

# Research Priorities for Understanding Ocean Acidification

Summary From the Second Symposium on the Ocean in a High-CO<sub>2</sub> World

BY JAMES C. ORR, KEN CALDEIRA, VICTORIA FABRY, JEAN-PIERRE GATTUSO,  
PETER HAUGAN, PATRICK LEHODEY, SILVIO PANTOJA, HANS-OTTO PÖRTNER,  
ULF RIEBESELL, TOM TRULL, ED URBAN, MARIA HOOD, AND WENDY BROADGATE

**ABSTRACT.** The first symposium on “The Ocean in a High-CO<sub>2</sub> World” in 2004 proved to be a landmark event in our understanding of the seriousness of ocean acidification, as reported in *Oceanography* (Cicerone et al., 2004). The scientific community reunited in 2008 for a second symposium on “The Ocean in a High-CO<sub>2</sub> World.” During the four years between the two symposia, more scientific papers were published on the topic of ocean acidification than during the preceding 55 years. Ocean acidification is now widely cited in the press and is familiar to many nonscientists. Participants at the 2008 symposium identified new research priorities and stressed the importance of improving international coordination to facilitate agreements on protocols, methods, and data reporting in order to optimize limited resources by greater sharing of materials, facilities, expertise, and data. Despite major uncertainties, the research community must find ways to scale up understanding of individual organisms’ responses to provide meaningful predictions of ocean acidification’s effects on food webs, fisheries, marine ecosystems, coastal erosion, and tourism. Easy-to-understand information, such as simple indicators of change and of thresholds beyond which marine ecosystems will not recover, is also needed for management and policymaking.

## INTRODUCTION

Fossil-fuel combustion releases carbon dioxide (CO<sub>2</sub>) to the atmosphere, leading to a warmer climate. But, increasing

atmospheric CO<sub>2</sub> is also changing the ocean’s chemistry, as one-fourth of the human-generated CO<sub>2</sub> is currently absorbed by the ocean. When CO<sub>2</sub>

dissolves in seawater, it forms carbonic acid, decreasing both ocean pH and the concentration of the carbonate ion, the basic building block of the shells and skeletons of many marine organisms. The following sections present scientific highlights from the second symposium on “The Ocean in a High-CO<sub>2</sub> World” and the recommendations from discussion groups that met at the symposium.

## SCIENCE SUMMARY

### Anthropogenic Ocean Acidification Is Rapid in the Context of Past Natural Changes

Surface ocean pH has dropped by 0.1 units since the beginning of the Industrial Revolution, equivalent to a 30% increase in hydrogen ion concentration (referred to here as acidity). Marine organisms have not experienced this acidification rate for at least many

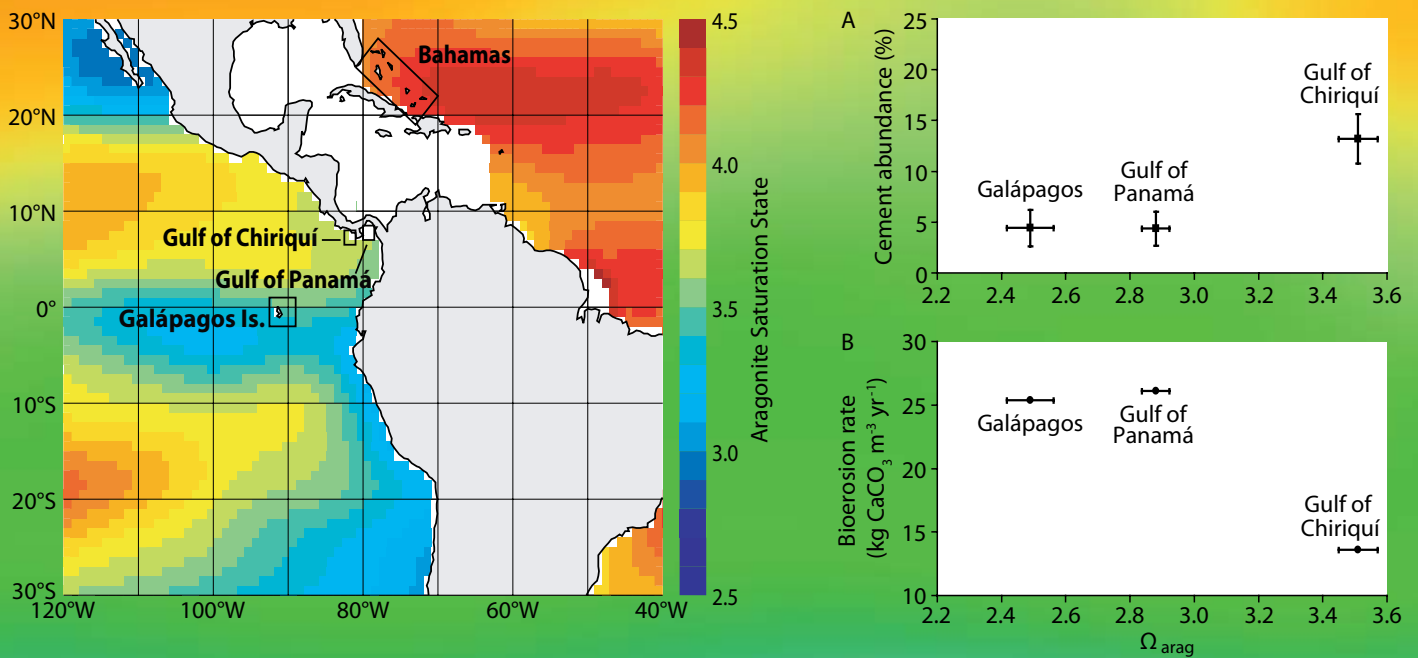


Figure 1. (Left) Map showing depressed aragonite saturation state across the eastern tropical Pacific Ocean in comparison to highly supersaturated waters that influence Caribbean reef sites. (Right) Aragonite saturation state for eastern tropical Pacific sites plotted against cement abundance (A) and bioerosion (B). From Manzello et al. (2008). ©2008 National Academy of Sciences, United States of America

millions of years. Previous natural acidification events may have been associated with the five major coral mass extinction events that are known to have occurred during Earth's history (Veron, 2008). The general characteristics of future chemical changes that will occur in the ocean as a result of increasing atmospheric CO<sub>2</sub> are highly predictable. Across the range of scenarios used by the Intergovernmental Panel on Climate Change (IPCC), surface ocean pH is projected to decrease by  $0.4 \pm 0.1$  pH units by 2100 relative to pre-industrial conditions (Meehl et al., 2007). Today's "acidification event" differs from past events because it is human-induced and is occurring much more rapidly. If ocean acidification continues to worsen to the end of this century, as projected, thousands of years may be required for the Earth system to reestablish even roughly similar ocean

chemistry (Montenegro et al., 2007; Tyrrell et al., 2007); hundreds of thousands to millions of years will be needed for coral reefs to be reestablished, based on past records of natural coral-reef extinction events (Veron, 2008).

### Ocean Acidification Is Already Detectable

Time-series records of ocean carbon chemistry over the past 25 years show clear trends of increasing ocean carbon and decreasing pH in lockstep with increasing atmospheric CO<sub>2</sub> (Bates, 2007; Dore et al., 2009). Over the past two decades, there have been measurable decreases in the calcium carbonate (CaCO<sub>3</sub>) shell weights of Southern Ocean pteropods (Roberts et al., 2008) and foraminifera (Moy et al., 2009), and corals on the Great Barrier Reef have shown a recent decline in calcification

(Cooper et al., 2008). However, more studies are needed to confirm whether these effects are due solely to ocean acidification.

### Severe Biological Impacts May Occur Within Decades

Projections of the saturation levels of aragonite (a metastable form of calcium carbonate used by many marine organisms) indicate that calcification rates in warm-water corals may decrease by 30% over the next century (Gattuso et al., 1998; Langdon and Atkinson, 2005). Areas with already-low aragonite saturation states show less-abundant inorganic cement deposits and higher bioerosion than do regions with higher aragonite saturation levels (Manzello et al., 2008; Figure 1); similar impacts may become more widespread as ocean acidification continues. By 2100, it is projected under

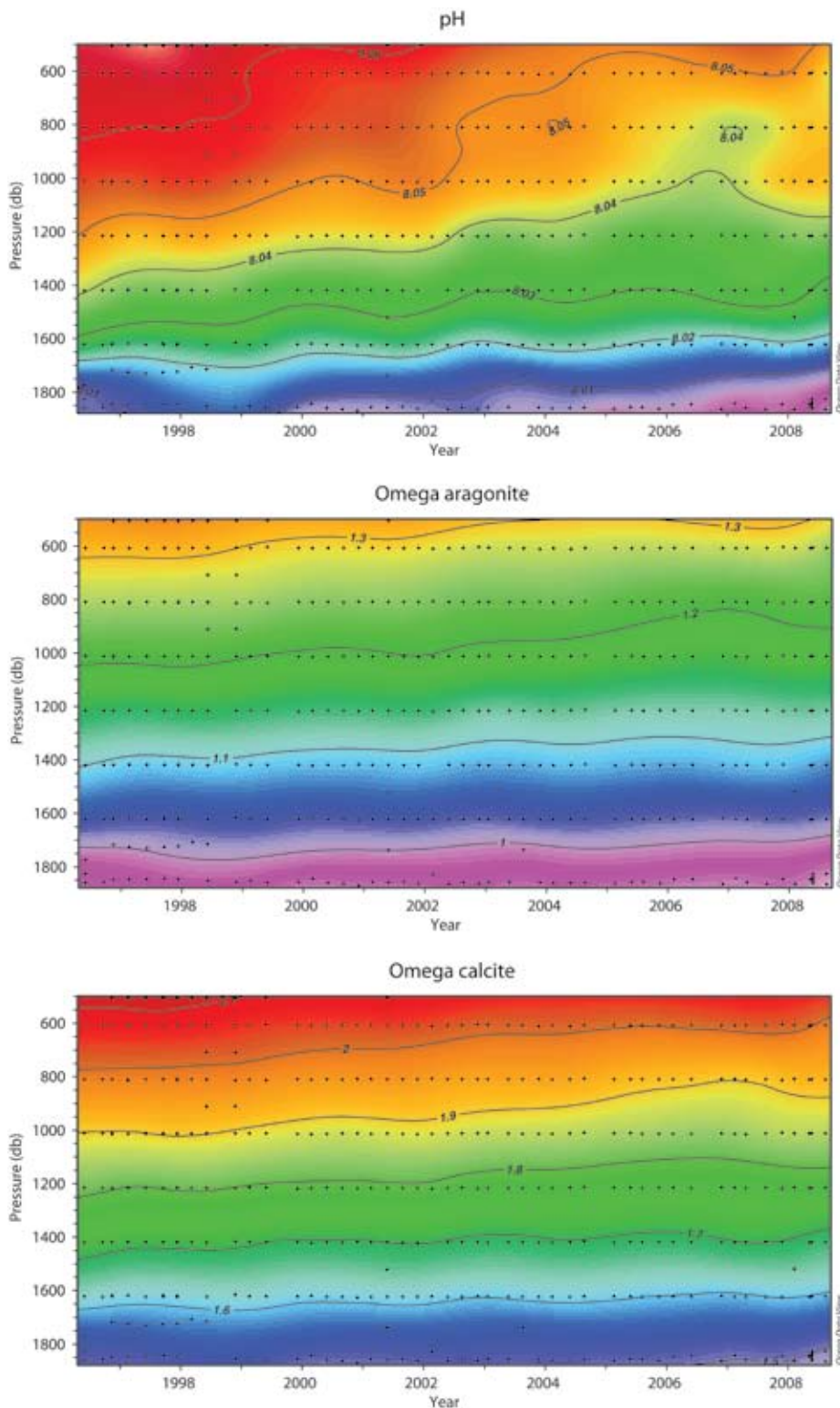


Figure 2. Time series of pH, aragonite saturation state, and calcite saturation state in the Iceland Sea between 500 and 1850 m during 1994–2008. From Olafsson et al. (2009).

the IPCC IS92a scenario that about 70% of cold-water corals will be exposed to waters that are undersaturated with respect to aragonite (Guinotte et al., 2006), and a field study has begun to evaluate the extent to which these conditions would be chemically corrosive to their skeletal material (Maier et al., 2009). Some ocean areas (coastal waters in the Northeast Pacific Ocean and north of Iceland) have already become undersaturated with respect to aragonite during some or all of the year (Feely et al., 2008; Olafsson et al., 2009; Figure 2). A transition to such corrosive conditions is projected to occur within decades in surface waters over much of the polar oceans (Orr et al., 2005; McNeil and Matear, 2008; Steinacher et al., 2009; Figure 3).

### Marine Organisms Exhibit a Range of Responses to Ocean Acidification

Studies of marine calcifiers indicate that most but not all of them exhibit reduced calcification with increased ocean acidification (Fabry et al., 2008). Marine calcifiers differ because they use various mechanisms to control their internal micro-environments where calcification takes place. Also, different life stages of marine calcifiers respond differently. These differences need to be taken into account when designing experiments to evaluate likely future changes in calcification rates due to ocean acidification (Havenhand et al., 2008). Laura Parker (University of Western Sydney, Australia) reported at the meeting that one oyster species that was selectively bred to resist disease was more resistant to acidification impacts, which raises the hope that some organisms might be able to adapt to some



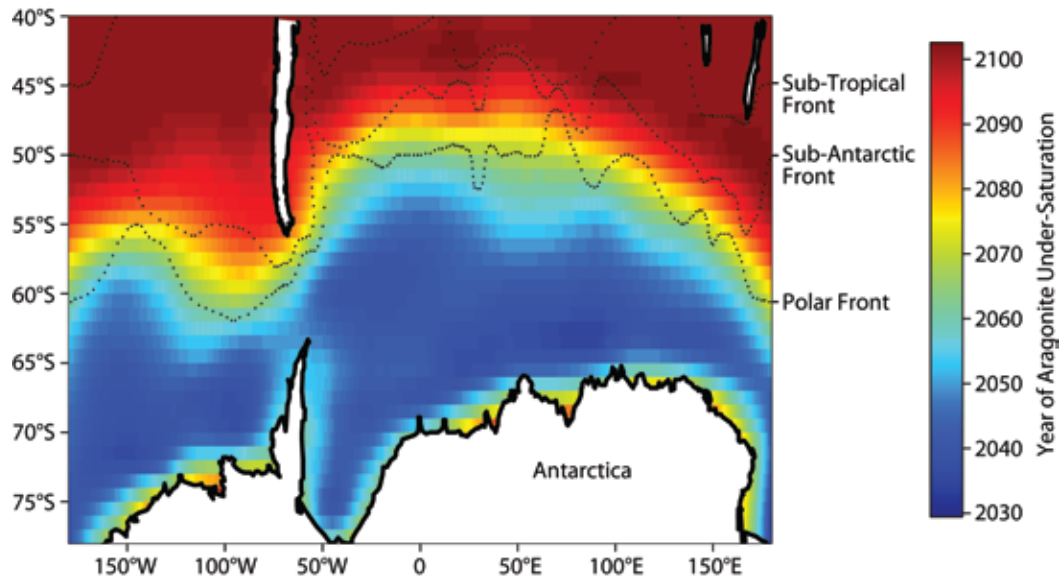


Figure 3. Projected year when surface waters in the Southern Ocean during winter reach undersaturation with respect to aragonite. From McNeil and Matear (2008). ©2008 National Academy of Sciences, United States of America

extent. Meanwhile, there is an ongoing discussion about the potential effects of acidification on coccolithophores (Iglesias-Rodriguez et al., 2008; Riebesell et al., 2008) and their ability to adapt to pH changes (Müller et al., in press). Diverse responses are expected because elevated CO<sub>2</sub> from ocean acidification affects a large suite of physiological mechanisms (Pörtner, 2008).

### Naturally Low-pH Environments Provide a Glimpse of Ecosystems in a High-CO<sub>2</sub> World

Insights into how ecosystems may adapt to high-CO<sub>2</sub> levels have been gained from natural environments near seafloor vents that emit CO<sub>2</sub> at ambient temperature as well as in regions with naturally varying pH gradients, such as coastal upwelling systems. The high-

CO<sub>2</sub>, shallow seafloor vent areas around Ischia, Italy, in the Bay of Naples show that when mean pH conditions reach values that are expected for the end of the century, there is a total absence of some species, generally reduced biodiversity, and regime shifts to completely different ecosystems where sea grasses and invasive species thrive (Hall-Spencer et al., 2008). Another case is the warm-

---

**James C. Orr** ([james.orr@lscce.ipsl.fr](mailto:james.orr@lscce.ipsl.fr)) is Commissariat à l'Énergie Atomique (CEA) Senior Scientist, Laboratoire des Sciences du Climat et de l'Environnement, CEA Saclay, Gif-sur-Yvette Cedex, France. **Ken Caldeira** is Staff Scientist, Carnegie Institution Department of Global Ecology, Stanford, CA, USA. **Victoria Fabry** is Professor, Department of Biological Sciences, California State University at San Marcos, San Marcos, CA, USA. **Jean-Pierre Gattuso** is Centre National de la Recherche Scientifique (CNRS) Senior Scientist, Laboratoire d'Océanographie, CNRS and Université Pierre et Marie Curie, Villefranche-sur-mer, France. **Peter Haugan** is Professor, Geophysical Institute, University of Bergen, Bergen, Norway. **Patrick Lehodey** is Head, Ecosystem Modeling, CLS, Space Oceanography Division, Ramonville, France. **Silvio Pantoja** is Professor, Department of Oceanography and COPAS Center, University of Concepción, Concepción, Chile. **Hans-Otto Pörtner** is Professor, Alfred-Wegener-Institute, Bremerhaven, Germany. **Ulf Riebesell** is Professor, Biological Oceanography, Leibniz Institute of Marine Sciences (IFM-GEOMAR), Kiel, Germany. **Tom Trull** is Associate Professor, University of Tasmania and CSIRO Marine and Atmospheric Research, Hobart, Tasmania, Australia. **Ed Urban** is Executive Director, Scientific Committee on Oceanic Research, University of Delaware, Newark, DE, USA. **Maria Hood** is Consultant, International Ocean Carbon Coordination Project, Intergovernmental Oceanographic Commission of UNESCO, Paris, France. **Wendy Broadgate** is Deputy Director, Natural Sciences, International Geosphere-Biosphere Programme, Stockholm, Sweden.

water coral reefs that are found in naturally high-CO<sub>2</sub>, low-pH waters of the eastern tropical Pacific, which are less cemented and more prone to bioerosion (Manzello et al., 2008).

## DISCUSSION GROUP REPORTS

Following the plenary oral presentations at the 2008 symposium, participants divided into three separate groups to discuss (1) perturbation studies, (2) observational networks, and (3) scaling up results and adaptability of organisms. Each group met for 2.5 hours and then returned to the final plenary session to report back on group discussions, make recommendations, and promote questions and further discussion. The following is a summary of the discussions. Greater detail can be found in the *Research Priorities Report* available at <http://www.ocean-acidification.net>.

### Discussion Group 1: Natural and Artificial Perturbation Experiments to Assess Acidification

Various natural and artificial perturbation approaches have been used to assess ocean acidification impacts. These approaches include highly (or fully) controlled single-species laboratory experiments, microcosms and mesocosms, natural perturbation studies from CO<sub>2</sub> venting sites and naturally low-pH regions (e.g., upwelling areas), and manipulative field experiments. Future experiments should include the most ecologically important species, not merely those species that are easy to maintain in the laboratory, and should integrate changes in multiple physiological processes into the whole-organism response to high CO<sub>2</sub>. Ecological

processes should be more thoroughly studied, including the importance of organisms' vulnerability at different life stages, competition, and trophic interactions. Experiments should strive to maintain natural conditions (e.g., food supply and animal densities).

New types of experiments and approaches are needed, including approaches to link pelagic and benthic mesocosm studies. Benthic and pelagic mesocosms and Free-Ocean CO<sub>2</sub> Enrichment Project-type systems should be used to validate scaled-up laboratory experiments. Long-term perturbation studies should investigate adaptation and micro-evolution. Methods to understand underlying calcification mechanisms for different species should be improved. Simple communities could be manipulated to study community-level responses and to identify indicators of vulnerability and tolerance.

### Discussion Group 2: Observational Networks for Tracking Acidification and Its Impacts

Tracking acidification and its impacts requires large-scale, sustained, in situ measurements. International cooperation is necessary to develop a coordinated global network of ocean observations that could leverage existing infrastructure and programs as far as possible, while identifying additional sites for monitoring and process studies aimed explicitly at ocean acidification. New instruments need to be developed for shipboard and autonomous measurements of CO<sub>2</sub> system parameters (particularly total dissolved inorganic carbon and alkalinity), particulate inorganic and particulate organic carbon,

and other indicators of impacts on organisms and ecosystems. Governments should establish new monitoring sites and repeat surveys in key areas that are likely to be vulnerable to ocean acidification while extending and enhancing existing long-term time series that are relevant for ocean acidification observations and research.

One of the most important needs in monitoring the impacts of ocean acidification is to identify tipping points—geochemical thresholds for ocean acidification (e.g., CaCO<sub>3</sub> mineral solubility)—that, if crossed, will lead to irreversible deleterious effects on species or ecosystems. To detect such tipping points, it will be important to establish a global observation network to routinely measure parameters that reliably detect biotic effects of ocean acidification, such as indicator-species abundance, calcification per cell, biochemical signatures of physiological stress, and ecosystem species composition.

### Discussion Group 3: Scaling Up Effects in Single Organisms to Populations and Adaptability of Organisms

Scaling up experimental results from individuals and populations to the ecosystem level requires understanding of the physiology and genetics of organisms and how they interact to affect energy flows and ecosystem structures. Several different research and analysis approaches could be used to understand scaling better, including laboratory experiments, mesocosm studies, observations of ocean ecosystems, and ecosystem perturbation experiments. It may be possible to examine analogs from other kinds of environmental

disturbance to understand food web effects (e.g., overfishing can lead to an explosion of sea urchin populations). Priorities are to: (1) identify key physiological processes related to calcification, acid-base control, and other processes affected by changes in pH and carbonate ion concentrations, (2) identify sensitive organisms, and (3) evaluate the role of these organisms in various ecosystems. Using these sensitive organisms, laboratory experiments should focus initially on sensitivity indicators such as mortality, stress, and changes in performance to try to understand the mechanistic basis for sensitivity.

It is a priority to determine how ocean acidification interacts with other changes in marine environments, such as changes in key variables, including temperature, salinity, light, nutrients, and oxygen; changes in weather and its variability; changes in ocean circulation and large-scale cycles of the climate system; changes in seasonal and interannual patterns (e.g., El Niño); and changes in human behavior (overfishing, pollution). It is also critical for experiments to be made with relevant conditions of temperature, pH, and other parameters.

More research is needed to understand how sensitive organisms may adapt and evolve over time, including the speed and extent to which adaptation can occur, how gene flow and dispersal affect adaptation, and whether there is evidence for adaptation already occurring. Scientists must strive to understand how adaptation may change interactions among species and to predict how long it takes adaptation and evolution to restore vulnerable ecosystems. After key genes are identified,

they should be monitored in natural populations to determine whether they are changing. Long-term laboratory and mesocosm experiments will be needed to study long-term changes at the genetic level under environmentally

but other measurements relevant to ocean acidification also need to be standardized. One of the greatest current limitations is the inability to compare experiments. The European Project on Ocean Acidification and other orga-

“TODAY’S “ACIDIFICATION EVENT” DIFFERS FROM PAST EVENTS BECAUSE IT IS HUMAN-INDUCED AND IS OCCURRING MUCH MORE RAPIDLY.”

relevant conditions (e.g., including seasonal variability and proper nutrient conditions). Some of these experiments should slowly ramp up CO<sub>2</sub> concentration to more closely mimic progressive change. Finally, selective breeding experiments should help provide information about the adaptability of organisms to changing pH and carbonate ion concentrations.

### CROSSCUTTING RECOMMENDATIONS

Some general topics arose in more than one of the discussion groups, as follows.

#### Need for Development of Best Practices for Ocean Acidification Research

Because many approaches for ocean acidification research are new, there are currently no common guidelines for best practices. It is important to develop best practices and community standards so that research carried out by different investigators can be easily compared. Dickson et al. (2007) provide an internationally agreed-upon guide to best practices for carbon measurements,

nizations are working on a “Guide for Best Practices in Ocean Acidification Research and Data Reporting” (see <http://www.epoca-project.eu/index.php/Best-Practices-Guide/>).

#### Data Management


Data management and dissemination for ocean acidification research must be planned before new data are collected. Data must be reported and archived in ways that make them readily accessible now and in the future. Likewise, data mining and archiving of historical data may provide useful insights into the evolution of ocean acidification over time. This effort needs to be approached carefully, however, as there are many historical data that are not of sufficient quality to address these issues.

#### Education, Outreach, and Engagement of Policymakers

Symposium participants recognized the need for interdisciplinary training of graduate students, postdoctoral investigators, and principal investigators to improve research, observations, modeling, and data management.

Multidisciplinary summer schools should bring together experimentalists and modelers. Meetings should be held with coral reef managers, fisheries

of results and conclusions should be accelerated. Communication among disciplines relevant to ocean acidification research should be expanded.

received from the following organizations and funding agencies: US National Science Foundation (grants OCE-0608600 and OCE-0813697 to SCOR), Prince Albert II of Monaco Foundation, Monaco Government, Musée Océanographique de Monaco, Centre Scientifique de Monaco, International Council for Exploration of the Seas, and North Pacific Marine Science Organization. 

“ ONE OF THE MOST IMPORTANT NEEDS IN MONITORING THE IMPACTS OF OCEAN ACIDIFICATION IS TO IDENTIFY TIPPING POINTS...THAT, IF CROSSED, WILL LEAD TO IRREVERSIBLE DELETERIOUS EFFECTS ON SPECIES OR ECOSYSTEMS. ”

managers, other stakeholders, and policymakers to engage them in formulating research questions that will enable scientists to provide results relevant for decision making. Participants recommended contributing to existing programs to advance public education. Readily accessible presentations and fact sheets on ocean acidification and its effects on marine life should be created for the public and schools, and made available via Web sites (see *Summary for Policymakers* at <http://www.ocean-acidification.net>). So far, only limited analyses have been conducted on potential economic impacts of ocean acidification (e.g., Cooley and Doney, 2009). There is a great need to expand such efforts.

### Communication Within the Ocean Science Community

The research community needs to hear about “mistakes” and conditions that produced no significant effects, so that we can learn from them. Dissemination

Results from this second symposium are being disseminated via several documents: a *Research Priorities Report*, a special issue of the peer-reviewed journal *Biogeosciences* (offering a subset of the contributed research papers), this article, and a *Summary for Policymakers*. Other articles are designed for a broader audience (e.g., Conference Declaration, press releases, IGBP Newsletter). All of these documents are accessible at <http://www.ocean-acidification.net>.

### ACKNOWLEDGEMENTS

This symposium was planned and executed by the Scientific Committee on Oceanic Research (SCOR), the Intergovernmental Oceanographic Commission (IOC) of UNESCO, the International Atomic Energy Agency (IAEA), and the International Geosphere-Biosphere Programme (IGBP). These scientific sponsors and the organizing committees of the symposium gratefully acknowledge the financial and in-kind support

### REFERENCES

- Bates, N.R. 2007. Interannual variability of the oceanic CO<sub>2</sub> sink in the subtropical gyre of the North Atlantic Ocean over the last 2 decades. *Journal of Geophysical Research* 112, C09013, doi:10.1029/2006JC003759.
- Cicerone, R., J. Orr, P. Brewer, P. Haugan, L. Merlivat, T. Ohsumi, S. Pantoja, H.-O. Poertner, M. Hood, and E. Urban. 2004. Meeting report: The ocean in a high-CO<sub>2</sub> world. *Oceanography* 17(3):72–78. Available online at: [http://www.tos.org/oceanography/issues/issue\\_archive/17\\_3.html](http://www.tos.org/oceanography/issues/issue_archive/17_3.html) (accessed October 29, 2009).
- Cooley, S.R., and S.C. Doney. 2009. Anticipating ocean acidification's economic consequences on commercial fisheries. *Environmental Research Letters* 4, doi:10.1088/1748-9326/4/2/024007.
- Cooper, T., G. De'ath, K. Fabricius, and J. Lough. 2008. Declining coral calcification in massive *Porites* in two nearshore regions of the northern Great Barrier Reef. *Global Change Biology* 14:529–538.
- Dickson, A.G., C. Sabine, and J. Christian, eds. 2007. *Guide to Best Practices for Oceanic CO<sub>2</sub> Measurements*. PICES Series Publication 3, IOCCP Report No. 8, 191 pp.
- Dore, J.E., R. Lukas, D.W. Sadler, M.J. Church, and D.M. Karl. 2009. Physical and biogeochemical modulation of ocean acidification in the central North Pacific. *Proceedings of the National Academy of Sciences of the United States of America* 106:12,235–12,240, doi:10.1073/pnas.0906044106.
- Fabry, V.J., B. Seibel, R.A. Feely, and J.C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* 65:414.
- Feely, R.A., C.L. Sabine, J.M. Hernandez-Ayon, D. Ianson, B. Hales. 2008. Evidence for upwelling of corrosive “acidified” water onto the continental shelf. *Science* 320(5882):1,490–1,492.
- Gattuso, J.-P., M. Frankignoulle, I. Bourge, S. Romaine, and R.W. Buddemeier. 1998. Effect of calcium carbonate saturation of seawater on coral calcification. *Global and Planetary Change* 18(1–2):37–46.

- Guinotte, J.M., J.C. Orr, S. Cairns, A. Freiwald, L. Morgan, and R. George. 2006. Climate change and deep-sea corals: Will chemical and physical changes in the world's oceans alter the distribution of deep-sea bioherm forming scleractinians? *Frontiers in Ecology and the Environment* 4:141–146.
- Hall-Spencer, J.M., R. Rodolfo-Metalpa, S. Martin, E. Ransome, M. Fine, S.M. Turner, S.J. Rowley, D. Tedesco, and M.C. Buia. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454:96–99.
- Havenhand, J.N., F.-R. Butler, M.C. Thorndyke, and J.E. Williamson. 2008. Near-future levels of ocean acidification reduce fertilization success in a sea urchin. *Current Biology* 18(15):R651–R652.
- Iglesias-Rodriguez, M.D., E.T. Buitenhuis, J.A. Raven, O. Schofield, A.J. Poulton, S. Gibbs, P.R. Halloran, and H.J.W. de Baar. 2008. Response to comment on “Phytoplankton calcification in a high-CO<sub>2</sub> world.” *Science* 322:1,466.
- Langdon, C., and M.J. Atkinson. 2005. Effect of elevated pCO<sub>2</sub> on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *Journal of Geophysical Research* 110, C09S07, doi:10.1029/2004JC002576.
- Maier, C., J. Hegeman, M.G. Weinbauer, and J.-P. Gattuso. 2009. Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences* 6:1,671–1,680.
- Manzello, D.P., J.A. Kleypas, D. Budd, C.M. Eakin, P.W. Glynn, and C. Langdon. 2008. Poorly cemented coral reefs of the eastern tropical Pacific: Possible insights into reef development in a high-CO<sub>2</sub> world. *Proceedings of the National Academy of Sciences of the United States of America* 105:10,450–10,455, doi:10.1073/pnas.0712167105.
- McNeil, B., and R. Matear. 2008. Southern Ocean acidification: A tipping point at 450-ppm atmospheric CO<sub>2</sub>. *Proceedings of the National Academy of Sciences of the United States of America* 105:18,860–18,864.
- Meehl, G.A., T.F. Stocker, W.D. Collins, P. Friedlingstein, A.T. Gaye, J.M. Gregory, A. Kitoh, R. Knutti, J.M. Murphy, A. Noda, and others. 2007. Global climate projections. Chapter 10 in *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller, eds., Cambridge University Press, Cambridge, UK, and New York, NY, USA.
- Montenegro, A., V. Brovkin, M. Eby, D. Archer, and A. Weaver. 2007. Long term fate of anthropogenic carbon. *Geophysical Research Letters* 34, L19707, doi:10.1029/2007GL03090.
- Moy, A.D., W.R. Howard, S.G. Bray, and T.W. Trull. 2009. Reduced calcification in modern Southern Ocean planktonic foraminifera. *Nature Geoscience* 2:276–280, doi:10.1038/NCEO46.
- Müller, M.N., K.G. Schulz, and U. Riebesell. In press. Influence of high CO<sub>2</sub> on two coccolithophore key species under long-term cultivation. *Biogeosciences*.
- Olafsson, J., S.R. Olafsdottir, A. Benoit-Cattin, M. Danielsen, T.S. Arnarson, and T. Takahashi. 2009. Rate of Iceland Sea acidification from time series measurements. *Biogeosciences* 6:2,661–2,668.
- Orr, J.C., V.J. Fabry, O. Aumont, L. Bopp, S.C. Doney, R.A. Feely, A. Gnanadesikan, N. Gruber, A. Ishida, F. Joos, and others. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681–686.
- Pörtner, H.-O. 2008. Ecosystem effects of ocean acidification in times of ocean warming: A physiologist's view. *Marine Ecology Progress Series* 373:203–217.
- Riebesell, U., R.G.J. Bellerby, A. Engel, V.J. Fabry, D.A. Hutchins, T.B.H. Reusch, K.G. Schulz, and F.M.M. Morel. 2008. Comment on “Phytoplankton calcification in a high-CO<sub>2</sub> world.” *Science* 322:1,466.
- Roberts, D., W.R. Howard, A.D. Moy, J.L. Roberts, T.W. Trull, S.G. Bray, and R.R. Hopcroft. 2008. Interannual variability of pteropod shell weights in the high-CO<sub>2</sub> Southern Ocean. *Biogeosciences Discussions* 5:4,453–4,480.
- Steinacher, M., F. Joos, T.L. Frölicher, G.-K. Plattner, and S.C. Doney. 2009. Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle-climate model. *Biogeosciences* 6:515–533.
- Tyrrell, T., J. Shepherd, and S. Castle. 2007. The long-term legacy of fossil fuels. *Tellus B* 59:664–672.
- Veron, J.E.N. 2008. *A Reef In Time: The Great Barrier Reef From Beginning To End*. Belknap Press, 304 pp.