconstructions for paleo-variability of pH based on data obtained from sediment and ice cores. The reconstructions made at SIO RAS point on cyclic character of the pH variability in the past.

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