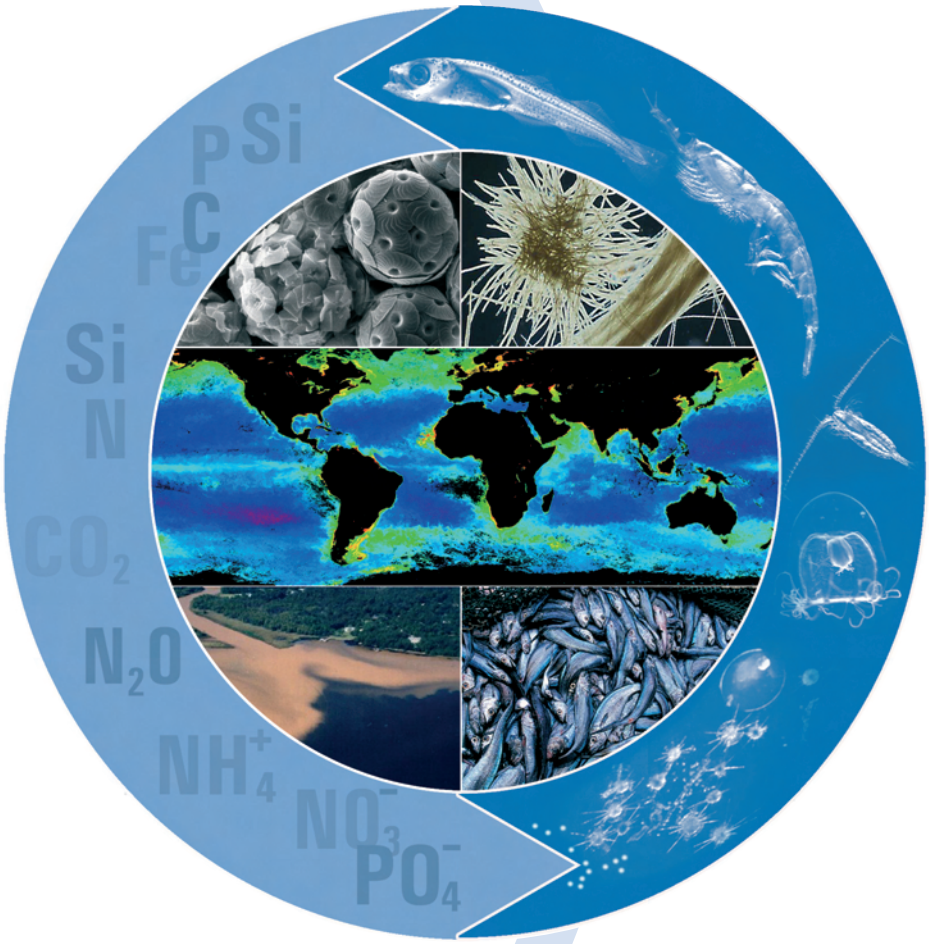
IMBER

Integrated Marine Biogeochemistry and Ecosystem Research

IGBP Report 52

Integrated Marine Biogeochemistry and Ecosystem Research



Science Plan and Implementation Strategy

International Council for Science
Scientific Committee on Oceanic Research

GLOBAL CHANGE
IGBP

Citation

This report should be cited as follows:
IMBER (2005) Science Plan and Implementation Strategy. IGBP Report No. 52, IGBP Secretariat, Stockholm. 76pp.

Cover image

Kath McLeod (NIWA) assisted in the production of the central IMBER diagram, for which Neil Bagley, Birgitta Bergman and Ulf Riebesell provided photographs.

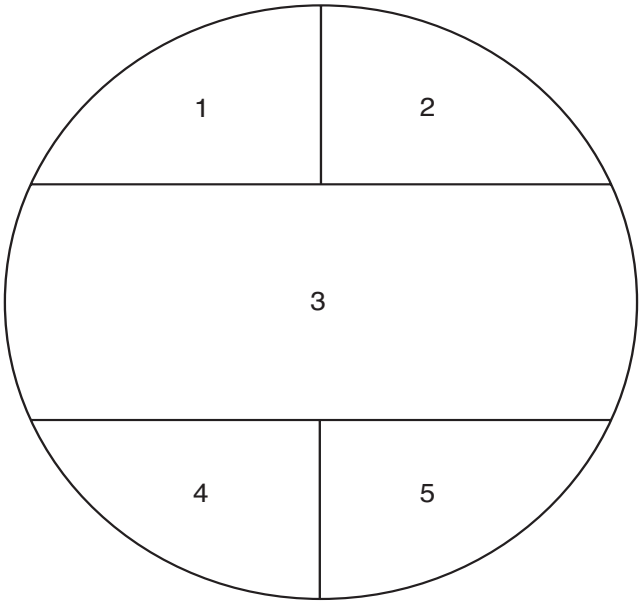


Photo 1: Coccolithophore *Calcidiscus leptoporus* grown at present and elevated CO_2 levels. Credits: Courtesy of Dr. U. Riebesell (IFM-GEOMAR).

Photo 2: *Trichodesmium spp*. appearing in Berman-Frank et al. 2001, Science 294:1534-1537. Credits: Courtesy of Dr. Pernilla Lundgren.

Photo 3: NASA satellite image of the surface cholorophyll pattern due to El-Niño climatic event (Dec. 1998). Credits: Courtesy of SeaWiFS and NASA.

Photo 4: Yangtze River meets the Yellow Sea, as seen from space. Credits: Courtesy of NASA.

Photo 5: Over fishing. Credits: Courtesy of NIWA.

Publication Details

Published by:
IGBP Secretariat
Box 50005
SE-104 05, Stockholm
SWEDEN
Ph: +46 8 166448, Fax: +46 8 166405
Web: www.igbp.net

Editors: Julie Hall, Wendy Broadgate, Penelope Cook, Claire Hamilton, Ed Urban, Bill Young

Series Editor: Bill Young
Technical Editor: John Bellamy

ISSN 0284-8105
Copyright © 2005

Copies of this report can be downloaded from the IMBER, IGBP and SCOR websites. Hard copies can be ordered from the IMBER International Project Office.

IMBER International Project Office
European Institute for Marine Studies
Technopôle Brest-Iroise
Place Nicolas Copernic
29280 Plouzané, France

Web: www.imber.info

Science Plan and Implementation Strategy

Prepared by the IMBER Scientific Steering Committee:

Julie Hall (Chair), New Zealand
Dennis A. Hansell (Vice-Chair), United States
Patrick Monfray (Vice-Chair), France
Ann Bucklin, United States
Jay T. Cullen, Canada
Wilco Hazeleger, Netherlands
David Hutchins, United States
Arne Körtzinger, Germany
Carina Lange, Chile
Jack Middelburg, Netherlands
Coleen Moloney, South Africa
S. Wajih A. Naqvi, India
Raymond Pollard, United Kingdom
Hiroaki Saito, Japan
Carol Turley, United Kingdom
Jing Zhang, China (Beijing)

Preface

The IMBER Science Plan and Implementation Strategy reflects the importance placed on the integration of biogeochemistry and ecosystems research for understanding the impacts of global change and the role of the ocean in the Earth System, by the marine science community, the International Geosphere-Biosphere Programme (IGBP) and the Scientific Committee on Oceanic Research (SCOR). The plan builds on the IGBP/SCOR Framework for Future Research on Biological and Chemical Aspects of Global Change in the Ocean and the OCEANS Open Science Conference held in Paris in 2003. The ideas from these have been woven into a framework of four themes, each with a series of issues and priority questions that form the basis of the IMBER Science Plan.

The Science Plan is ambitious and sets out not only the significant scientific challenge of integrating biogeochemical and ecosystem research, but also the challenge of bringing together the natural and social science communities to address questions of common interest regarding the impacts of global change on the marine system. IMBER will encompass research from the continental margins to the deep sea, and from Antarctica through the equatorial seas to the Arctic Circle.

I encourage scientists from all areas of marine science to come together to address the challenges laid out in this Science Plan and Implementation Strategy, and I encourage this community to work hand-in-hand with the social sciences community to ensure that the questions posed are addressed in a fully integrated manner.

Julie Hall
Chair, IMBER Scientific Steering Committee
June 2005

Acknowledgements

The following people contributed to writing and reviewing this Science Plan and Implementation Strategy:

Keith Alverson, PAGES IPO
Bob Anderson, United States
Vladimir Anikiev, Russia
Bernard Avril, JGOFS IPO
Manuel Barange, GLOBEC IPO
Wendy Broadgate, IGBP Secretariat
Antonio Busalacchi, United States
Howard Cattle, CLIVAR IPO
Hervé Claustre, France
Nicolas Dittert, Germany
Richard Dugdale, United States
Syma Ebbin, IDGEC IPO
Richard Feely, United States
John Field, South Africa
Jean-Pierre Gattuso, France
Alison Gilbert, Netherlands
Wulf Greve, Germany
Wei Hao, China (Beijing)
Richard Hasler, United States
Carlo Heip, Netherlands
Maria Hood, IOC
Keith Hunter, New Zealand
John Huthnance, United Kingdom
David Hydes, United Kingdom
Andreas Irmish, Germany
George Jackson, United States
Richard A. Jahnke, United States
Ian Joint, United Kingdom
Hartwig Kremer, LOICZ IPO
S. Prasanna Kumar, India
Anne Larigauderie, DIVERSITAS Secretariat
Han Lindeboom, Netherlands
Peter Liss, United Kingdom
Kon-Kee Liu, China (Taipei)
Michel Loreau, France
Liana McManus, United States
William Miller, Canada
Ron Mitchell, United States
João Morais, IGBP Secretariat
Raghu Murtugudde, United States
Shoichiro Nakamoto, Japan
John Parslow, Australia
Olivier Ragueneau, France
Casey Ryan, SOLAS IPO
Christopher Sabine, United States
Dork Sahagian, GAIM IPO
Michael St John, Germany
Shubha Sathyendranath, Canada
Richard Sempere, France
Ino Shuji, Japan
Martin Solan, United Kingdom
Cosimo Solidoro, Italy
Tapani Stipa, Finland
Jilan Su, China (Beijing)
Svein Sundby, Norway
Sergei Tambiev, Russia
Qisheng Tang, China (Beijing)
Paul Treguer, France
Kyozo Ueyoshi, United States
Ed Urban, SCOR Secretariat
Cisco Werner, United States
Douglas Wallace, Germany
Richard Wanninkhof, United States
Paul Wassmann, Norway
Nalin Wikramanayake, Sri Lanka
Oran Young, United States
Ein-Fen Yu, China (Taipei)
SOLAS SSC members
GLOBEC SSC members
LOICZ SSC members

Financial support for IMBER and its interim Project Offices was provide by ICSU, IOC, IGBP, NIWA (New Zealand), Plymouth Marine Laboratory (United Kingdom), SCOR and the U.S. National Science Foundation (Grants OCE-0003700, OCE-326301 and OCE-0228863 to SCOR).

Julie Hall
Chair, IMBER Scientific Steering Committee

June 2005

Contents

Executive Summary 1

Introduction 3

Scientific Background 4
Structure of the Science Plan and Implementation Strategy 5
Collaboration 6
IMBER Outcomes 7

Science Plan 8

Theme 1: Interactions Between Biogeochemical Cycles and Marine Food Webs 8

Issue 1.1: Transformation of Organic Matter in Marine Food Webs 9

Issue 1.2: Transfers of Matter Across Ocean Interfaces 13

Issue 1.3: End-to-end Food Webs and Material Flows 17

Theme 2: Sensitivity to Global Change 22

Issue 2.1: Impacts of Climate-Induced Changes Through Physical Forcing and Variability 23

Issue 2.2: Effects of Increasing Anthropogenic CO_2 and Changing pH on Marine Biogeochemical Cycles, Ecosystems and Their Interactions 27

Issue 2.3: Effects of Changing Supplies of Macro- and Micronutrients 30

Issue 2.4: Impacts of Harvesting on End-to-end Food Webs and Biogeochemical Cycles 33

Theme 3: Feedbacks to the Earth System 36

Issue 3.1: Oceanic Storage of Anthropogenic CO_2 37

Issue 3.2: Ecosystem Feedback on Ocean Physics and Climate 40

Theme 4: Responses of Society 43

Integrated Modelling 45

Implementation Strategy 47
Research Approaches 47
Process Studies 48
Sustained Observations 48
Synthesis and Modelling 50
Palaeoceanography 51
Molecular Genetics and Genomics 52
Data Management and Mining 53
Project Organisation and Management 53
Scientific Steering Committee 53
Working Groups 54
Regional Projects 55
International Project Office 55
National Committees and Contacts 56
Recognition of IMBER Research 57
Capacity Building 58
Communication 58
Linkages with Other Projects and Programmes 59
Global Ocean Ecosystem Dynamics (GLOBEC) Project 59
Surface Ocean–Lower Atmosphere Study (SOLAS) 60
Land-Ocean Interactions in the Coastal Zone (LOICZ) 60
Past Global Changes (PAGES) 60
Analysis, Integration and Modelling of the Earth System (AIMES) 61
Climate Variability and Predictability (CLIVAR) 61
DIVERSITAS 62
International Human Dimensions Programme on Global Environmental Change (IHDP) 62
Global Carbon Project (GCP) 62
Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) 62
International Ocean Carbon Coordination Project (IOCCP) 63
GEOTRACES 63
The Census of Marine Life (CoML) 63
Other IMBER-SCOR Affiliated Projects 63
Global Ocean Observing System (GOOS) and Global Climate Observing System (GCOS) 63

References 65

Appendices 72
Appendix I: Acronym List 72
Appendix II: Data Policy Template for IGBP and SCOR Large-Scale Ocean Research Projects 74
Appendix III: Application Process for IMBER Endorsement 76

Executive Summary

IMBER (Integrated Marine Biogeochemistry and Ecosystem Research) is a decade-long international project that will develop new knowledge of ocean biogeochemical cycles and ecosystems. The past decade of internationally coordinated marine research has greatly increased our ability to describe and model the ocean's many biological, chemical and physical processes. The Joint Global Ocean Flux Study (JGOFS) led to significant improvements in the understanding of carbon cycling and quantification of its fluxes in the ocean, and the Global Ocean Ecosystem Dynamics (GLOBEC) project continues to identify processes key to the functioning of marine ecosystems. IMBER will build on the successes of these projects and will seek to merge the knowledge bases of marine biogeochemistry and ecosystem research.

The vision of IMBER is:

to provide a comprehensive understanding of, and accurate predictive capacity for, ocean responses to accelerating global change and the consequent effects on the Earth System and human society.

This vision stems from the recognition that human activities are rapidly altering Earth System processes that directly and indirectly influence society. Informed decisions require an understanding of which parts of the Earth System are most sensitive to change, and the nature and extent of anticipated impacts. This requirement is the basis of the IMBER goal, which is:

to investigate the sensitivity of marine biogeochemical cycles and ecosystems to global change, on time scales ranging from years to decades.

To achieve this goal IMBER will identify key interactions between marine biogeochemical cycles and ecosystems, and will assess how these interactions respond to complex natural and anthropogenic forcings. Important forcings include large-scale climate variations, changing physical and biological dynamics, changing carbon cycle chemistry and nutrient fluxes, and widespread marine harvesting. The major drivers of change considered are physical dynamics, seawater CO_2 (controlling ocean pH), nutrients (with changing inputs to the euphotic zone from the subsurface waters, sediments and land), and intensive fish harvesting. This research will fill the critical gap between short-term climate events (seasonal scale) and anthropogenic climate and global change (century scale).

In pursuit of its goal, IMBER is structuring its research around four themes, each addressing a number of specific issues. Theme 1 brings together biogeochemical and ecosystem research and provides the scientific underpinning for the remaining themes. Theme 2 is the heart of IMBER research and considers the impact of global change on biogeochemical cycles, ecosystems and their interactions. Theme 3 considers feedbacks to the Earth System, and Theme 4 considers the interactions between the open ocean (its biogeochemical cycles and ecosystems) and human society.

Theme 1: Interactions Between Biogeochemical Cycles and Marine Food Webs

What are the key marine biogeochemical cycles and related ecosystem processes that will be impacted by global change?

Understanding how biogeochemical cycles interact with food web dynamics is a major intellectual challenge for IMBER. Key issues are: (i) the transformation of organic matter in food webs, (ii) transfers of matter across ocean interfaces, and (iii) material flows in end-to-end food webs. Interactions between biogeochemical cycles and food webs are expected to differ between environments such as continental margins associated with coastal upwelling, high latitude and polar regions, and tropical and subtropical oligotrophic gyres. Comparisons of different systems will provide new insights for identifying and understanding fundamental interactions between marine biogeochemical cycles and ecosystems.

Theme 2: Sensitivity to Global Change

What are the responses of key marine biogeochemical cycles, ecosystems and their interactions, to global change?

This theme is central to IMBER and will lead to advances in understanding and predicting how marine biogeochemical cycles and ecosystems respond to the complex suite of forcings associated with global change. Identification of components that respond directly to global change is a primary concern. In this theme, responses are partitioned into four major issues: (i) effects of climate-induced changes in the physical dynamics of the ocean, (ii) effects of increasing CO_2 levels and decreasing pH, (iii) effects of changes in macro- and micronutrient inputs to the ocean, and (iv) impacts of marine harvesting. These issues must be considered from diverse interdisciplinary perspectives, with scientific approaches guided by defined priority questions and implementation strategies.

Theme 3: Feedbacks to the Earth System

What are the roles of ocean biogeochemistry and ecosystems in regulating climate?

This theme will focus on key issues to address the present and future capacity of the ocean to affect the climate system via ocean effects on atmospheric composition and ocean heat storage. Key issues include: (i) the varying capacity of the ocean to store anthropogenic CO_2, (ii) ecosystem feedbacks on ocean physics and climate, and (iii) how changes in low-oxygen zones affect the nitrogen cycle, especially transformations involving N_2O. Modelling the potential feedbacks from marine biogeochemical cycles and ecosystems to the Earth System, will require detailed understanding of local and regional manifestations of global change in the ocean, and their interactions with other parts of the Earth System.

Theme 4: Responses of Society

What are the relationships between marine biogeochemical cycles, ecosystems and the human system?

This theme focuses on interactions between human and ocean systems. Its motivation stems from recognition that humans not only influence ocean systems, but that humans also depend on ocean systems for goods and services. The overall theme goal is to promote an understanding of the multiple feedbacks between human and ocean systems, and to clarify what human institutions can do, either to mitigate anthropogenic perturbations of the ocean system or to adapt to such changes. The achievement of this goal depends on inputs from both the natural and social sciences. A major challenge of this theme will therefore be to bring together scientists from a wide range of disciplines, to identify areas of joint concern and interest, and to create an ongoing natural-social science marine research community.

Implementation

IMBER will take advantage of new and innovative approaches to conducting marine research, ranging from new molecular techniques to sustained *in situ* and remotely sensed observations. The development of new sustained observation sites will be an important part of the implementation strategy for IMBER, which will be complemented by targeted field-based process studies, *in situ* mesocosm studies, and both field and laboratory experiments. An interdisciplinary approach will be adopted to bring together biological and biogeochemical oceanographers.

A suite of hierarchical models will be developed to test hypotheses, analyse data and extrapolate in space and time, and identify crucial knowledge gaps that require new observations. Extrapolation to the global scale will require integration and assimilation of data from basin-wide surveys. To support the modelling and synthesis efforts of IMBER, interconnected biological, geochemical and physical databases will be built, extended, and updated in near real-time.

Answering the broad interdisciplinary questions of IMBER will require an effort much larger than any single nation can mobilise. Multiple investigators spanning several disciplines, and intercomparisons of data across a wide range of systems will also be needed. Interfacing the natural and social science communities to study the key impacts and feedbacks between marine and human systems will be a major challenge.

IMBER will encourage the development of collaborative activities that will draw on the expertise of other international research projects and programmes, including the Global Ocean Observing System, to avoid unnecessary duplication and to ensure that IMBER adopts a truly interdisciplinary approach.

Introduction

The past decade of internationally coordinated marine research has greatly increased our ability to describe and model the ocean's many biological, chemical and physical processes. Previous research has quantified the global fluxes of major elements – with an emphasis on carbon – and has identified the organisms and processes central to the functioning of marine ecosystems. A newly emerging challenge, dictated by society's need to understand and respond to the impacts of global change, is to bridge and merge the knowledge bases of the marine biogeochemical and ecosystem disciplines. In response to this need the Integrated Marine Biogeochemistry and Ecosystem Research (IMBER) project has been formed as an activity jointly sponsored by IGBP and SCOR.

The long-term vision for IMBER is:

to develop a comprehensive understanding of, and accurate predictive capacity for, ocean responses to accelerating global change and the consequent effects on Earth System and human society.

The challenge to the scientific community is to understand inter-relationships between biogeochemical cycles and ecosystems, and to quantify and predict responses of the marine system to natural and anthropogenic perturbations.

This has led to the IMBER goal, which is:

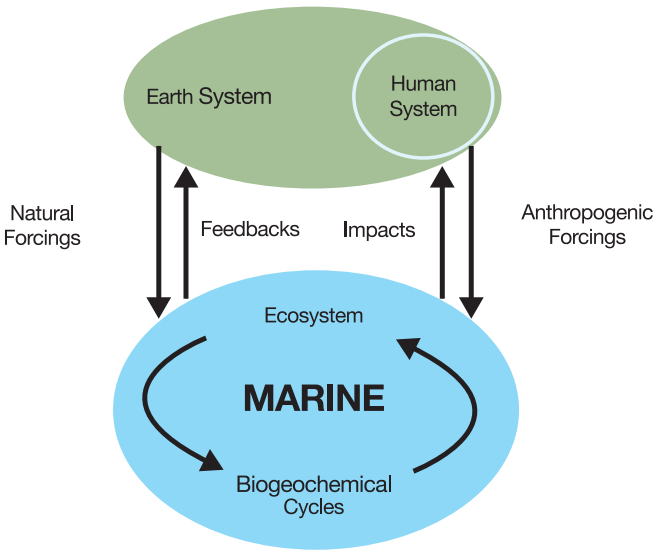
to investigate the sensitivity of marine biogeochemical cycles and ecosystems to global change, on time scales ranging from years to decades.

IMBER research will seek to identify the mechanisms by which marine life influences marine biogeochemical cycles, and how these, in turn, influence marine ecosystems (Figure 1). Central to the IMBER goal is the development of a predictive understanding of how marine biogeochemical cycles and ecosystems respond to complex forcings, such as large-scale climatic variations, changing physical dynamics, carbon cycle chemistry and nutrient fluxes, and the impacts of marine harvesting. Changes in marine biogeochemical cycles and ecosystems due to global change will also have consequences for the broader Earth System.

Advancing our knowledge and quantification of these feedbacks will be an important aspect of IMBER research. The time frame of years to decades is one that can be realistically modelled, is amenable to testable predictions and is pertinent to those ocean processes that are susceptible to global change impacts. At shorter time scales (daily to seasonal) variability is strongly influenced by stochastic processes rather than primarily reflecting long-term change. At longer time scales (centuries) changes would not be directly observable during the project life time, and predictions would not be truly testable.

IMBER science priorities are founded on the advances of previous internationally coordinated projects, particularly the completed JGOFS (www.uib.no/jgofs) and WOCE (www.soc.soton.ac.uk/OTHERS/woceipo) projects and the ongoing GLOBEC (www.globec.org) project. The primary focus of these projects has been understanding the current state of the ocean, and they have been extraordinarily successful (e.g. Fasham et al., 2001; Siedler et al., 2001; Stenseth et al., 2004). JGOFS focused on the lower

Figure 1. Essential features of IMBER, including impacts of natural climatic and anthropogenic influences on marine biogeochemical cycles and ecosystems, and their interactions and feedbacks to the Earth System including the human system.



trophic levels of marine food webs (phytoplankton and microbial processes) and their relations to biogeochemical cycles. GLOBEC considers the higher trophic levels focusing on physical environmental forcing of zooplankton and fish. These projects were not mandated to establish linkages from micro-organisms to top predators. IMBER however, will work collaboratively with GLOBEC to achieve a more complete understanding of end-to-end food web structure and function. Critical questions of how ocean ecosystems are changing under global change have evolved from these projects, and IMBER will seek to address these. IMBER will also address the ocean's role in the Earth System and the links between the open ocean and human society.

The IMBER Science Plan and Implementation Strategy is largely based on science priorities developed at the broadly inclusive OCEANS Open Science Conference (Paris, January 2003; www.igbp.net/obe/), and the IGBP/SCOR Framework for Future Research on Biological and Chemical Aspects of Global Change in the Ocean (IGBP/SCOR, 2002).

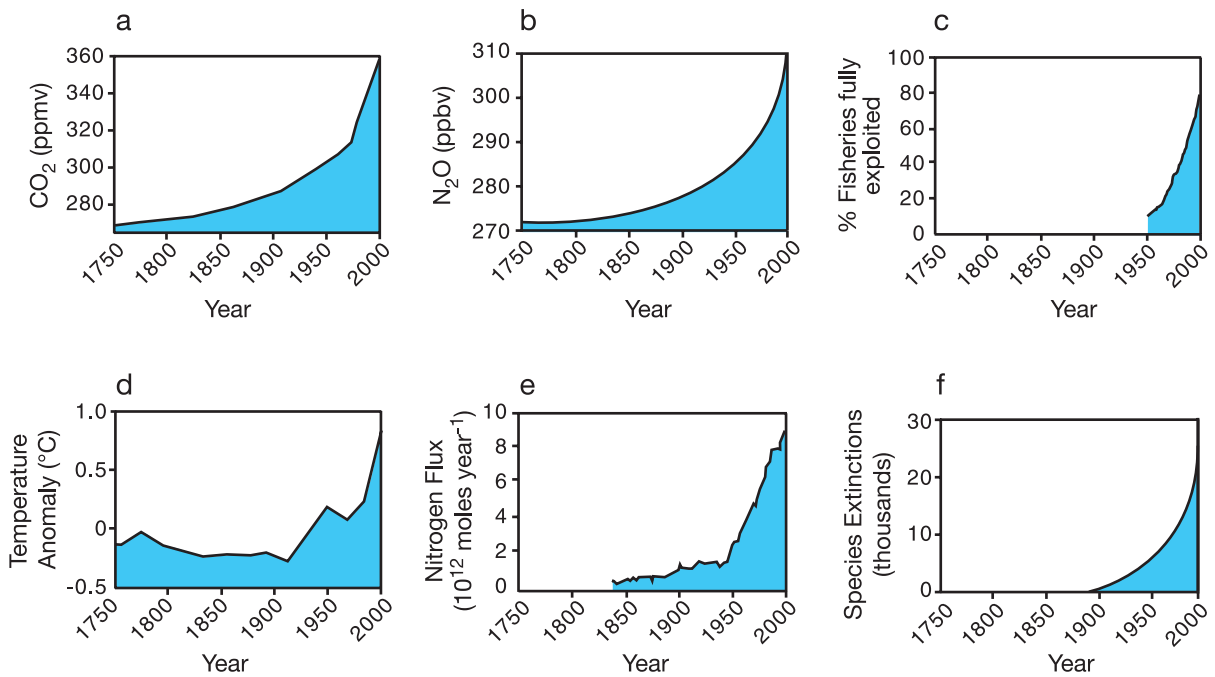
Scientific Background

The ocean has a vast capacity for storage and exchange of heat and gases and thus exerts a major control on the global climate. It is also the most extensive and yet least understood component of the Earth System. Significant advances in marine understanding have been achieved using coupled models, but key biogeochemical and ecosystem questions remain unanswered and material sources and sinks are not fully identified.

The global ocean is experiencing unprecedented stresses due to human activities. These include increasing discharges of macro- and micronutrients caused by land use changes, rapid changes in marine biodiversity and marine ecosystem structure due to heavy fishing pressure and other human activities, invasion of anthropogenic CO_2 into the surface ocean and increasing temperature (Figure 2). These changes have direct impacts on marine physics, chemistry and biology, and direct consequences for society.

Increased release of anthropogenic CO_2 is driving large-scale climate change, affecting both terrestrial and marine

Figure 2. Responses of the Earth System to increasing pressure from human activities: (a) atmospheric CO_2 concentrations, (b) atmospheric N_2O concentrations, (c) percent of ocean fisheries that are fully exploited, (d) Northern Hemisphere average surface temperature anomalies, (e) global nitrogen flux to the coastal zone, and (f) estimated global species extinctions. Adapted from Steffen et al. (2004).



ecosystems. These changes will not only affect atmospheric chemistry and temperature, but also ocean chemistry and temperature, and potentially, ocean physics (e.g. circulation and stratification). Understanding how such change will cascade into key biogeochemical cycles and marine food webs is critical for understanding the impacts of global change on the marine system. GLOBEC studies and JGOFS time-series observations suggest that low-frequency variability in the physical system (e.g. changes in stratification, circulation, ventilation, wind transport and mixing) can have major impacts on the lower trophic levels of marine food webs and the associated biogeochemical cycles. In particular, introduction of macro- and micronutrients to the euphotic zone is strongly controlled by physical processes, the mechanisms and strength of which are directly altered by variations and changes in the climate system.

Nutrients from terrestrial and coastal sources enter the open ocean via the atmosphere and via exchange with the continental margin. This stimulates primary production and affects species composition and complexity of marine ecosystems, impacting flux patterns of the major elements. Over the past century significant amounts of fertiliser have been released into the environment, impacting freshwater systems, estuaries and semi-enclosed and enclosed seas. How far these impacts penetrate into the coastal ocean and offshore regions is unresolved in terms of biogeochemical cycles and marine food webs.

Previous studies of marine ecosystems have demonstrated the effects of both climate and human activity on marine food webs. Palaeoceanographic records, for example, indicate that the abundance of anchovies off California has fluctuated by a factor of 20 over the past two millennia – well before commercial fishing began. On shorter time scales, it has been suggested that catch trends of several pelagic and demersal fish species varied in or out of phase with global atmospheric indices over the past 50–70 years (Klyashtorin, 1998; Schwartzlose et al., 1999). Recruitment success of higher trophic levels is highly dependent on synchronisation with pulsed planktonic production, which is particularly vulnerable to changes in ocean conditions (Edwards and Richardson, 2004).

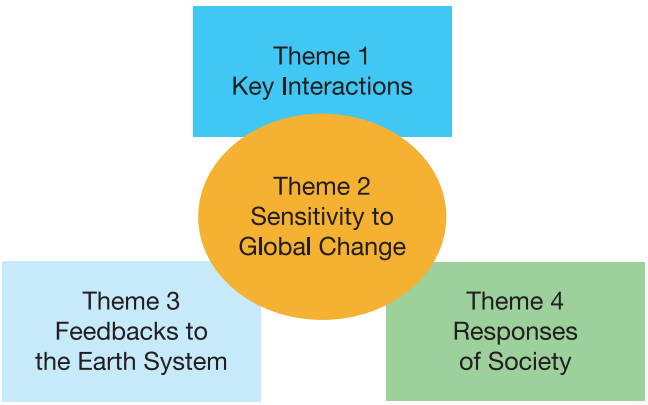
Changes in the decadal pattern of climate variability, as reflected in the Pacific Decadal Oscillation (PDO) and the North Atlantic Oscillation (NAO) indices has been related to major ecosystem disruptions and population changes, ranging from phytoplankton to top predators such as fish and sea birds (Reid et al., 2001; Thompson and Ollason, 2001; Beaugrand et al., 2002; Chavez et al., 2003). The mechanisms by which climate influences marine food webs are, however, poorly understood. Climatic variations cause physical changes in the ocean that directly affect organisms at each trophic level, and these variations also alter transfers through biogeochemical cycles, from nutrients up through food webs, thus affecting organisms indirectly.

Selective exploitation of marine organisms can change the size and age structure of populations, with subsequent impacts on population dynamics and hence ecosystems via food web interactions (Marshall, 1999; Köster et al., 2001). For example, excessive removal of large fish (Myers and Worm, 2003) alters trophic structure (Pauly et al., 1998), interfering with the flow of matter within the pelagic domain and between the pelagic and benthic domains. This has the potential to affect marine biogeochemical cycles.

Structure of the Science Plan and Implementation Strategy

The IMBER Science Plan is structured around the four major research themes (Figure 3), each highlighting issues of particular importance; within each issue priority questions are posed. Theme 1 focuses on identifying and characterising interactions of the key biogeochemical and ecosystem processes that will be impacted by global change. Theme 2 is the core of

Figure 3. Linkages and relationships of the IMBER themes.



IMBER research and considers the sensitivity of these key processes and their interactions to global change, with an emphasis on quantification and prediction. Theme 3 investigates the roles of ocean biogeochemistry and ecosystems in impacting the larger Earth System through direct and indirect feedbacks. Finally, Theme 4 will integrate natural and social sciences, drawing on information from the previous three themes to investigate key interactions with the human system and the options for mitigating or adapting to the impacts of global change on marine biogeochemical cycles and ecosystems.

Modelling the complex system of biogeochemical and ecosystem interactions is an important integrative activity across IMBER. Research will also address interactions of the marine system with other components of the Earth System. Developing, validating, and testing predictions of Earth System models is impossible without a solid understanding of the interactions between biogeochemical cycles and ecosystems. IMBER will investigate the regional manifestations of global change on marine biogeochemical cycles and ecosystems and the resulting feedbacks to the Earth System.

The time domain of IMBER research is years to decades including intra-seasonal and inter-annual variability. Modelling and observational activities will specifically emphasise longer-than-annual time scales. Consequently, IMBER will work in space domains affected by processes corresponding to these time scales, for example, the mesopelagic layer, shallow benthos and basin-scale gyres.

The IMBER Implementation Strategy addresses implementation issues that cut across the science themes, including modelling, sustained observations and data management. It also covers project structure and management and the pathways for engaging scientists worldwide. The approaches described in the Implementation Strategy will be augmented by detailed implementation plans for specific research topics development by groups of scientists working together with the IMBER Scientific Steering Committee.

Both the Science Plan and the Implementation Strategy will undergo a mid-project review to ensure that the project builds on research undertaken in this and other projects over the next five years. IMBER research may be augmented at that point, particularly in relation to key research identified in GLOBEC synthesis and integration activities.

Collaboration

Collaborative relationships with other marine programmes and projects will be critical to the success of IMBER. IMBER will build on the approaches taken and the knowledge gained in previous projects, and will establish collaborative links with related projects to fill important research gaps. In particular, IMBER will foster a close partnership with GLOBEC to enable studies on interactions of biogeochemistry and end-to-end food webs, and studies on the impacts of marine harvesting on end-to-end food webs and biogeochemical cycles.

On topics in which global change science and ocean science intersect, IGBP and SCOR work closely together. On these and other ocean science topics IMBER will collaborate with the following projects/programmes (sponsors indicated in brackets):

- LOICZ (IGBP and IHDP) in studies on the continental margins, including coastal material fluxes and anthropogenic drivers;
- SOLAS (IGBP, SCOR, WCRP and CACGP) on the effects of atmospheric inputs on marine biogeochemistry and ecosystems, and on the carbon and nitrogen cycling in the ocean;
- GEOTRACES (SCOR) in the global study of trace elements;
- CoML (SCOR-affiliated project) on marine biodiversity descriptions, especially microbes and zooplankton;
- GEOHAB (SCOR and IOC) on the effects of physical, chemical and biological conditions on phytoplankton population dynamics; and
- IOCCP (SCOR and IOC) on observations of carbon cycling and storage in the ocean.

The ocean is an integral component of the Earth System and is affected by the other system components. IMBER will therefore collaborate with the following projects (sponsors indicated in brackets) in the IGBP family and in the Earth System Science Partnership (ESSP: DIVERSITAS, IGBP, IHDP and WCRP) to achieve its own goal and to advance Earth System understanding:

- PAGES (IGBP) – particularly IMAGES – in understanding physical and biogeochemical marine processes operating on time scales beyond the instrumental records;

- AIMES (IGBP) in the development of Earth System models that incorporate ocean processes;
- CLIVAR (WCRP) on the role of physical processes – particularly climate variability and change – on marine biogeochemical cycles, ecosystems and their direct feedbacks to physics;
- GCP (ESSP) in the study of global carbon cycling;
- DIVERSITAS on the impacts of biodiversity changes on marine biogeochemical cycles and ecosystems; and
- IHDP on integrating social science and the development of Theme 4.

In addition, IMBER will work closely with the global observations systems, particularly GCOS and GOOS, to ensure effective development and use of sustained observations.

Details of how these collaborations will be implemented are outlined in *Linkages with Other Projects and Programmes*. Linkages to national and regional activities will be established as these activities develop.

IMBER Outcomes

Over its ten-year life IMBER will develop a significantly increased understanding of how the interactions between marine biogeochemical cycles and ecosystems respond to, and force, global change. This increased understanding will provide policy makers with sound scientific knowledge to make informed decisions on the management of global change. This will include the identification of potential options for adapting to, or mitigating, the impacts of global change. The increased understanding will be based on internationally shared, publicly available datasets from a wide range of experiments, existing and new high-technology time-series stations, sustained ocean observations and results from a hierarchy of integrated models. The models will link the mechanisms of biogeochemical cycles with ecosystem processes, and provide a predictive understanding of the impacts of global change on the ocean system. Of equal importance will be IMBER's development of a new generation of interdisciplinary marine scientists from developed and developing countries, that uses a systems approach to answer research questions.

Science Plan

Theme 1: Interactions Between Biogeochemical Cycles and Marine Food Webs

What are the key marine biogeochemical cycles and related ecosystem processes that will be impacted by global change?

Understanding how the transformation and transport of elements involved in biogeochemical cycles relates to food web dynamics, is a major intellectual challenge for marine science and IMBER. Three key issues have been identified within this theme: (i) transformation of organic matter in food webs, (ii) transfers of matter across ocean interfaces, and (iii) material flows in food webs from end-to-end.

The inputs, losses, dynamics and chemical forms of macro- and micronutrients influence autotrophic and heterotrophic organisms in the ocean (Bruland et al., 2001; Mann et al., 2001; Svensen et al., 2002; Granger and Ward, 2003). These factors can cause non-linear impacts on metabolic rates and processes, population and community dynamics, and food web and community structures. For example, macro- and micronutrients can be required for the functioning of specific enzymes and metabolic pathways, and thus may exert considerable control on the species composition of marine communities. The relationships between the life cycles of marine organisms and the distributions of macro- and micronutrients are reciprocal, and are coupled on a wide range of space and time scales. Changes in microbial and phytoplankton activity due to changes in the concentrations, types and ratios of macro- and micronutrients, can alter the composition, production and subsequent degradation of organic matter (Madin et al., 2001). Differential remineralisation may lead to decoupling of nutrient cycles within the water column (Karl, 1999; Karl et al., 2001b).

Through uptake, metabolic transformations, active and passive transport, extracellular complexation and recycling, biological communities exert considerable control on the oceanic abundance and distribution of macro- and micronutrients and other particle-reactive elements.

Biogeochemical cycles may also be influenced by higher-level characteristics of marine food webs, such as species composition and biodiversity.

Interactions between biogeochemical cycles and food webs are expected to differ among environments such as continental margins associated with coastal upwelling, high latitude and polar regions, and tropical and subtropical oligotrophic gyres. For example, upwelling regions are characterised by intermittent high phytoplankton production, but trophic transfer up the food web may be less efficient in these regions because grazers cannot keep pace with phytoplankton growth, resulting in higher export of particles to the seafloor. Comparisons between different systems will provide new insights for identifying and understanding fundamental interactions between marine biogeochemistry and ecosystems. The three issues in this theme have been identified as the key science to underpin the other project themes, and to address the impacts of global change on marine biogeochemical cycles and ecosystems.

Issue 1.1: Transformation of Organic Matter in Marine Food Webs

Organisms continuously require a complex set of inorganic and organic substances that they obtain from their environment. During the millions of years of evolution, marine life forms have become increasingly complex. This evolution has been largely driven by the selective advantage in meeting the basic requirements for maintenance and reproduction, by capturing and ingesting other organisms. Organic matter is continuously transferred from lower to higher trophic levels, and transferred back through decomposition/remineralisation to constituent elements by microbes and scavengers. This continuous transfer and transformation in the food web from inorganic to organic substrates and back again, explains why biological processes drive almost all biogeochemical cycles.

Marine food webs consist of individual organisms that are adapted to a specific range of environmental conditions and interact with other organisms. In the past, food webs have been studied firstly by looking at "state variables" – such as populations, species, and trophic levels – in which the properties of organisms were aggregated, and secondly by quantifying the flows of energy and matter between these state variables. This simplification allowed the development of a large body of scientific knowledge that can be coupled in a straightforward way to elemental cycles, especially where processes involving nutrients and lower trophic levels (phytoplankton and bacteria) are considered. For zooplankton and fish, the emphasis has been more on population-level biological processes, such as recruitment, competition and predation, in an implicit or explicit evolutionary context. Simultaneous top-down (by predation) and bottom-up (by nutrient availability) control of marine food webs may confound attempts to establish the relative importance of macrobiological versus microbial food webs, but it is recognised that this approach may be necessary to advance the ability to model ecosystems.

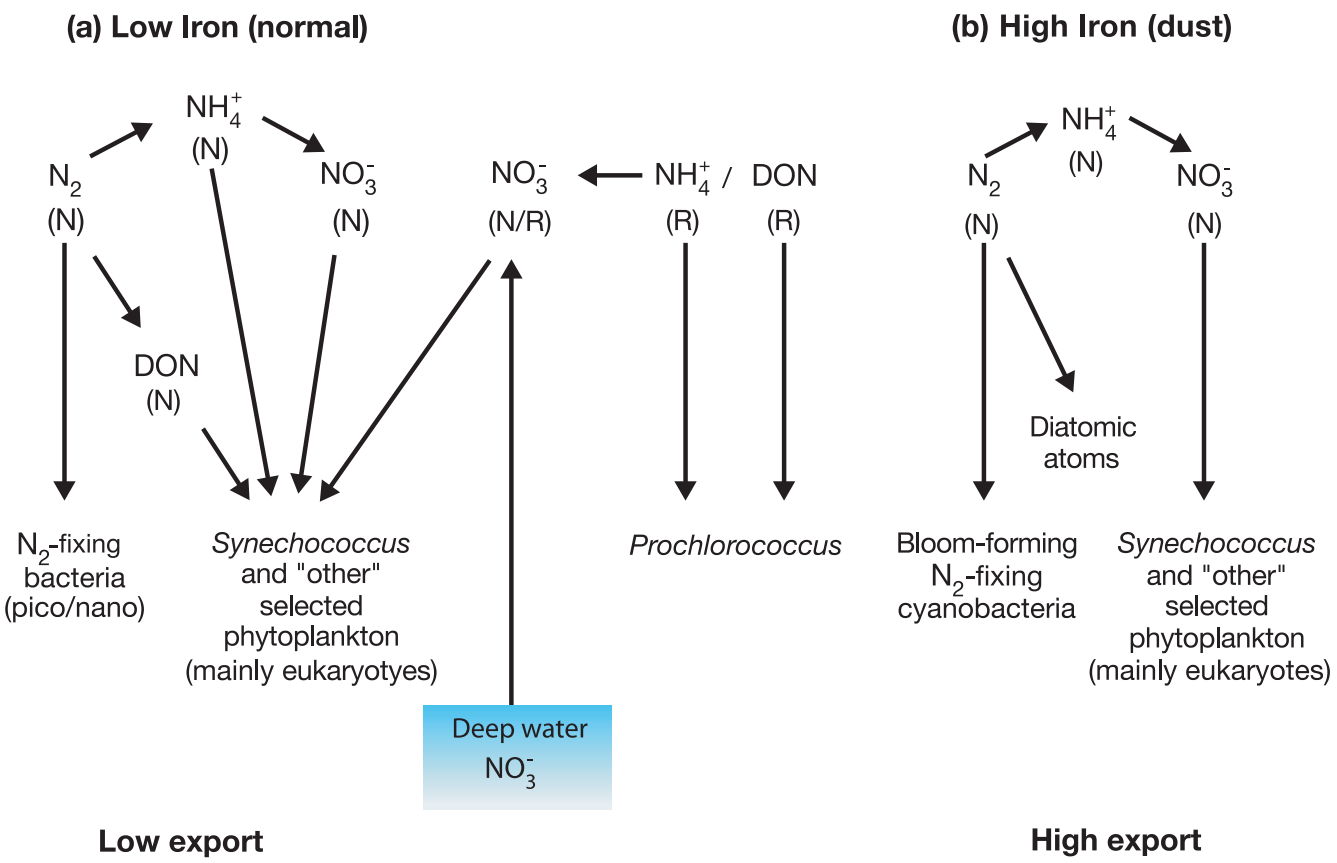
Knowledge of the connections between biological, physical and chemical factors influencing nutrient uptake and remineralisation in the ocean is rapidly increasing, but is still insufficient for construction of realistic predictive models. A holistic view of the impact of macro- and micronutrients on food web structure and function in different ocean regimes is needed. Although the basic processes of organic matter production and breakdown are well known, their interconnectedness and overall regulation requires more study. From projects like JGOFS have come general descriptions of the cycling of many essential elements (carbon, oxygen, nitrogen, phosphorus, silicon) in selected marine ecosystems (especially the surface ocean and oligotrophic gyres), and an understanding of many fundamental processes such as photosynthesis, respiration, nitrogen fixation and denitrification (Fasham et al., 2001). It is important that research is extended to regions such as polar and high-latitude ecosystems, continental margins (especially those that exhibit strong coastal upwelling) and the mesopelagic layer. These areas are predicted to be more sensitive to global change than other areas, and/or are hot spots of biogeochemical-ecosystem coupling. From remote sensing and decades of shipboard expeditions, there are now measurements for a number of variables in nearly all areas of the global ocean. Biogeographical provinces have been described for all ocean basins (Longhurst, 1995), although new species, particularly within the microbial and benthic realms, continue to be discovered and described.

Estimates of the mean oceanic residence times and average vertical profiles for most elements in the periodic table have been published (Nozaki, 1997). These profiles generally indicate whether an element displays a nutrient-like profile or more chemically conservative behaviour. However, this information is generally not adequate for understanding the specific interactions between biogeochemical cycles and food webs, because the profiles integrate a multitude of processes. Important unresolved issues include (i) whether all of the important sources and sinks have been identified and quantified for specific elements, (ii) whether all or only a few specific forms of the element are available for uptake and utilisation by organisms, and (iii) how efficiently each element is transported vertically via the biological pump.

One factor that has confounded these studies is anthropogenic activities, which alter exchange rates on time scales that are short relative to the mean oceanic residence times of important elements. Inputs, outputs and ocean inventories are not in balance for some elements – including fixed nitrogen (Middelburg et al., 1996; Codispoti et al., 2001).

Over evolutionary time the emergence of organisms with a key function, such as photosynthesis, nitrogen fixation, nitrification, denitrification, silicification and calcification, repeatedly induced dramatic changes in marine biogeochemistry and Earth System chemistry (Holland, 1984). Such ecosystem-biogeochemistry interaction is also observed over shorter time scales. The biological activity related to nutrient uptake influences marine physical and chemical systems, for example, by (i) releasing radiatively active gases (Charlson et al., 1987), (ii) converting photon energy absorbed by pigments into heat in the euphotic layer (Nakamoto et al., 2001), (iii) changing N:P stoichiometry by nitrogen fixation and denitrification (Karl et al., 2001b), (iv) changing ratios between macro- and micronutrients by differential uptake, regeneration and export rates (Takeda, 1998), and (v) carrying particle-reactive micronutrients and isotopes across isopycnals (Butler, 1998). Another example is the variable iron supply from the land to the ocean, which may have increased the abundance and production of diazotrophs, inducing changes in N:P stoichiometry in the equatorial Pacific Ocean ecosystem on a time scale of less than a few decades (Karl, 2002) (Figure 4).

Figure 4. Revised conceptual view of new (N) versus regenerated (R) nitrogen based on observations from the Hawaii Ocean Time-series programme in the North Pacific subtropical gyre. (a) Normal, low-iron condition that is observed during most of the year. (b) High-iron condition resulting from increased dust deposition. Nitrogen-fixing pico- and nano-plankton incorporate new N_2, part of which cycles locally through new ammonium (NH_4^+) to new nitrate (NO_3^-); new dissolved organic nitrogen is also produced during this process. All of these substrate pools are used for photosynthesis by the various groups of photo-autotrophs. From Karl (2002); reprinted with permission from Elsevier.



Priority Questions

What controls the stoichiometry and form of "bioreactive" elements in space and time?

It has long been known that the biological availability and accumulation of micronutrients in the ocean (i.e. Fe, Cu and Hg) are strongly influenced by their chemical speciation, which is controlled by chelators produced by phytoplankton and bacteria (Moffett, 1995; Moffett and Brand, 1996). Of the elements that have complex interactions with ecosystem function, one of the best understood is iron. The bioavailability of iron depends directly on its oxidation state, complexation by siderophores or other unknown organic ligands, and its partitioning between particulate, colloidal and dissolved forms. In the past decade our understanding of the chemical speciation of iron and its interaction with biological systems has changed considerably (Turner and Hunter, 2001). Although thought to be completely complexed by inorganic hydroxides as recently as 10–15 years ago, iron is now believed to be almost completely complexed by organic ligands. This new picture of iron chemistry in seawater greatly changes the conceptual ideas of the interactions between iron and ecosystems. The chemistry of other biologically important micronutrients may be equally misunderstood, and consequent relations to biological function and ligand production may also require new examination.

Lessons learned from iron chemistry in the ocean suggest that micronutrient bioavailability is intimately tied to the physical and chemical speciation of elements in seawater. Indeed, processes that partition micronutrients between the dissolved and particulate phase, like the formation and dissolution of the primary biogenic mineral phases, may be primary factors affecting bioavailability. Many elements are known to be scavenged by inorganic particles in seawater. For example, calcium carbonate ($CaCO_3$) and opal can serve as ballasting materials, enhancing vertical fluxes of particle-reactive elements (Armstrong et al., 2002). Production and dissolution of $CaCO_3$ can also modulate seawater pCO_2 levels. These transformations may control the availability of micronutrients to organisms and the reactivity of these elements in abiotic processes.

Global and regional changes in seawater pH, oxygen levels and other factors, could lead to widespread changes in speciation and partitioning of important elements. These factors are therefore of particular importance in understanding the potential impacts of global change. For example, as anthropogenic CO_2 invades the ocean the pH of surface waters is expected to decrease (Feely et al., 2004). Increases in water column stratification due to surface warming could lead to increased hypoxia in deep waters. There is a need to understand the sensitivity of micronutrient speciation to reduction-oxidation (redox) conditions, and how this speciation affects bioavailability, toxicity, solubility and other critical properties.

What controls production, transformation and breakdown of organic matter in marine food webs?

Factors that control the flows of organic matter in marine food webs must be further elucidated. The traditional view of marine food webs often considers the production of organic matter by diverse autotrophic communities to be limited primarily by a single factor (e.g. light or nutrients), and does not consider the interactions among factors or the characteristic temporal and spatial scales of processes. Food web structure is usually described in static terms, and does not consider, for instance, the large differences in time and space scales relevant at different trophic levels – for example, bacteria operating at microns and whales at thousands of kilometres. Descriptions of organic matter flows in food webs must use, and link, appropriate time and space scales.

To understand how food web structure and function may impact production, remineralisation, transport and transformation of organic matter, better descriptions are needed of the cycles of macro- and micronutrients in marine ecosystems, the relationships between the genetic, morphological, physiological and behavioural characteristics of organisms, and the interrelated major biogeochemical cycles. Grazing and predation relationships and the rates of predation among key species need to be measured and analysed quantitatively, taking into account morphological and behavioural characteristics of species and transfer efficiencies between predator and prey. It is necessary to explicitly recognise that predator-prey and plant-herbivore interactions have evolved, and that because of selective pressures the fundamental characteristics of these interactions may continue to evolve over relatively short time intervals. As the primary currency for the transfer of energy within marine food webs, it is necessary to understand – at the molecular level – the nature (e.g. size, composition and turnover rates) of particulate organic carbon (POC) and dissolved organic carbon (DOC) pools. Food web transfers represent an organic-to-organic transition, but also impact

the partitioning between POC, DOC and dissolved inorganic carbon (DIC) pools; for instance, through the fraction of organic material that is respired or lost during feeding. In addition, quantifying food web transfers is critical to quantifying secondary productivity and export from surface waters (Steinberg et al., 2000).

Remineralisation processes are difficult to quantify because although they are dispersed throughout the water column, they are concentrated in the difficult to observe mesopelagic layer. It is important to determine roles of particular species, functional groups and genes for remineralisation processes. One of the most challenging aspects of food web and biogeochemical studies alike, is that important components of marine food webs, and therefore new and possibly important biogeochemical processes, remain to be discovered. This is true for both the micro- and the macrobiological components in surface waters, and especially, in deeper waters. Examples include pelagic Archaea in meso- and bathypelagic microbial communities, organisms capable of anaerobic ammonium oxidation, and the widespread occurrence of mixotrophic, symbiotic and parasitic relationships.

Issue 1.2: Transfers of Matter Across Ocean Interfaces

Evaluation of the interactions and feedbacks between marine biogeochemistry and ecosystems requires knowledge of the distribution and residence times of biologically important elements. Reactions and transfer of macro- and micronutrients, particle-reactive elements, and isotopes occurring at ocean interfaces (air-sea, land-sea, and sediment-water) and across ocean boundaries (epipelagic-mesopelagic), represent the fundamental means whereby changes in source and sink strengths propagate into the marine environment and alter the oceanic biogeochemical state. In the reverse sense, transfer across these interfaces also represents the means by which the ocean influences other parts of the Earth System. IMBER research seeks to advance the understanding of how the transfer of materials and energy across these interfaces influences, and is influenced by, marine biogeochemical and ecosystem interactions. The rate and magnitude of potential interface-dependant reactions are strongly controlled by specific sets of chemical and ecological processes. New insight into the processes that control the input, internal cycling and ultimate fate of biologically important elements in the ocean system will provide the means to describe and evaluate the potential for significant non-linear responses of the ocean to even modest changes in global change forcings transmitted across interfaces. Predictive biogeochemical models must accurately represent remineralisation processes and interfacial transfers on time scales relevant to global change. However, substantial uncertainties remain in our understanding and quantification of the processes involved, and many basic questions must be answered before accurate parameterisations can be developed.

Imbalances in nutrient use and regeneration within the surface ocean food web propagate downward with consequences for the biological carbon pump. The role of interfaces is important in nutrient cycling: especially between the euphotic surface layer and the mesopelagic layer, between continental margins and the open ocean, and within the benthic boundary layer.

Priority Questions

What are the time and space scales of remineralisation of organic matter in the mesopelagic layer?

The mesopelagic layer, located between the photosynthetic surface ocean and ≈1000 m depth, connects the two main interfaces for exogenous sources and sinks of biologically important elements in the ocean. Processes occurring in the mesopelagic layer control the remineralisation of organic material produced by organisms in the overlying euphotic zone. These processes release macro- and micronutrients affecting the consequent quantity and stoichiometry of material delivered to the deep waters and seafloor. The mesopelagic layer is also critical for the reflux of biologically important elements back into the sunlit surface ocean, and hence plays a critical role in controlling primary production on global change time scales. Processes in the mesopelagic layer are driven by mesopelagic ecosystems; the vertical and horizontal structures of these ecosystems are controlled by the changing biochemistry of particles and dissolved organic matter, the movements and migrations of organisms, and currents and mixing processes.

Knowledge of the structure and functioning of mesopelagic ecosystems is needed to understand the exchanges between the photic zone, the benthic zone and the ocean margins. Better quantification of the magnitude of fluxes and the rates of chemical transformations that control the stoichiometry of material passing through the mesopelagic layer is required. The dominant processes involved in the transformations must be identified and evaluated as to their role in oceanic responses to global change. Because transfer across the mesopelagic layer varies regionally, it is necessary to determine basin-wide distributions of chemical components that result from vertical exchange, input and removal at boundaries and lateral transport.

Remineralisation processes are difficult to observe and quantify, particularly in the mesopelagic layer, and con-

sequently they remain poorly characterised throughout the entire water column. This situation requires immediate attention, since biogeochemical models designed to predict fluxes and material transformations in the mesopelagic layer must include information about the depth dependence of nutrient remineralisation, the factors that control it and the rates of remineralisation under different conditions. Better characterisation of these processes should lead to models that can better estimate the responses of these fluxes to perturbations as diverse as climate change, iron fertilisation, CO_2 injection and harvesting of mesopelagic fish stocks. Processes in the euphotic zone play an important role in the character of exported material, and hence affect how remineralisation occurs in the mesopelagic layer, such as in determining the depth range over which material is degraded. Thus observations, experiments and models must link the two systems.

Association of organic matter with mineral grains may impact the rate and depth of remineralisation by protecting organic molecules from enzymatic attack, and by acting as particle ballast to increase sinking velocities. Differential remineralisation of biologically important elements may lead to the decoupling of nutrient cycles within the water column, creating changes in the levels of specified nutrients that limit plant growth, and resulting in subsequent ecosystem shifts to favour species that are less affected by the new limitations and/or thrive on the increased nutrient levels. A better understanding is required of the relationships between remineralisation depth, vertical scales of stratification, circulation and isopycnal ventilation, which determine the time scales of nutrient sequestration and reflux.

Globally, the residence time of particulate carbon in phytoplankton is only a few weeks, whereas the turnover of carbon and nutrients via export, remineralisation and water mixing in the mesopelagic layer occurs on seasonal-to-decadal time scales.

Changes in surface-water circulation driven by climate affect mesopelagic water masses and their chemistry (including nutrient content) on decadal-to-centennial time scales. On a global scale therefore, the vertical and horizontal redistribution and return of nutrients to the euphotic zone control the biological state and processing in the upper ocean on these time scales, not only the nutrient concentrations themselves, but also the ratios of nutrients in the surface ocean supplied to the euphotic layer (Dugdale and Wilkerson, 1998). Food web structure, from organisms as small as viruses to as large as whales, influences the depth and rates at which particulate organic matter (POM) is recycled by controlling the composition of POM, and the sinking speed of cells, faecal pellets and aggregates (Beaumont et al., 2002). Food web structure in the mesopelagic layer then controls how much POM passes through to deeper water, and how much is remineralised.

How does nutrient exchange between continental margins and the ocean interior impact biogeochemical cycles?

One of the important domains identified by IMBER is the continental margin, which includes continental shelf, slope and rise areas, and inland and marginal seas. Physical, chemical and biological processes on the continental shelf and slope transport and transform material entering the open ocean. Many transport and reaction processes are unique to, or intensified at, the land-sea boundary, and contribute to the high spatial and temporal variability of these systems (Figure 5). Examples include wind-driven upwelling and associated high biological productivity, accelerated cross-isopycnal mixing and input of materials from terrestrial sources, submarine groundwater discharges and related chemical inputs, and input from cold vents related to gas hydrates and hydrocarbon seepage. Furthermore, the transport of macro- and micronutrients on and off the shelf has been reported to impact the dynamics of both shelf and offshore ecosystems (Gallego et al., 1999). It has been suggested that ocean margin systems are globally significant in the oceanic uptake of anthropogenic CO_2 (Tsunogai et al., 1999; Yool and Fasham, 2001), in the deep vertical flux of organic matter (Jahnke, 1996; van Weering et al., 2001; Wollast and Chou, 2001a; Wollast and Chou, 2001b), in the removal of fixed nitrogen from the ocean via denitrification (Middelburg et al., 1996; Codispoti et al., 2001) and in the burial of opaline silica (DeMaster, 2002). More than 90% of the organic carbon burial in sediments occurs in these boundary regions (Hedges and Keil, 1995).

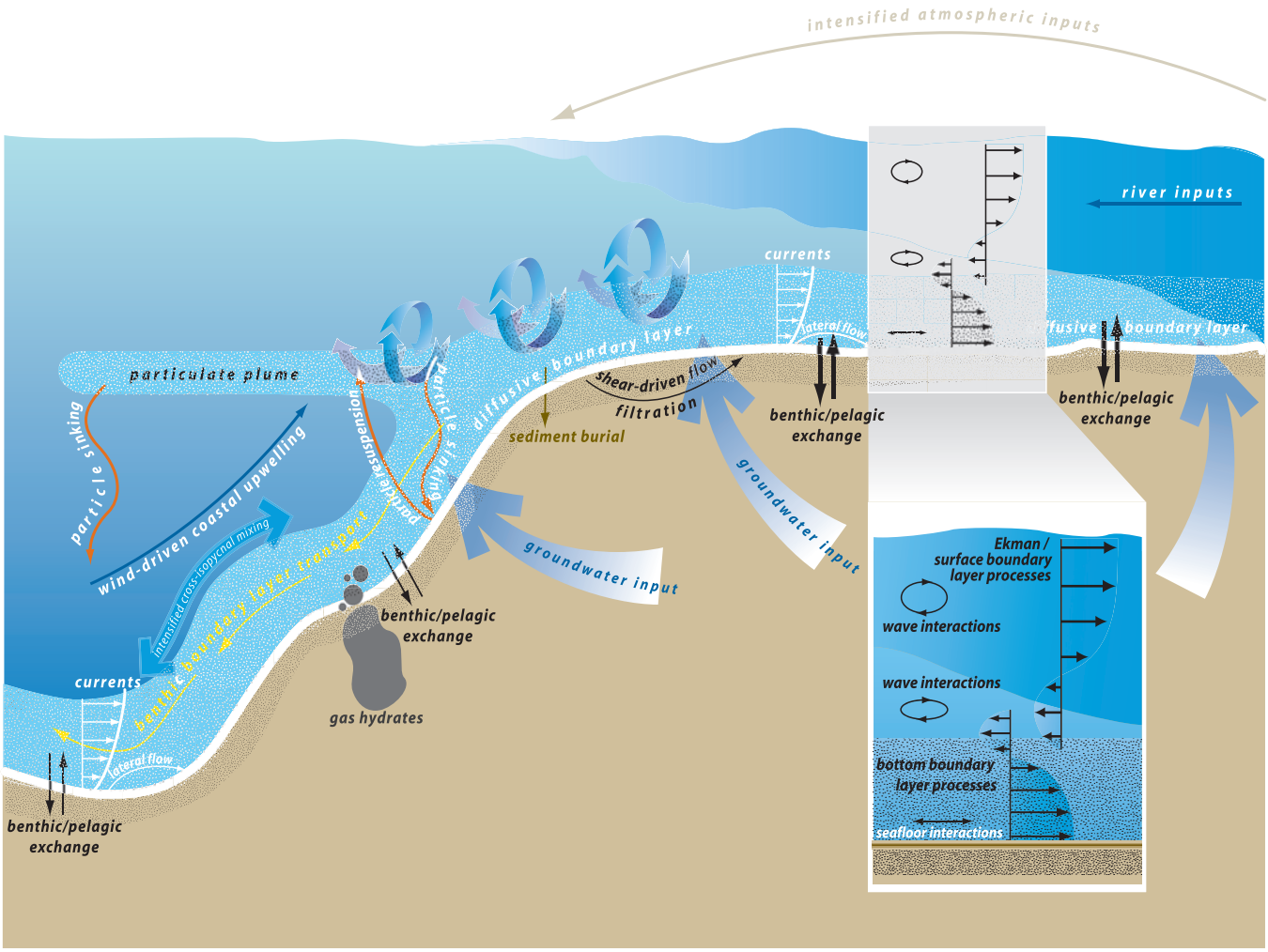
Recent evidence shows that iron limitation can control primary productivity, not only in open ocean high-nutrient–low-chlorophyll (HNLC) areas, but also in highly productive coastal upwelling regimes (Hutchins and Bruland, 1998; Hutchins et al., 2002) and even in estuaries (Lewitus et al., 2004). Furthermore, the flux of dissolved iron from coastal anoxic sediments and the extraction of iron from resuspended sediment particles have been suggested as sources of bioavailable iron (Berelson et

al., 2003). New results also suggest that advection from continental shelves could provide a large, but previously unrecognised portion of the bioavailable iron supply to open ocean regimes (Elrod et al., 2004). Precisely how iron inputs from margins affect global productivity and biogeochemical cycles still remains to be determined.

Although less well documented than iron limitation, other trace metals – such as zinc – could also be important in controlling biological community structure (Crawford et al., 2003) or critical biogeochemical processes such as calcification (Schultz et al., 2004). A great deal of work on trace metals other than iron is needed before we can claim to fully understand their effects on marine food webs and nutrient cycles.

Many different types of benthic communities exist on the continental margin; they are usually highly diverse and exhibit dramatic small-scale spatial and temporal variability (Thrush, 1991). The role of these communities in biogeochemical processes is poorly known because of their complexity and variability and the lack of large-scale studies. Estimates of primary production in the coastal zone based on measurements of phytoplankton are between 375–575 TmolC yr^{-1}. These estimates do not include primary production from benthic micro-algae (Jahnke

Figure 5. Schematic depiction of processes impacting coastal benthic exchange dynamics, many of which are sensitive to global change with local- and global-scale consequences for biogeochemical cycles and foods webs. This figure was developed from a workshop that sought to define the role of coastal observing systems in the study of coastal benthic processes; an NSF-funded initiative arose from the workshop as the ORION Program's (www.orionprogram.org) inaugural research effort. From Reimers et al. (2004).



et al., 2000), macro-algae, coral reefs, seagrasses, marshes and mangroves, which may account for as much as half of the total coastal primary production. While most studies report global coastal benthic respiration rates of 150–200 TmolC yr^{-1}, these studies clearly underestimate total coastal benthic respiration by a factor of 3–4 if reefs, macro-algae, seagrasses and other macrophyte communities are also considered. The question of how benthic communities contribute to cycling of nutrient elements (e.g. Fe, N, P and Si) and ecosystem functioning as a whole clearly needs more attention.

How does exchange between the seafloor and the water column impact food web structure and function?

The linkages between benthic and pelagic systems are clearly identified as critical components in the study of continental margin and deep-water biogeochemistry. The understanding of the physical, biological and chemical controls of sediment-water exchange must be advanced. Benthic exchange of nutrients can alter nutrient ratios in coastal upwelling waters, impacting surface ocean food webs and consequent export fluxes. The spatial extent of the deep seafloor and known deep-seafloor exchange processes suggest that this interface must also be understood to fully constrain the large-scale cycling of biologically important elements in the ocean. Implicit in research on the sediment-water interface is the need to further characterise the diagenetic processes that control the intricate balance between deposition, recycling and burial rates which ultimately control the present and future biogeochemical state of the ocean. These studies will also improve the accuracy with which the sedimentary record can be related to oceanic conditions and processes, a requirement for determining the temporal variability of oceanic biogeochemical and ecological systems and climate, as well as for understanding the sedimentary record of past conditions.

Another process that has been known for several decades is the direct input of micronutrients (many of which are biologically relevant) to the ocean via high-temperature seawater plumes exiting the seafloor at mid-ocean ridges and mid-plate volcanoes. Significant exchange of material also occurs more subtly via low-temperature circulation of water through the extensive flanks of mid-ocean ridges. In such zones large quantities of deep-ocean water are processed (at temperatures lower than those found in vent systems) through the sediment and aging crust, providing a mechanism for altering the stoichiometry of chemical elements in the emerging water and for supporting microbial life (Cowen et al., 2003). Some elements are preferentially removed from seawater flowing through ridge flanks and other elements are enriched in this seawater. This hydrothermal circulation exerts considerable control on the chemical composition of the entire ocean over the long term, and may affect local chemistry in ridge crest areas and ridge flanks on shorter time scales.

Issue 1.3: End-to-end Food Webs and Material Flows

In keeping with the IMBER goal, project research must approach marine food webs as comprehensive and integrated systems, from viruses to top predators. Perturbations at any point in these systems can propagate both up and down through trophic levels. Thus the focus on specific trophic levels typical of past ecosystem studies may have failed to identify important cascading effects resulting from anthropogenic and natural forcings. Although food webs are essentially continuous systems, research on marine food webs has been fragmented. In the past, research on pelagic food webs tended to focus on either the phytoplankton and microbial food web, or on zooplankton, fish and top predators. Another evident dichotomy is between pelagic and benthic food webs.

The complexity introduced by considering multiple trophic levels can be simplified somewhat by focusing on key species, and/or identifying functional groups within marine food webs. For IMBER research, species should be grouped based on similar biogeochemical roles, rather than taxonomic or genetic similarity. In either case, the goals are to quantify the flow of energy and materials through an ecosystem, and to characterise responses to external forcings.

Understanding of species composition, biodiversity and structure of marine food webs is still limited, especially in the under-sampled mesopelagic and benthic domains. A comprehensive examination of marine life will almost certainly reveal new species – even among well-studied groups – that may be important in ocean elemental cycling and ecosystems. The Census of Marine Life (CoML, www.coml.org) has estimated that as many as 5,000 fish species may be undiscovered. Recent CoML discoveries have included new cetacean (Wada et al., 2003) and gigantic cephalopod species (Veccione et al., 2001). Most of the marine biodiversity probably lies at the other end of the size spectrum, in the microbial food web including viruses, bacteria, algae and microzooplankton. Species richness of Archaea, bacteria and eukaryotes in the ocean may number at least in the millions, and most of those species have not yet been identified or scientifically described (Venter et al., 2004). Very little is understood about how internal and external factors influence biodiversity of these components of marine food webs.

The production of fish depends on the structure of food webs (GLOBEC, 1999), with important implications for human society in terms of food security, biodiversity and the management of marine resources (IHDP, 1999; Loreau and Oliveri, 1999; DIVERSITAS, 2002; Perry and Ommer, 2003). Recent evidence shows that heavy fishing has removed larger commercially valuable fish worldwide, leaving primarily smaller, less commercially valuable fish (Pauly et al., 1998; GLOBEC, 1999). Observational and theoretical evidence suggests that such large changes at the top of marine food webs can induce switches in equilibrium states at lower trophic levels (Spencer and Collie, 1997). How far downward into lower trophic levels this effect propagates is unknown.

Priority Questions

How do food web dynamics affect nutrient availability?

Marine food webs are structured by complex interactions between the concentration, distribution and bioavailability of macro- and micronutrients, and biological processes such as primary production, grazing and predation. Conversely, it is currently unclear how extensively food web structure influences the stoichiometry of micronutrients. Through the JGOFS time-series studies it was shown that phytoplankton species composition and the contribution of nitrogen fixers to primary production varied temporally. Such a change in phytoplankton species composition also changes the function of the ecosystem in biogeochemical cycles (Karl et al., 2001b; Madin et al., 2001; Chiba et al., 2004) (Figure 6), and influences the stoichiometry of important minor elements in seawater. Ecosystem changes (including regime shifts) may occur on a wide range of time scales in response to human activities and inputs, as well as in response to short- and long-term natural cycles (Chavez et al., 2003) – particularly related to climate modes. Greater understanding of such changes in the open ocean and at continental margins is needed.

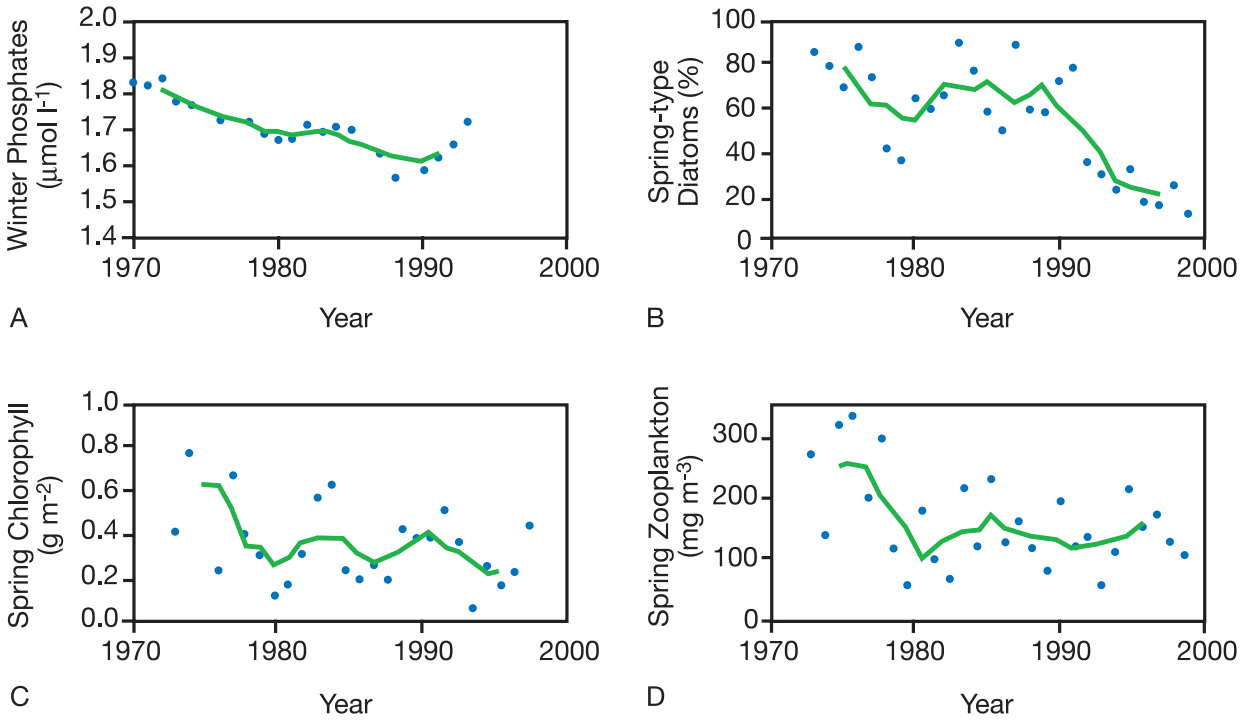
An example is the response of HNLC regions to natural and manipulated iron addition. Iron addition changes phytoplankton species composition, abundance and production, such that dramatic changes in nutrient uptake processes and elemental flux often occur (Wong and Matear, 1999; Bishop et al., 2002). Iron addition experiments tend to produce large diatoms (de Baar et al., in press) which are more prone to sinking than smaller iron-limited phytoplankton, and thus more effective in exporting carbon from the surface layer. Iron availability also influences nitrogen fixation because the functioning of nitrogenase and the other nitrogen fixation processes require more iron than do ammonium and nitrate uptake (Kustka et al., 2003). N:P stoichiometry in marine ecosystems is thus influenced by the amounts of nitrogen fixation and denitrification in the benthic and hypoxic mesopelagic layer.

How do key functional groups, species, and genes affect biogeochemical cycles?

In marine ecology the "structure" of ecosystems is most often condensed to a food web in which all species are aggregated by size, or aggregated into functional or trophic groups. For some studies a more suitable approach is to focus on "key" species that may be expected to explain major characteristics of food webs and ecosystem functioning, and thus reduce ecosystem analysis to a tractable modelling problem. In recent years, it has become clear that many characteristics of global elemental cycles depend on the characteristic properties of relatively few key species or functional groups. For example, variations in community composition and resulting production and metabolic pathways, may produce deviations from the Redfield ratio (Redfield, 1934) with consequences for export ratios and remineralisation length scales (Karl, 1999).

Key species may have high abundance and/or biomass, or have significant impact on a particular biogeochemical process. They may structure the physical and chemical environment; for example, "engineering species" in the benthos. Top predators often moderate the populations of their prey species, which may ultimately affect biogeochemical cycles. In some cases, particularly for micro-organisms, key species may not have been identified because they cannot be cultured. However, it is now possible to use a genomic approach (studying genes and their functions), targeting the diversity and expression of

Figure 6. Evolution over 30 years of the spring bloom environment off Oyashio, Japan. (a) winter phosphate concentration (mixed-layer average, μmol l^{-1}), (b) spring-type diatom abundance (%), (c) integrated column spring chlorophyll (g m^{-2}), (d) spring zooplankton biomass (mg m^{-3}). Points indicate year-to-year values, lines correspond to five-year running means. Adapted from Chiba et al. (2004).



specific genes or portions of the genome of one or more species, and relating this to particular ecosystem processes.

Rapid advances in genomics and analysis of gene expression (the creation of proteins from genes), are being used to detect the occurrence of specific metabolic traits and to study recently discovered metabolic pathways in marine animals. Such techniques allow identification of groups of organisms that perform certain functions within food webs, for example, production of dimethylsulphide (DMS), nitrogen fixation and calcification.

IMBER will advance our understanding of how organisms respond to environmental variation and change at the molecular and genetic levels, and the extent to which these responses are adaptive. Specific research areas may include comparative genome architecture of marine organisms, quantitative variation of life history traits, differential gene expression, molecular mechanisms underlying phenotypic variation, genetic structure of natural populations, ecological significance of molecular variation, genomic analysis of bacteria and viruses, maintenance of intra-specific variation by biotic and abiotic factors, and molecular evolution of regulatory processes.

Introduced or invasive species and the emergence of rare species to become dominant species are special cases for studies of the impacts of key species. Mesoscale iron fertilisation in the western subarctic Pacific dramatically increased the abundance of the previously rare centric diatom *Chaetoceros debilis* within 10 days, resulting in the drawdown of previously high macronutrient levels (Tsuda et al., 2003). Species invasions are occurring with ever-increasing frequency, particularly in coastal waters (Grosholz, 2002) and have devastated some marine ecosystems, including the introductions of the ctenophore *Mnemiopsis leidyi* into the Black Sea (Kideys, 2002), the scyphozoan *Chrysaora melanaster* into the Bering Sea (Brodeur et al., 2002), and other species elsewhere (Hoffmeyer, 2004; Lynam et al., 2004). Similar changes in food web components and species abundances are observed during harmful algal blooms in coastal ecosystems.

How do species biodiversity and species interactions affect food web functioning and biogeochemical cycling?

The composition of food webs in terms of how many and which species are present, can have significant impacts on ecosystem dynamics (Irigoien et al., 2004) and biogeochemical cycling (Legendre and Rivkin, 2002; Bertilsson et al., 2003; Quigg et al., 2003). Studies of ecological stoichiometry are needed in ocean ecosystems (Sterner and Elser, 2002). At present, it is not known how differences in the biodiversity of marine communities yield different flows of energy and matter through marine food webs, or how these differences impact food web structure and function.

Unravelling interrelationships among species diversity, food web functioning and biogeochemical cycling, will require a simplified description of biodiversity, reducing the descriptors to a manageable number. Why are a few species dominant, while most are rare (McGowan, 1990), and what are the consequences of this for biogeochemical cycles? It can be hypothesised that biodiversity increases the functional redundancy of marine ecosystems, and that such redundancy plays an important role in the ability of an ecosystem to withstand natural and anthropogenic disturbance (Fonseca and Ganade, 2001). This hypothesis has been tested extensively for terrestrial ecosystems, but not for marine ecosystems. The impact of changes in biodiversity on food web structure and function and on the stability of marine ecosystems, may prove to be a key determinant of the impacts of global change.

The potential number of interactions among species is almost infinite, but strong selective pressure seems to shape both individual adaptations and the characteristics of marine food webs. To understand how species interactions contribute to marine ecosystem stability, it is necessary to understand how natural selection operates in this highly variable environment, and across a wide range of spatial and temporal scales – from viral infections of cyanobacteria (Bratbak et al., 1994) to orcas feeding on whales.

Species interactions between primary producers and zooplankton are important because they are a crucial step in the transfer of organic matter from the photic zone to deep waters (Madin et al., 2001; Steinberg et al., 2001) and upper trophic levels. Species interactions are also important in determining energy flows in marine food webs. It is important to consider the functional flexibility of species in order to understand biogeochemical cycling and food web structure. For example, some copepod species switch their ecological function from herbivore to carnivore depending on prey availability (Saiz and Kiørboe, 1995), and dinoflagellates can switch from autotrophy to heterotrophy depending on the availability of light and nutrients (Stoecker et al., 1997). Although significant knowledge has been gained on

growth rates of marine organisms through experimentation and modelling, very little is known about mortality induced by predation, grazing, viruses, bacteria and parasites (Ohman and Wood, 1995), or the effect of mortality on food web structure and the recycling of nutrients and carbon.

How are the interactions between biogeochemical processes and food webs recorded in palaeo-proxies?

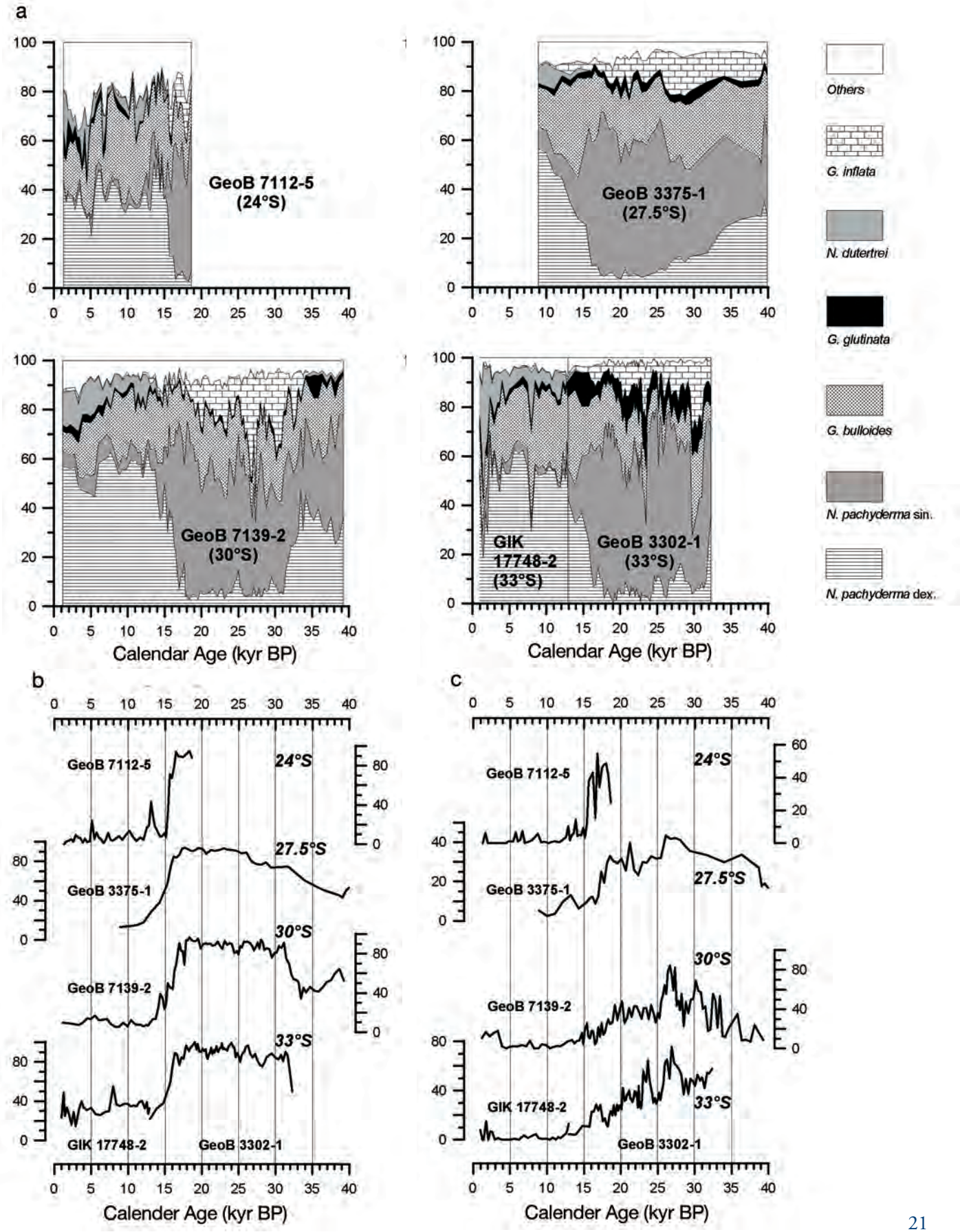
Palaeoceanographic records over the past four glacial cycles indicate clearly that during the maximum glacial conditions (e.g. around 20–30 kyr BP) sea level was 120–140 m below present (Labeyrie et al., 2002). During past warm periods (interglacials), such as 125–130 kyr BP, sea level was higher by 5–10 m because global continental ice cover was less extensive than today. During glacial sea-level lows the enlargement of exposed continental areas probably led to changes in the input of terrestrial material and runoff. All of these processes can provide potential links to ocean systems, but the magnitude and the time scales of modulation in response to human and climate perturbations remain poorly quantified.

The temporal stability of marine food webs and their ecological successions over time are generally unknown. Specifically, it is unknown whether present-day communities are in balance with present-day conditions, and how organisms and the food web structure may adapt over time to global changes in terms of new nutrient, pH or temperature regimes. The available time-series data seldom cover a period sufficiently long to predict species or functional group succession in response to changes in nutrient or physical regime characteristics, and are currently limited to a very narrow range of ecosystem types. In order to predict how marine biogeochemistry and ecosystems will respond to future global change, palaeo-records are required that provide details of past communities and key controls and trigger points and hotspots in biogeochemical cycles and ecosystems. The search for palaeo-proxies that would extend the record of climatic and biogeochemical variability and changes in the structure, function and dynamics of marine food webs, is important in developing a predictive understanding of marine biogeochemical cycles and ecosystems. Palaeoceanographic records suggest large variations in marine food webs in the past that are correlated with changes in the marine chemical and physical regimes. For example, several proxies show glacial-interglacial fluctuations in temperature, salinity, pCO_2 and sediment redox states, synchronised with changes in composition of planktonic and benthic communities (Figure 7).

Changes in biodiversity, from plankton to higher organisms, may provide critical information on pre-anthropogenic ecosystem evolution. Species that do not leave an obvious fossil record, such as cyanobacteria and phytoplankton species such as *Phaeocystis*, may be indicative of past physical and chemical environmental conditions, and tools for their detection in the sedimentary record should be developed. Documenting shifts in marine ecosystems, understanding the causes of such shifts and combining insights from modern oceanographic experiments and multiproxy sedimentary records at key sites, will provide insights into biogeochemical feedback processes that control the carbon cycle.

Improvement of chronology and calibration for marine palaeo-proxies with instrumental records is necessary to better interpret the palaeoceanographic records from sediments, corals and other sources. Multiple proxies that reveal synchronous variations in food web composition and function and nutrient distribution will be particularly useful. Documenting evolutionary shifts in ecosystem states and understanding their causes will provide insights into the physical and geochemical processes that drive ecological change and biogeochemical feedbacks.

Figure 7. (a) Time-series records of cumulative percentage of planktic foraminiferal species composition in cores from the Chilean continental slope; the vertical line at 13 kyr on the graph for the cores from 33°S separates core GeoB 3302-1 from core GIK 17748-2. (b) Ratio of *N. pachyderma* sin to *N. pachyderma* dex (%). (c) Ratio of *G. inflata* to *G. bulloides (%)*. Note the differing vertical scales. From Mohtadi and Hebbeln (2004).



Theme 2: Sensitivity to Global Change

What are the responses of key marine biogeochemical cycles, ecosystems and their interactions, to global change?

IMBER will focus not only on observation and analysis of current marine biogeochemical cycles and ecosystems, but also on understanding and predicting how these will respond to the complex forcings associated with global change. Identification of components of biogeochemical cycles and ecosystems that may respond most directly to global change is important. In this theme such responses have been partitioned into four major issues: (i) effects of climate-induced changes in physical ocean dynamics, (ii) effects of increasing CO_2 levels and decreasing pH, (iii) effects of changes in macro- and micronutrient inputs to the ocean, and (iv) impacts of marine harvesting.

IMBER will investigate how large-scale climate phenomena that alter the physical forcing on seasonal to inter-decadal time scales affect the ocean, and how these oceanic changes can directly alter the temperature and light environment and distribution of carbon and nutrients in the upper ocean. IMBER will also consider how changes in pH and carbon system parameters can alter biogeochemical cycles and ecosystems (including organism physiology, population levels and food web composition and structure). Further, IMBER will examine how global change affects the controls on biological growth (and related biogeochemical processes) which are exerted by oceanic distributions of macro- and micronutrients, and by the complex roles of iron and other nutrients from continental sources. Fishing pressure is heavily impacting marine food webs – and possibly biogeochemical cycles – although our understanding of potentially complex feedback effects like trophic cascades is rudimentary. These issues must be considered from diverse interdisciplinary perspectives, with scientific approaches guided by carefully defined objectives and implementation strategies.

The combined effects of all of these global change impacts may be very different from the sum of the individual effects, and at present there is no way to reliably predict how concurrent changes in multiple factors will affect marine ecosystem structure and function. IMBER will encourage an integrated approach to understanding the consequences of global change for ocean food webs and biogeochemistry, by examining the potential synergistic and antagonistic effects of key variables including CO_2, pH, temperature, light, nutrients and shifts in top-down control mechanisms. Though some data exist on the individual effects of these variables, research needs to determine the net effect of simultaneous changes in multiple variables. IMBER aims to provide an understanding of the net effects of global change on marine biota, and to supply vital information on how biogeochemical and ecosystem changes are linked through feedback mechanisms to oceanic and atmospheric chemistry.

Issue 2.1: Impacts of Climate-Induced Changes Through Physical Forcing and Variability

Biogeochemical cycles and ecosystems in the ocean are strongly affected by a wide range of physical processes, including temperature changes, horizontal and vertical transport, and upwelling and mixing of deep water. The critical time scales of biogeochemical and physical processes are not necessarily matched, leading to intrinsic spatial and temporal variability in ocean biology. Moreover, coupled ocean-atmosphere models predict significant changes in ocean circulation on time scales from decades to centuries and on spatial scales ranging from regional to global.

Such changes will result in modification of both the mean state and the spatial and temporal variability of the uptake, distribution and sequestration of biologically important substances throughout the ocean. These modifications have been linked to changing atmospheric composition and subsequent climatic effects in the past, through proxy records such as the Vostok Ice Core. Climate changes will also induce variability in direct physical forcing, which is probably just as important in controlling biological distributions and adaptations. The physical processes controlling major ecosystem processes and elemental fluxes, and how these will be affected by global change, must be identified and quantified.

Our incomplete understanding of the physical evolution of atmosphere-ocean interactions and the potentially non-linear ecological and biogeochemical responses to global changes hinder our ability to create accurate scenarios of the future effects of climate change on marine ecosystems. Predictions of how changes in climate will affect marine biogeochemical cycles and ecosystems will require a much better understanding of how climate change will affect physical conditions in the ocean, and how specific changes in these physical conditions will affect processes important to biogeochemical cycles and ecosystem structure. Particularly important will be a better understanding of the effects of changes in ocean physics on (i) carbon exchange, transport and storage, (ii) dynamics of key species and functional groups (e.g. biodiversity, biogeographical ranges, blooms of gelatinous zooplankton, migration and transport pathways of organisms), (iii) metabolic processes and life history strategies of organisms, and (iv) benthic-pelagic and continental shelf–open ocean coupling.

Priority Questions

What are the impacts of changes in circulation, ventilation and stratification?

It is likely that human-induced climate change will alter ocean circulation and its variability. For example, simulations of the climate effects of increased CO_2 by Sarmiento et al. (1998) predict reduced meridional overturning circulation and meridional heat transport, less vigorous wind mixing and greater stratification in the future. These effects will lead to reduction in global new primary production, but with complex regional patterns (Bopp et al., 2001; Snyder et al., 2003). At higher latitudes global warming could result in increased wind mixing (Debernard et al., 2002; Danard et al., 2003) and turbulence, influencing plankton contact rates and growth (Rothschild and Osborn, 1988). All these physical properties are linked, and they influence marine organisms directly as well as indirectly through the food web (Sundby, 2000).

Evaluation of the physical mechanisms that control biogeochemical cycles of major elements and distributions of key species is important. Climatic conditions favouring stratification, for instance, may shift the balance in sources of new nitrogen from vertically mixed nitrate (and phosphate) to fixed atmospheric nitrogen, with commensurate shifts in food web structure. Such shifts will be reflected in the magnitude, form and fate of organic matter constituting the biological pump, and will resonate throughout the ecosystem over seasonal-to-decadal time scales. The redistribution of nutrients and changes in circulation and stratification will lead to alteration of the rates, modes and patterns of biological production (Boyd and Doney, 2003). For example, changes in subtropical and tropical circulation related to the El Niño-Southern Oscillation (ENSO) have been implicated in significant biological and biogeochemical shifts in the Pacific Ocean (Karl, 1999; Karl et al., 2001b) (Figure 8).

Figure 8. Shifts at ALOHA station (Pacific Ocean) over time between phosphorus limitation and nitrogen limitation as indicated by time-series of 3-point running nutrient ratio values for: (a) total dissolved matter in 0–100 m, (b) suspended particulate matter in 0–100 m, and (c) exported (deposited) particulate matter (trapped at 150 m depth). The dashed lines correspond to the Redfield ratio; points above this line correspond to phosphorus limitation and points below the line correspond to nitrogen limitation. From Karl et al. (2003).

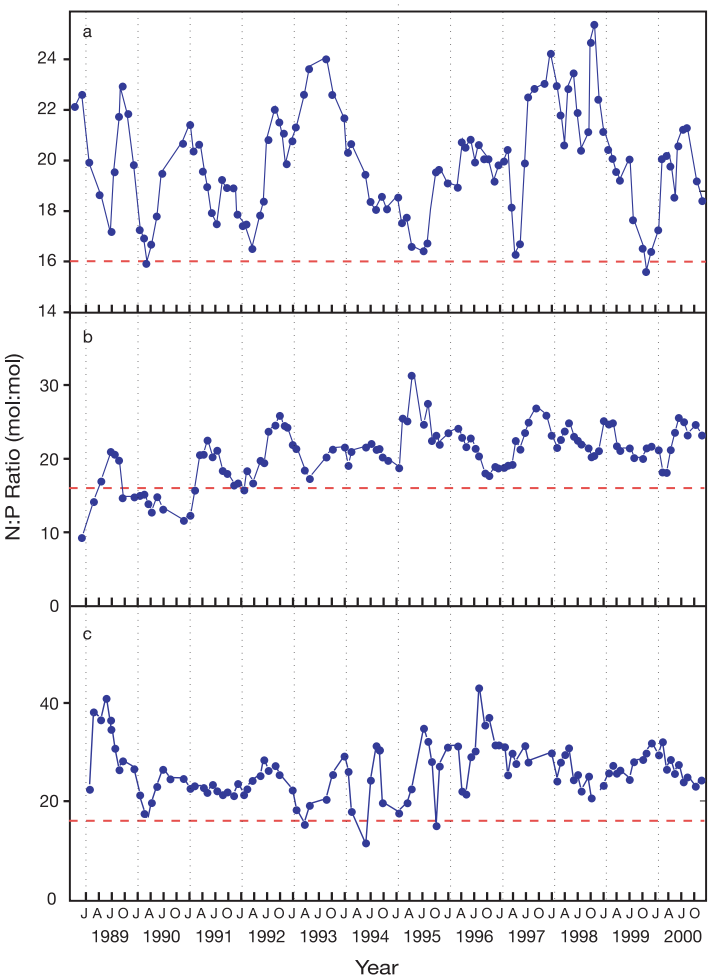
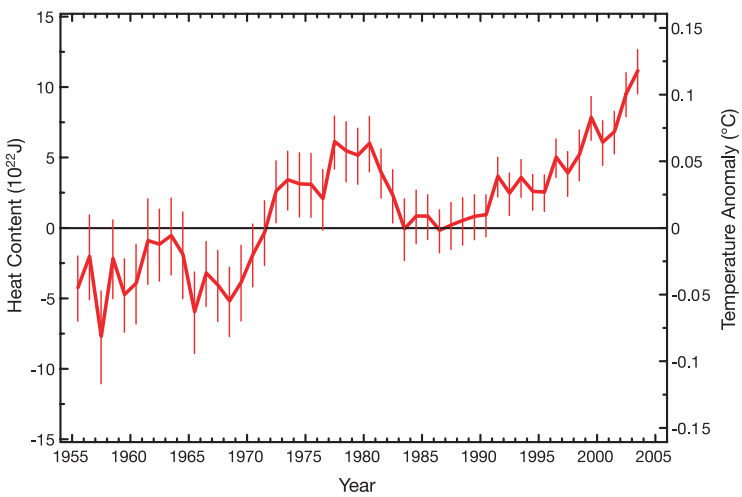


Figure 9. Time series of yearly ocean heat content for the 0–700 m layer. Each yearly estimate is plotted at the midpoint of the year. From Levitus et al. (2005).



Decadal climate modes (e.g. ENSO, NAO and PDO) and related teleconnections are likely to introduce signals into the ocean system, such as variations in heat content (Levitus et al., 2005, Figure 9), changes in carbon storage in the subtropical thermocline (Bates et al., 2002) and changes in iron delivery as dust (Prospero, 1999). Long-term evolution of nutrient concentrations in response to changes in physics are also observed off Japan (Ono et al., 2002). Such climatic oscillations result in the decoupling of major nutrient cycles (particularly nitrogen and phosphorus) and imply a previously unexpected fluidity in the large-scale elemental cycles. In addition to such shifts, significant large-scale changes in the magnitude of new production in the Equatorial Pacific Ocean may be a response to ENSO forcing (Turk et al., 2001). Changes in ocean-margin upwelling substantially alter productivity and subsurface oxygen distribution (Grantham et al., 2004). These changes may propagate into the ocean interior, and ultimately throughout the entire marine system. Although such regional-scale perturbations have been observed, extrapolation to basin and global scales is not practical using current understanding and given the existing level of observations of basic biological, physical and biogeochemical processes. Gaining a better understanding of physical global change processes and their impacts on food web–biogeochemical interactions will be an area of emphasis for IMBER.

What are the direct effects of changes in ocean temperature and light environment?

Models suggest that sea surface temperature (SST) will increase by 1–4°C over the next century in some parts of the ocean (Bopp et al., 2001). This will most likely have direct impacts on marine ecosystems, including changes in productivity, biodiversity and biogeographical ranges. Temperature changes will also affect the rates of critical physiological processes, such as respiration and photosynthesis, with potentially large biological and biogeochemical consequences. It has been suggested that export production may be lower in a warming future ocean (Laws et al., 2000; Bopp et al., 2001). At present however, the nature and degree of many of the effects of future SST increase are poorly understood.

Temperature changes can shift seasonal cycles of planktonic and benthic species' abundances (Greve, 2001; Edwards and Richardson, 2004), growth and recruitment of fish (Brander, 1995; Sundby, 2000) and

food web dynamics (McGowan et al., 2003). Geographic range displacements resulting from temperature change have been reported for diverse marine organisms (Nakken and Raknes, 1987; Southward et al., 1995; Molenaar and Breeman, 1997; Beaugrand et al., 2002; Parmesan and Yohe, 2003), and have been inferred from population genetic analysis (Bucklin and Wiebe, 1998). Unprecedented recent blooms of the coccolithophorid *Emiliania huxleyi* in the Bering Sea have been linked to changing climate regimes, including decreased mixed-layer depths and increased SST (Sukhanova and Flint, 1998; Napp and Hunt, 2001; Stockwell et al., 2001).

Critical marine ecosystems could potentially sustain serious damage and losses of biodiversity from long-term ocean warming. Coral reef systems worldwide have already begun to exhibit signs of thermal stress, including increasing frequency and severity of coral bleaching events and mass mortalities (Hughes et al., 2003; Bellwood et al., 2004). Reduced viability of reef-building coral species will also lead to widespread losses of the exceptionally diverse biological communities that rely on them (Jones et al., 2004). High-latitude sea ice melting could severely alter the food web dynamics of the polar seas, with possible concomitant losses of crucial biological communities, functional groups and species richness. It is expected that climate warming will significantly reduce the sea ice cover (Sarmiento et al., 2004) – especially in summer, while in winter some local extension could occur due to stratification or change in deep-water ventilation areas. Because the seasonal productivity cycle in marginal sea ice zones is strongly driven by melt-water during the period of ice retreat, consequences for marine ecosystems are expected and should be investigated. Arctic sea ice is a key area where strong changes are observed and where summer disappearance is expected (Houghton et al., 2001).

The light environment experienced by marine phytoplankton communities is also likely to change as a result of increased ocean stratification and shallower mixed layers (Bopp et al., 2001); the result will be an increase in the average integrated light intensity experienced by phytoplankton. Marine organisms are directly impacted by changes in light intensity (Huse, 1994; Macy et al., 1998), which can alter ecosystem dynamics such as trophic and competitive interactions (Fiksen et al., 1998). Biological, biogeochemical and molecular processes are significantly altered by changes in ultraviolet radiation resulting from both natural and anthropogenic causes (Boucher and Prezelin, 1996; Shick et al., 1996; Speekmann et al., 2000; Grad et al., 2001; Helbling et al., 2001). Thus light-driven effects of increased surface-ocean stratification could influence not only total phytoplankton biomass and productivity, but also the taxonomic composition of phytoplankton assemblages. In the Ross Sea, for instance, deeper mixed layers have been suggested to favour the haptophyte *Phaeocystis*, while shallower mixed layers along melting ice edges promote diatom blooms (Arrigo et al., 1999). Light is a key variable controlling primary production and ecosystem structure in the ocean, and the consequences of possible global change-mediated alterations in surface-ocean irradiance need to be carefully evaluated.

What are the impacts of changes in the frequency and intensity of extreme and episodic events?

Global change is often taken to imply slow but steady trends in the averages of variables such as SST, primary productivity or carbon flux, where averages are taken over wide areas and times. Certainly such changes in the averages of marine physical, ecosystem and biogeochemical variables are expected to result from global change, but they do not represent the entirety of change in ecosystem processes, nor do they necessarily reflect the changes of greatest impact on ocean systems. Changes in ocean processes will also arise from alterations in the frequency, duration and timing of extreme events, such as winter storms and hurricanes, coastal floods and droughts, extended periods of cold or warmth and variability in the extent of sea ice. The state of climate modes controls the frequency, location and strength of extreme events, which may have a great impact on ocean ecosystems and biogeochemical states.

As an example, hurricanes in the Sargasso Sea leave a track on the ocean surface: a path of lower SST which is visible in satellite images. In the wake of hurricanes, zooplankton biomass (Roman et al., 1993) and primary productivity (Malone et al., 1993) are reduced because the mixed-layer depth is increased. Hurricane-induced mixing may also enrich the surface ocean in nutrients due to enhanced upwelling from the mesopelagic layer, thus increasing productivity in the longer term. The air-sea exchange of CO_2 is increased (Bates et al., 1998) during and following hurricanes, due to changes in the variables controlling the rate of flux, such as SST and wind speed.

The magnitude of coastal flooding also can be controlled by the state of climate modes. ENSO events change the locations and amounts of precipitation, affecting riverine inputs to the ocean margin on the North American west coast (Pavia and Badan, 1998), the South American west coast and Australia. Flooding delivers nutrients, particulates, organic matter and pollutants to the ocean margins, thus impacting directly, broadly and immediately the margin ecosystems (Justic et al., 2003).

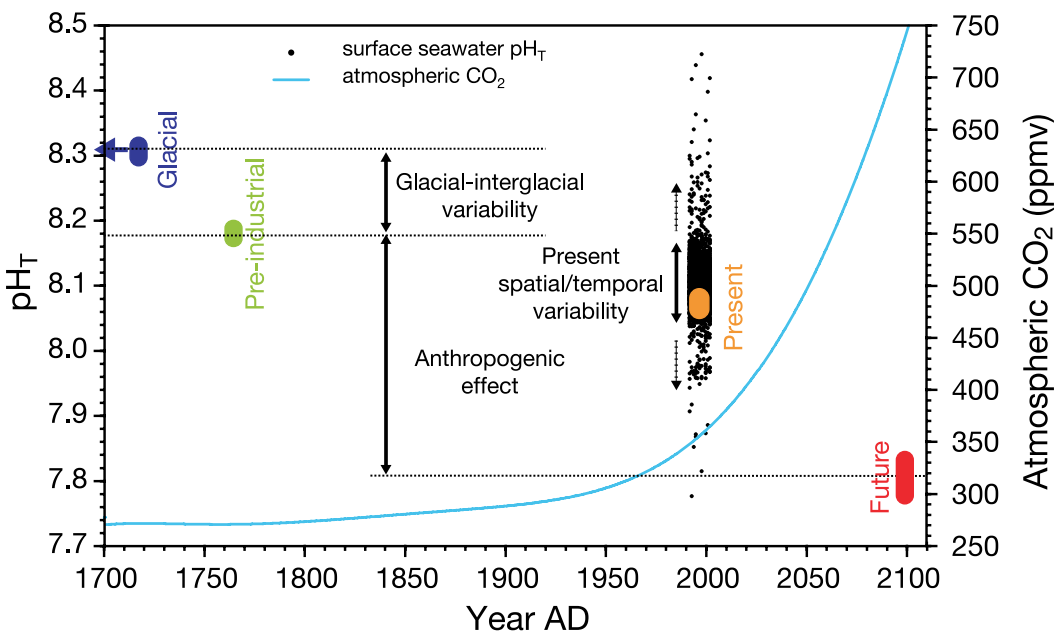
Biological extreme events also have major biogeochemical impacts. For instance, unpredictable and infrequent salp blooms have been implicated as playing an important role in highly efficient scavenging of biomass from the water column, speeding delivery of carbon to the ocean depths with particularly large faecal pellets (Naqvi et al., 2002). Diazotroph blooms or periods of extended diazotrophy will force changes in the grazer food web, the stoichiometry of remineralisation and remineralisation length scales. These currently unpredictable episodic events (Justic et al., 2003), which are undoubtedly affected by changes in oceanographic conditions such as water column stability, must be evaluated. It is important to understand which episodic and extreme events have the most impact on marine ecosystems and biogeochemical cycles, and which of these will be most impacted by changing ocean physical conditions. Changes in the frequency, duration and strength of these physical events ripple through the ecosystem, but how far, and with what result? Establishing how global changes in, for example, ocean stratification, acidity or nutrient availability, will cascade through marine ecosystems via extreme and episodic events is important.

Issue 2.2: Effects of Increasing Anthropogenic CO_2 and Changing pH on Marine Biogeochemical Cycles, Ecosystems and Their Interactions

Projected CO_2 emissions to the atmosphere over the next century will approximately double surface seawater CO_2 concentrations, with a resulting drop in pH of about 0.35 (Wolf-Gladrow et al., 1999); by 2250 ocean pH is projected to decrease by 0.77 (Calderia and Wickett, 2003). Currently, most surface waters have a pH of 8.1 ± 0.1 (Figure 10). Even glacial-interglacial ocean pH changes, as driven by variations in atmospheric CO_2 concentrations, represent a comparatively small perturbation of 0.10–0.15. During the past 23 million years the atmospheric CO_2 concentration probably never exceeded 300 ppm (Pagani et al., 1999; Pearson and Palmer, 1999; Petit et al., 1999), thus marine organisms have had a long time to adapt to a fairly narrow equilibrium pH range. Although marine organisms may experience pH values above this range from time to time due to intense CO_2 drawdown during algal blooms, values below this range are rarely, if ever, encountered in surface waters.

A better understanding of the effects of changing pH and carbon system parameters on marine biogeochemical cycles and organisms is urgently needed for two reasons: firstly, global-scale alterations of these variables are already well underway and will become more pronounced in the near future, and secondly, there are current suggestions that increasing atmospheric CO_2 concentrations could be mitigated by purposeful sequestration of carbon in the ocean. The impacts of such activities on biogeochemical cycles and ecosystems could be substantial. Current limited understanding of pH (and CO_2) effects does not allow evaluation of different scenarios of CO_2 -increase and -mitigation strategies.

Figure 10. Surface seawater pH_T values and atmospheric CO_2 concentrations. Surface seawater pH_T values include 3000 values for 1990–2002 (from the upper 25 m across all oceans) calculated from measured DIC and alkalinity; typical values for glacial times (blue), pre-industrial times (green) and the present (orange); and predicted future values (red). Future values are based on predicted atmospheric CO_2. Atmospheric CO_2 values are based on historic measurements and an exponential future increase from simple scenario calculations. Prepared by Arne Körtzinger on the basis of WOCE data (Schlitzer, 2000).



Priority Questions

What are the effects of CO_2-driven changes in carbonate chemistry?

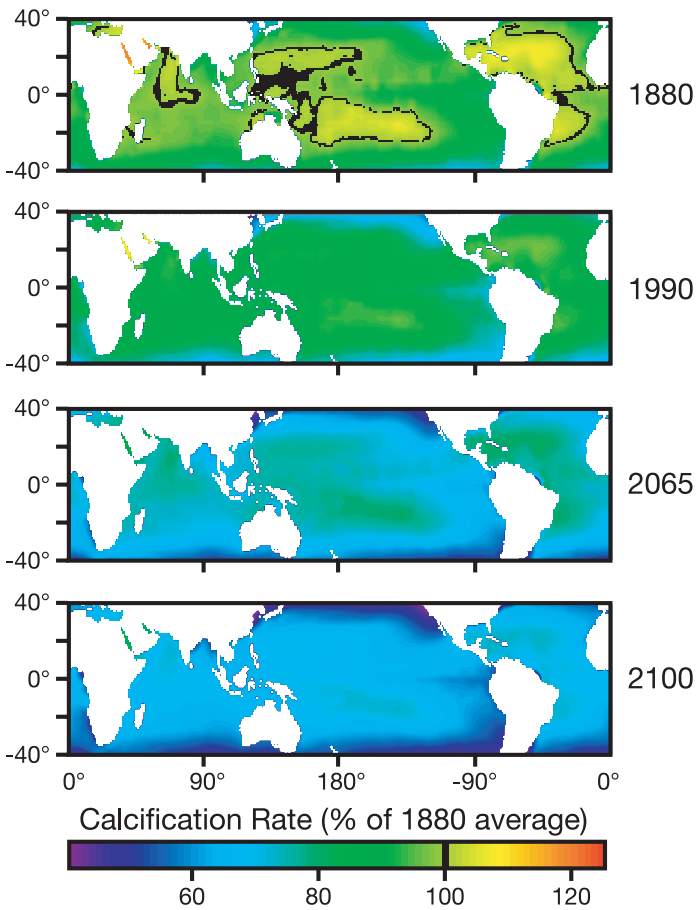
The chemical speciation within the marine CO_2 system is the major factor determining seawater pH. The significant acidification of the surface ocean will cause major shifts in the speciation of the marine CO_2 system, namely a marked increase in CO_2 (aq) and a strong decrease in carbonate ion (CO_3^{2-}) concentrations. The expected dramatic changes in pH and the marine carbonate system are very likely to affect marine organisms and metabolism in various ways, possibly leading to shifts and changes in biogeochemical cycles, ecosystems and their interactions.

Several direct effects of increasing CO_2 (aq) on biological productivity and the biological pump have been recognised. Existing experimental evidence suggests that changes in CO_2 availability can have large effects on algal physiology, community composition and nutrient cycling (Raven, 1997; Wolf-Gladrow et al., 1999; Burkhart et al., 2001; Tortell et al., 2002). Observed taxon-specific differences in CO_2 sensitivity suggest that changes in CO_2 availability may influence phytoplankton species succession and distribution (Rost et al., 2003). However, there is contradictory evidence about whether increasing CO_2 concentrations in the ocean will actually enhance oceanic productivity (Hein and Sand-Jensen, 1997).

CO_2-driven changes in Redfield C:P ratios have been observed in culture experiments (Burkhardt et al., 1999), challenging the commonly accepted notion of CO_2-independent Redfield ratios. Flexibility in these ratios allows for the possibility of CO_2-related changes in the stoichiometry and strength of the biological carbon pump. Mesocosm experiments show that elevated CO_2 levels may lead to increased exudation of carbon-rich DOC (Engel et al., 2004). As DOC has been shown to be a precursor of transparent exopolymer particles (TEP), which appear to be strongly involved in particle aggregation in the ocean, CO_2-driven changes in TEP abundances may impact particle flux in the ocean and lead to stimulation of the biological pump.

As its carbonate ion concentration decreases, surface seawater becomes less supersaturated with respect to calcite and aragonite mineral phases, simply as a consequence of the uptake of anthropogenic CO_2. There is strong evidence that such decreases in calcite and aragonite supersaturation in seawater have negative impacts on calcification success of corals and coralline macro-algae (Figure 11, Kleypas et al., 1999; Langdon et al., 2000). Calcification by coccolithophorids is also reduced at elevated CO_2 (Riebesell et al., 2000). It remains to be seen how this will affect net community production (Langdon et al., 2003) in the marine environment, as well as $CaCO_3$ dissolution at depth and feedbacks to atmospheric CO_2 concentrations (Zondervan et al., 2001). Furthermore, changes in marine calcification may directly impact organic carbon export via the proposed role of $CaCO_3$ as mineral ballast in POC export (Armstrong et al., 2002; Klaas and Archer, 2002). Despite recent research effort in this area major questions remain unanswered regarding the ultimate impacts of changing carbonate chemistry in the ocean.

Figure 11. Projected change in coral reef calcification rate based on average calcification response of two species of tropical marine algae and one coral in a marine mesocosm. From Kleypas et al. (1999); reprinted with permission from the American Association for the Advancement of Science.



What are the effects of pH-driven changes in nutrient and trace metal speciation?

In addition to direct effects of changing carbonate chemistry on the marine biota, there is a strong likelihood of indirect changes via pH effects on the availability and speciation of macro- and micronutrients and toxic trace metals. Concentrations of micronutrients may be influenced by pH changes through pH-dependent sorption-desorption equilibria (Granéli and Haraldsson, 1993), which may either enhance or inhibit marine phytoplankton production. The speciation of trace elements may be affected by pH changes (Kester, 1986) with both beneficial (e.g. Co and Fe) and inhibitory (e.g. Cu) consequences for biological productivity. Major nutrient speciation could also be affected by ocean acidity changes; for instance, the particle reactivity of phosphate increases markedly with lowered pH, potentially favouring the removal of this nutrient from seawater through particle-scavenging processes (Sañudo-Wilhelmy et al., 2004). All of these processes will be further complicated by redox chemistry under changing oxygen levels and hypoxia extent in the ocean, and thus may be considerably amplified in the coastal zone. Although more subtle than direct pH or CO_2 effects on the biology, these types of changes in limiting nutrient chemistry and cycling also have the potential to drive very large indirect changes in ocean ecosystem structure and function.

Which organisms and biological processes are most sensitive to pH and CO_2 changes, what are the consequences and to what extent can organisms adapt in response to these changes?

The pH of seawater is a "master variable" in the marine system. Changes in pH may therefore result in a significant impact on marine ecosystems via a number of possible mechanisms. The importance of pH is illustrated by the effects of pH on enzymes – especially those with exogenous substrates. Depending on an enzyme's pH optimum, decreasing seawater pH may increase or decrease enzyme activity. Maintaining a specific optimal intracellular pH may cause cells to use more (or less) energy under conditions of changing ambient pH (Raven and Lucas, 1985), and may affect a cell's overall performance. These examples demonstrate that changing pH will affect food webs by multiple mechanisms simultaneously, in different directions and to varying degrees. An extensive review of the effects of pH on coastal phytoplankton by Hinga (2002) revealed significant differences in pH sensitivity and pH ranges, but provided limited insight into the underlying mechanisms of pH effects.

Recognising the strong potential impact of pH changes on marine organisms and ecosystems, it will be important to develop ideas and techniques to investigate the adaptive capabilities of marine biota to a low-pH environment. Predictions of the impacts on marine systems of decreased pH will depend critically on whether adaptation by both organisms and ecosystems as a whole can keep pace with predicted pH changes. An important feature of such research would be to attempt to determine the physiological and genetic components of organism adaptations to pH changes.

A broad understanding should be developed of the pH sensitivity of marine biogeochemical cycles and ecosystems, ranging from organisms and their metabolic processes to overall food web structure and function. Understanding is currently lacking on how changes in the marine CO_2 system will impact the broad spectrum of biological processes such as primary and secondary production, key species' dynamics and energy flow in food webs. Such changes will likely stimulate a multitude of responses caused and controlled by mechanisms that may not yet be understood or anticipated. On the basis of such knowledge it will be essential to develop a better understanding of the integral effects of pH changes on the quantity and quality (e.g. organic: inorganic carbon ratio, opal:carbonate ratio) of the biological pump and the resulting potential feedback on atmospheric CO_2 concentrations. In the future it will be necessary to answer questions and provide sound scientific guidance from a biogeochemical and ecosystem perspective in the context of proposed purposeful deep-ocean CO_2 sequestration schemes. These studies should also be extended to deep-sea ecosystems and to the pH ranges to be expected locally and regionally in the course of such attempted technological fixes.

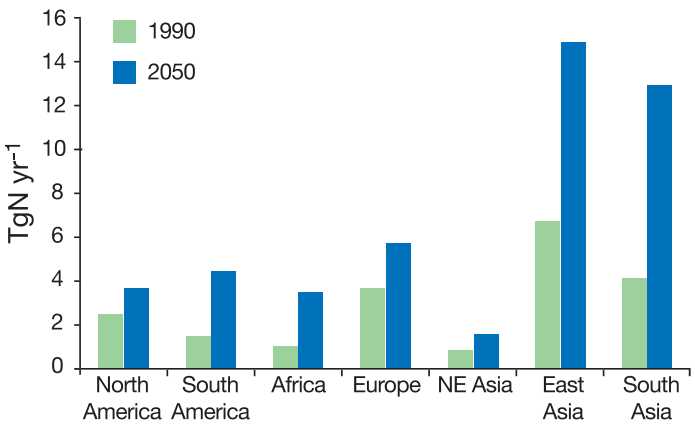
Issue 2.3: Effects of Changing Supplies of Macro- and Micronutrients

Human activities have been significantly modifying chemical transfers across the ocean-land and ocean-atmosphere boundaries for decades. Despite a great deal of research, the cumulative impacts of cultural eutrophication continue to be uncertain. A quantitative understanding must be developed of the coupled responses of marine biogeochemical cycles and food webs to such anthropogenic additions of both macro- and micronutrients.

Macronutrients generally occur naturally in seawater in fairly constant ratios that can be altered by anthropogenic additions. Currently, inputs of nitrogen and phosphorus from land to the ocean due to eutrophication are several times their natural values. However, damming of rivers has resulted in reservoir entrapment of some nutrients, particularly silicon – and to a lesser extent phosphorus (Zhang et al., 1999; Ittekkot et al., 2000; Rabalais and Nixon, 2002). Another two-fold increase in land-source nutrient fluxes to the ocean is projected to occur by the middle of this century (Figure 12). The human alteration of nutrient fluxes has been geographically uneven, with the largest changes occurring in areas of high population density and extensive agricultural production, and within marginal seas and over continental shelves.

Further changes in nutrient ratios can be brought about by shifts in biogeochemical processes in the ocean itself. For example, continuing global expansion of oxygen-depleted zones resulting from eutrophication is expected to lead to an increase in denitrification rates (Diaz and Rosenburg, 1995). This change will be associated with remobilisation of phosphorus and micronutrients from continental shelf sediments, resulting in a decrease in the N:P ratio in the water column, and an increase in the availability of micronutrients such as iron for assimilation by organisms. Results of time-series observations in the North Pacific Ocean indicate that changes in nitrogen fixation may be associated with alternating nitrogen and phosphorus control of production on decadal time scales (Karl et al., 2001a). Decoupling of macronutrient cycles in the ocean – in which micronutrients probably play key roles – is now widely regarded as being of key ecological importance.

Figure 12. Predicted riverine fluxes of dissolved inorganic nitrogen for various regions in 1990 and 2050 for the "business-as-usual" scenario. From Seitzinger et al. (2002); reprinted with permission from the Estuarine Research Federation.



Priority Questions

How will changes in macro- and micronutrient inputs to the ocean affect the cycles of these elements?

The effects of increased inputs of macro- and micronutrients from land to the ocean via the atmosphere, freshwater runoff and submarine groundwater discharge, on the biogeochemical processes and fluxes in the ocean are not fully understood. There are unanswered questions regarding the net effect of counter-balancing processes; for example, nitrogen loss through denitrification will lower the fixed N:P ratio, thereby setting the stage for nitrogen fixation. Conversely, processes that stimulate nitrogen fixation (such as iron inputs) will tend to raise the N:P ratio. What the net effect of these opposing processes will be on the global fixed nitrogen inventory and how this will affect fluxes and the stoichiometric composition of organic matter in different domains remains poorly understood. Human activities tend to contribute N and P to the coastal ocean, while Si inputs still originate mainly from natural weathering processes. Cultural eutrophication therefore usually increases N:Si and P:Si ratios, with

possible impacts on the relative biological availability and removal processes of these nutrients. Human-driven increases or decreases in aeolian iron inputs are also likely. How this will affect the cycling of this limiting micronutrient and the biogeochemistry of major nutrients like nitrogen is far from certain.

How will changes in the abundance, distribution and stoichiometry of nutrient elements affect food web structure and function?

Changes in the structure and dynamics of marine food webs will impact, and be impacted by, altered chemical forcing; that is, changes in the quality and quantity of macro- and micronutrients from the land, atmosphere and bottom sediments. Since species differ in their nutrient requirements, changes in the levels and ratios of nutrients entering the ocean can be expected to change the relative abundance of different groups. Modified nutrient ratios can significantly impact marine food web structures and biodiversity (Sterner and Elser, 2002). Under conditions of abundant silicon and iron, diatoms may become the dominant primary producers and food webs will support commercially important fisheries. Where diatom productivity is limited by a low Si:N ratio (or insufficient Fe supplies), the food web is more complex and flagellates may dominate, with a smaller fraction of production reaching the higher trophic levels (Turner, 2002). Food web structure also determines the extent of export from the surface waters (Michaels and Silver, 1988). Other consequences of eutrophication and associated changes in relative abundance of nutrients in coastal waters may include increases in the number and severity of blooms of toxic dinoflagellates and other harmful algal species (Anderson et al., 2002), and shifts in the abundance, diversity and harvest of fish in affected regions (Breitburg, 2002). The impacts of increased terrestrial supply of dissolved and particulate matter may extend from shallow waters to well offshore. The nature and extent of such changes and the possible feedback loops of biological processes to chemical forcing, remain open questions.

How will increases in hypoxia and anoxia affect food webs and cycles of key macro- and micronutrients?

Oceanic distribution of dissolved oxygen is expected to be significantly altered by changes in water circulation and organic loading arising from human activities. Models suggest that stronger stratification associated with impending global warming may cause an expansion of oxygen-minimum zones. Decreases in subsurface oxygen levels have already been recorded in several areas of the open ocean; in addition, eutrophication driven by terrestrial inputs of nutrients is turning vast stretches of near-bottom waters hypoxic, and even anoxic, over several continental shelves. Nutrient over-enrichment may be responsible for recent discoveries of hypoxia in coastal waters in regions not previously known to experience oxygen depletion (Hearn and Robinson, 2001; Rabalais and Turner, 2001; Li et al., 2002; Weeks et al., 2002). There are several important yet poorly understood aspects of coastal anoxia and hypoxia, including how exposure of sediments to reducing conditions facilitates mobilisation of redox-sensitive metals such as iron and manganese. Aside from serving as an unquantified source of these bioactive elements to surface and intermediate waters, such mobilisation may interact through redox chemistry with the nitrogen cycle. The contribution of such interactions to the nitrogen cycle should be evaluated.

Intensification of subsurface oxygen-deficiency is expected to significantly impact biogeochemistry and ecosystems in several ways. Firstly, anaerobic conditions greatly affect cycles of polyvalent elements – some of which serve as important macro- (e.g. N) and micronutrients (e.g. Fe). Loss of the oxidized nitrogen to gaseous forms (denitrification) changes the speciation and inventory of fixed nitrogen and the ratios between the major macronutrients (N:P), thus affecting rates of primary production and food web structure. Secondly, hypoxia and anoxia in coastal waters have significant impacts on marine biota, including organism metabolic changes, species distributions, biodiversity and food web dynamics (Ross et al., 2001; Breitburg, 2002; Cooper et al., 2002; Baden and Neil, 2003). Thirdly, sedimentary cycling of biogenic elements (e.g. C, N, P, S and Fe) and their exchanges across the sediment-water interface are greatly modified, and fourthly, biogeochemical transformations involving climatically important gases such as nitrous oxide are extremely sensitive to changes in oxygen concentrations at low concentrations.

Linkages between nutrient inputs, oxygen concentration of coastal waters, biogeochemical cycling and benthic fauna should be explored (Justic et al., 1997; Rabalais and Turner, 2001). The rate of organic carbon accumulation per unit area of the seafloor can be up to 30 times higher in coastal areas than in the open ocean (Chen et al., 2003). Eutrophication and related hypoxia and anoxia in coastal waters may be expected to favour preservation of carbon in the marginal sediments, and possibly

carbon export to the ocean interior. However, sedentary benthic animals cannot benefit from the enhanced food availability due to hostile conditions arising from the absence of oxygen (Rabalais and Turner, 2001). Moreover, the lower pH in anoxic areas may suppress the growth of benthic animals with calcareous shells. Hypoxia can also alter benthic-pelagic coupling and transfers across the sediment-water interface over continental margins. While an increased carbon supply to sediments supports sedimentary denitrification and sulphate reduction, the decreased oxygen penetration to sediments arising from bottom-water oxygen depletion and reduction of bioturbation limit nitrate availability for denitrification. Thus the extent to which sedimentary denitrification can serve as a buffer to increased nitrate loading in coastal waters is still unclear.

Issue 2.4: Impacts of Harvesting on End-to-end Food Webs and Biogeochemical Cycles

It is now well established that harvesting has drastically reduced various fish stocks (FAO, 2000). Quantitative estimates of the relative decline of some species are given by Christensen et al. (2003) and Myers and Worm (2003) – amongst others, with estimates ranging from several-fold up to an order of magnitude. Harvesting began in coastal areas centuries ago (Jackson et al., 2001), expanding into the North Atlantic and North Pacific oceans in the early 20th century, and finally to oceans worldwide after the 1970s following the development of industrialised fisheries (Figure 13). The effects of fishing on non-target species and on the diversity of the ecosystem are also potentially substantial, although the direction of this impact is not always predictable (ICES, 2003).

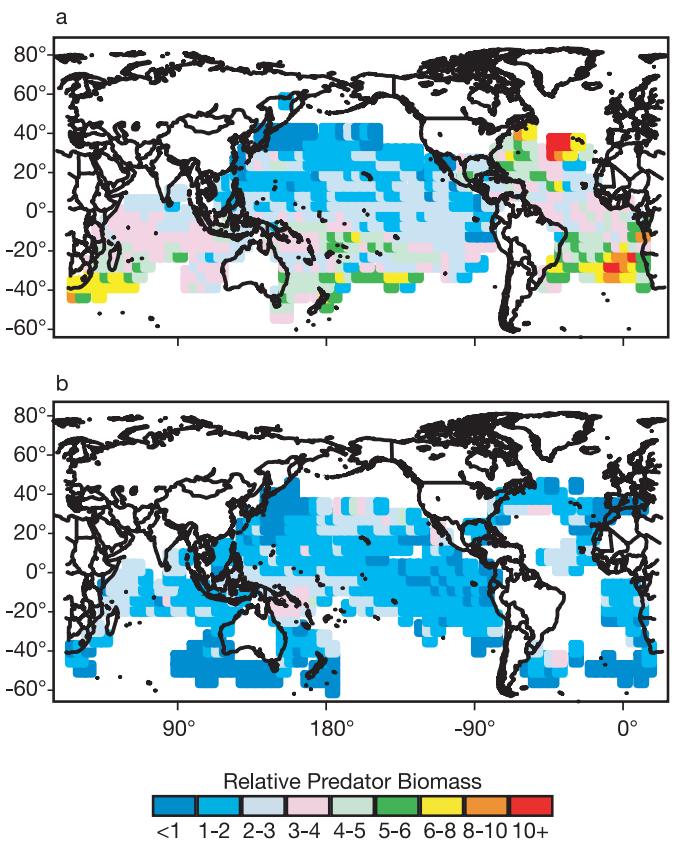
Trophic links in the marine ecosystem are dynamic, responding both to natural biomass fluctuations (Baumgartner et al., 1992) and to fishing (Rice, 2001). Severe exploitation of particular fish species is likely to impact both predators and prey, thus restructuring entire food webs. Work conducted by GLOBEC (Barange and Harris, 2003) has demonstrated the crucial linkages between *Calanus* copepods and predatory cod in the North Sea (Beaugrand et al., 2003), tuna populations in the equatorial Pacific and their El Niño-forced prey populations (Lehodey, 2001), and the dynamic balance between cod, sprat and their zooplankton prey in the Baltic Sea (Möllmann et al., 2003). However, most studies have not considered the impacts of harvesting on food webs from end-to-end, nor on biogeochemical cycles. Top-down and bottom-up effects caused by removal of key fish species have been observed in the form of alterations in the abundance, biomass or productivity of a community across more than one trophic link, in terrestrial, limnic and oceanic ecosystems (Pace et al., 1999). However, these alterations, also known as trophic cascades, are not easily observed in open-ocean communities without hard substrata (Rice, 2001). It is also unclear to what extent trophic cascade effects can be manifested down to the level of basic biogeochemical cycles of carbon and nutrients. This issue will be studied in collaboration with GLOBEC, to ensure effective end-to-end food web research and to take advantage of ongoing and planned GLOBEC research.

Priority Questions

How do harvesting-induced changes in food web structure impact biogeochemical cycles?

Harvesting of fish can impact a variety of ocean processes, including diseases of marine species, toxic blooms and population explosions of the microbes that are responsible for increasing eutrophication (Officer et al.,

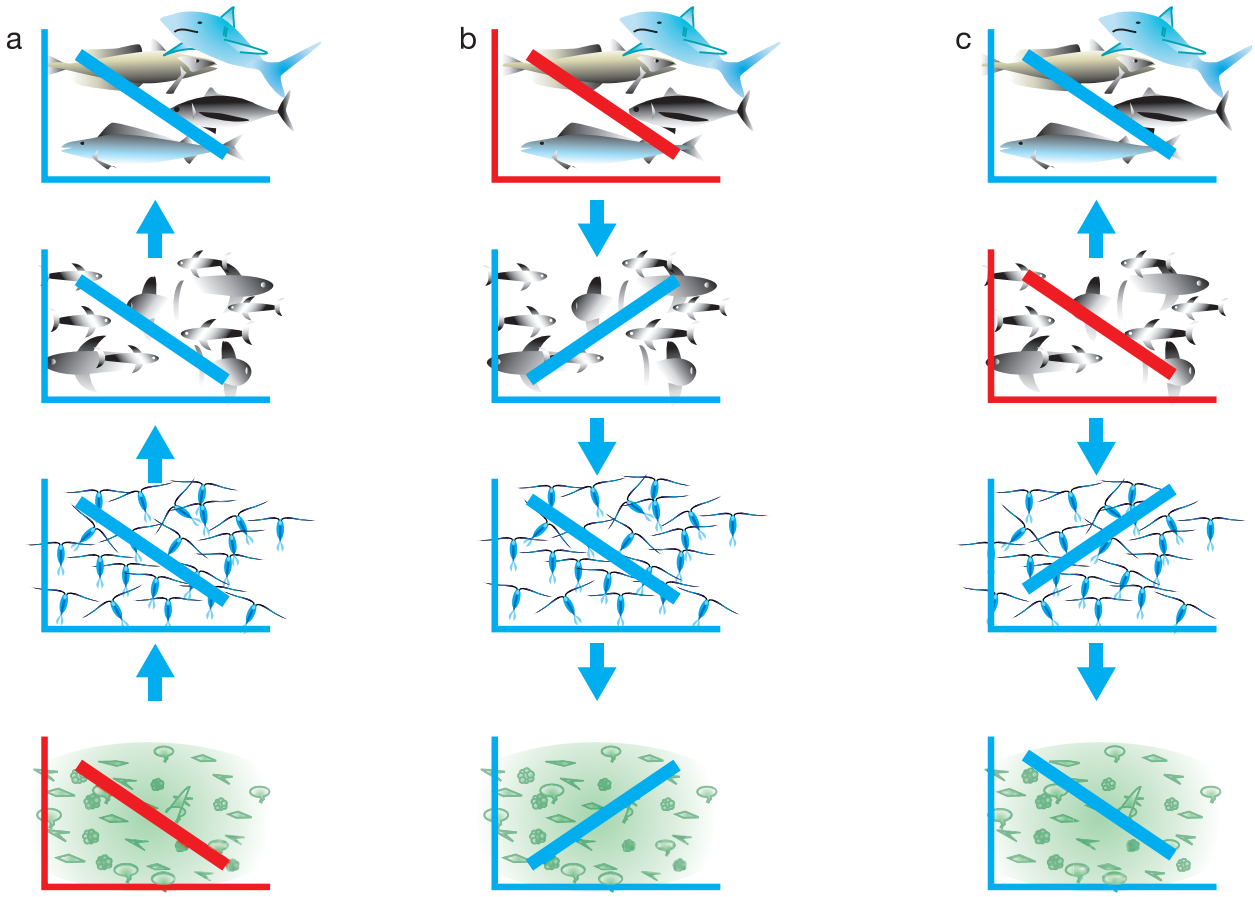
Figure 13. Spatial patterns of relative predator biomass (number of fish caught per 100 hooks on pelagic longlines set by the Japanese fleet) in (a) 1964 and (b) 1980. Data are binned in a global 5° × 5° grid. From Myers and Worm (2003); reprinted from Nature with permission from Macmillan Magazines Limited.



1984; Jackson et al., 2001). Harvesting an entire trophic level makes ecosystems more vulnerable to other natural and human disturbances, such as nutrient loading and eutrophication, hypoxia, disease, storms and climate change (Jackson et al., 2001), with possible synergies among different disturbances (Myers, 1995). However, the ultimate small- and large-scale impacts of harvesting on cycles of biologically important elements such as nitrogen, iron and phosphorus, are unknown.

Meta-analyses of 47 marine mesocosm experiments manipulating nutrients and consumers, and of time-series data of nutrients, plankton and fish from 20 natural marine systems, revealed – as expected – that nutrients generally enhance phytoplankton biomass, and that carnivores depress herbivore biomass (Micheli, 1999). The impact of changing predation on zooplankton and the subsequent impact on phytoplankton species composition is an open question. Because specific phytoplankton groups mediate important biogeochemical processes such as nitrogen fixation, calcification and carbon export, such selective top-down effects could impact important biological feedbacks on the ocean-atmosphere system. Ultimately, trophic cascades could also affect the utilisation and recycling of both macro- and micronutrients, including changes in the microbial loop and shallow sediments. Continental margins appear to be key areas for investigation, as these are regions where compounding effects could occur, for example harvesting, trawling, eutrophication and stratification. The effect of trawling on sediment structure and biogeochemistry is likely to be of importance when considering the indirect impacts of harvesting.

Figure 14. Schematic responses of a simplified four-level (phytoplankton, zooplankton, forage fish, predatory fish) marine food web: (a) bottom-up control, (b) top-down control, and (c) wasp-waist control. Red lines indicate a anthropogenically- or environmentally-driven decrease in biomass at one trophic level with subsequent changes at other trophic levels (blue lines). From Cury et al. (2003); reprinted with permission from the Food and Agriculture Organisation of the United Nations.



What are the impacts of harvesting living marine resources on end-to-end food webs?

Palaeo-ecological, archaeological and historical data show that time lags of decades to centuries may have occurred between the onset of over-fishing and consequent changes in coastal ecological communities. This is because unfished species of similar trophic level assumed the ecological roles of over-fished species, until they in turn were over-fished or died of epidemic diseases related to overcrowding (Jackson et al., 2001). Such time lags can only be investigated with long-term observations and data-mining. Retrospective research is being conducted though the CoML *History of Marine Animal Populations* and *Future Animal Populations* projects, and is contributing valuable information to deal with the time-lag impacts of harvesting.

Early conceptual and theoretical analyses built around simple food chains are not easily applied to most complex natural systems. Nevertheless, some trophic interactions generate strong effects, and there is a growing number and diversity of reports of cascade-type responses (Dayton, 1985; Paine, 1994). Questions regarding trophic cascades have shifted from "whether" to "when, where and how often". Exciting frontiers remain in discerning and modelling the variability generated by trophic cascades, as well as in understanding ecological mechanisms that dampen or prevent cascades (Pace et al., 1999). Figure 14 schematically illustrates responses to harvesting and environmental perturbations.

In many of the highly productive ecosystems of the world there tends to be a crucial intermediate trophic level that is typically dominated by few species. GLOBEC studies have focused attention on the role of mesozooplankton such as *Calanus* in the North Atlantic Ocean, *Neocalanus* in the North Pacific Ocean (Mackas and Tsuda, 1999; Greene et al., 2003) and small planktiverous pelagic fish in eastern boundary-current upwelling systems (Bakun, 1996). Furthermore, strong local impacts on euphausiid abundance have been demonstrated in upwelling areas when high aggregations of jack mackerel were present (Quiñones et al., 1997). The impacts of harvesting on organisms such as microzooplankton and phytoplankton that have short life spans (days to weeks) are still poorly understood.

Finally, a well recognised problem with the concepts of "top-down" and "bottom-up" control is that they are difficult to separate in practice. In many situations some form of resource (bottom-up) and predatory (top-down) control are both operative, but at different temporal and spatial scales. Thus, it is crucial to not consider marine ecosystems as being in a near-equilibrium state, but rather as undergoing a succession of transitional phases. This argues for the need for extensive and integrated datasets, and for collaborative research efforts by GLOBEC and IMBER to capture system variability and to identify key interactions.

Theme 3: Feedbacks to the Earth System

What are the roles of ocean biogeochemistry and ecosystems in regulating climate?

This theme will focus on the present and future capacity of the ocean to control the climate system via atmospheric composition and ocean heat storage by assessing (i) the varying capacity of the ocean to store anthropogenic CO_2, (ii) how changes in ecosystem structure feed back to climate through modulation of solar heating of the upper ocean and consequently physical structures, and (iii) how changes in low-oxygen zones affect the nitrogen cycle including N_2O. Modelling the potential feedbacks from marine biogeochemical cycles and ecosystems to the Earth System will require detailed understanding of local and regional manifestations of global change in the ocean and their interactions with other parts of the Earth System.

The impact of human activities on the Earth System is manifested in many ways including increasing global mean temperature, changing precipitation and changing ocean chemistry. The rate of these changes, and more importantly, their local and regional manifestations, depend crucially and inextricably on how the components of the Earth System respond individually and together. Existing data and present knowledge will be used to develop a modelling capacity to enable prediction of the impacts of global change on the Earth System. This requires dynamic, process-based models that are able to capture the range of possible changes (Goddard and Graham, 1999; Stocker, 1999; Knutti and Stocker, 2002). Understanding and predicting interactions and feedbacks between components of the Earth System can only be achieved with extensive, well-planned observational programmes supported by modelling and data assimilation activities that span across projects and programmes.

The oceanic component of the Earth System includes many non-linear processes (Patten et al., 1995). One of the consequences of perturbations to the ocean system are regime shifts in ecosystems (Hare and Mantua, 2000), which may lead to altered efficiency and strength of the biological carbon pump, changed rates of primary and secondary production and release of radiatively active gases such as N_2O. While it is generally believed that the ocean acts as a buffer in Earth System dynamics (due to its capacity to absorb atmospheric heat and CO_2 – that is, a negative feedback mechanism), it is evident that such a complex system may also be a trigger in the evolution of global change trajectories, leading to positive feedbacks and amplifying global change. Solar penetration into the mixed layer is significantly affected by the absorption of infrared radiation by organic and inorganic particles. Therefore, ecosystem dynamics and properties could contribute significantly to stratification of the upper ocean, and consequently affect the global climate system (Murtugudde et al., 2002).

The ocean has a wide range of physical, biogeochemical and biological characteristics that result in "hot spots" and "choke points," many of which, are undoubtedly unknown. High-latitude ocean areas could be important choke points in marine biogeochemistry, with significant potential for positive feedbacks to the coupled climate system; for example, through oceanic regulation of atmospheric CO_2, as occurred during glacial periods (Sarmiento and Toggweiler, 1984). Coastal zones are important hot spots for biogeochemical and ecosystem feedbacks to the Earth System. The predicted sea-level rise over the next century (Houghton et al., 2001) will affect different coastal benthic ecosystems in different ways. The biogeochemical and ecosystem feedbacks could be manifested through reduction-oxidation (redox) state changes – and related impacts on the global nitrogen cycle – and changes in water quality, habitats and fish populations.

The most significant feedback loops must be described to guide observational and modelling activities. The feedbacks to the Earth System being studied by IMBER will be reviewed regularly as new data are available and as our knowledge on feedbacks improves. New studies will be added to this theme when appropriate. One important feedback is related to changes in DMS produced by marine plankton and the formation of aerosols and cloud condensation nuclei. This feedback will be studied in detail by SOLAS, and so is not considered here.

Issue 3.1: Oceanic Storage of Anthropogenic CO_2

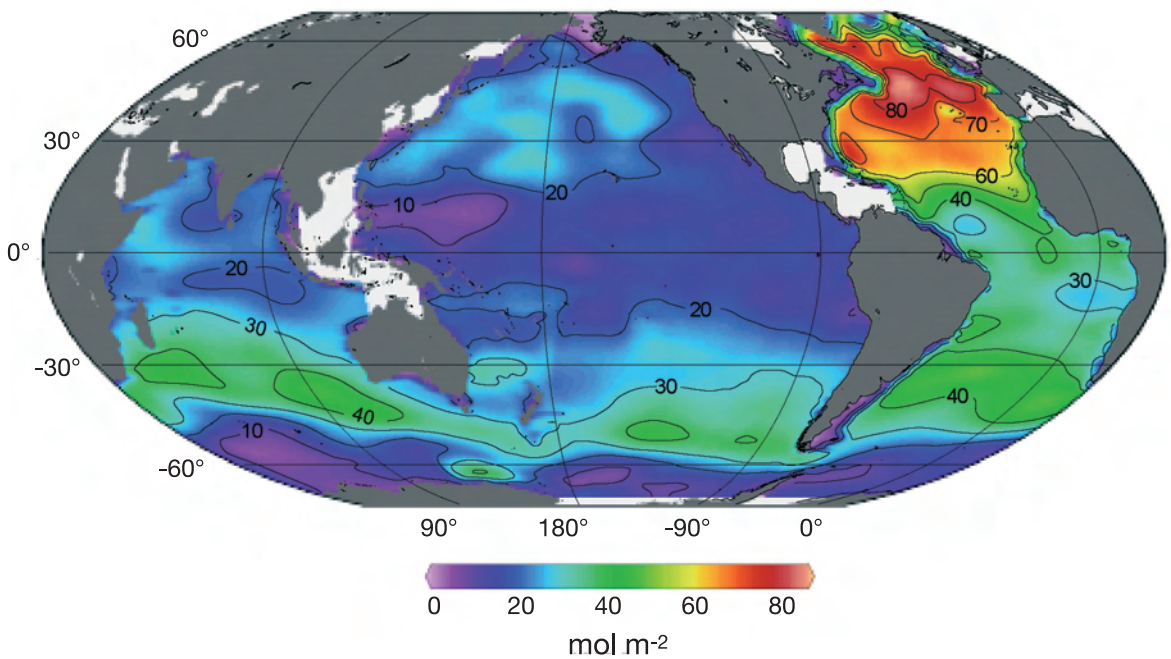
The most direct, and probably strongest, feedback from marine biogeochemistry and ecosystems to the Earth System will occur through oceanic regulation of atmospheric CO_2. The ocean absorbs nearly one-third of current anthropogenic CO_2 emissions; however, the assumption that the ocean will continue to be such an efficient sink of anthropogenic CO_2 may be incorrect.

Atmospheric CO_2 concentrations are now probably higher than at any time in the past 20 million years (Pagani et al., 1999; Pearson and Palmer, 1999; Petit et al., 1999). The anthropogenic increase of atmospheric CO_2 has led to enhanced accumulation of carbon in the upper and intermediate ocean (Sabine et al., 2004) (Figure 15). The variability of atmospheric CO_2 associated with natural modes of climate variability such as ENSO is not well constrained by available observations (Keeling et al., 1995; Bousquet et al., 2000; Le Quéré et al., 2000; Feely et al., 2002), and palaeo-environmental data indicate surprisingly small fluctuations of atmospheric CO_2 since the last glacial period (Indermühle et al., 1999).

Unlike cyclic glacial-interglacial atmospheric CO_2 variations, the anthropogenic perturbation of atmospheric CO_2 is occurring too rapidly to allow equilibration of the atmosphere with the deep ocean or with marine sediments. Marine export and physical recirculation have become de-coupled due to the combined kinetics of the different ocean carbon pumps: the physical (or solubility) pump driven by intermediate and deep water formation, and the biological pump, which can be separated into a soft tissue (or organic carbon) pump and a hard tissue (or alkalinity/carbonate) pump.

Global change is likely to have already had an impact on the ocean's carbon cycle, which could be mediated in many ways including vertical supply of nutrients, high-

Figure 15. Column inventory of anthropogenic CO_2 in the ocean (mol m^{-2}). Total inventory of shaded regions is 106 ± 17 PgC. From Sabine et al. (2004); reprinted with permission from the American Association for the Advancement of Science.



latitude convection activity and the strength of the thermohaline circulation, changes in calcification, efficiency and elemental composition of the biological pump, and the supply of macro- and micronutrients to the ocean. It is currently unclear, quantitatively and even qualitatively, what the integrated effects of such changes will be on the ocean carbon cycle, and how these will feed back to atmospheric CO_2 concentrations.

Regarding longer time scales, the correlation between glacial-interglacial changes in temperature and atmospheric CO_2 concentrations is striking – radiative forcing due to CO_2 probably accounts for a significant part of past glacial-interglacial climate variation. Although it is clear that the ocean is most likely a major driver of CO_2 changes observed in glacial cycles, the mechanisms for this are not understood (Archer et al., 2000). Moreover, analysis of short-term transients, such as during Dansgaard-Oeschger or Heinrich events, should provide key insights on responses at decadal or centennial time scales. Although the Earth System is currently operating in a no-analogue state, the perspectives gained from palaeo-proxies is likely to provide important insights into the functioning of the Earth's climate system, which will certainly help in interpreting the comparatively fast changes of the "Anthropocene." Glacial-interglacial CO_2 cycles represent an important test case for Earth System understanding.

Nitrous oxide (N_2O) is a trace constituent of the atmosphere that contributes significantly to global warming; the exchange of N_2O between the ocean and atmosphere accounts for about one-third of all N_2O inputs to the atmosphere (Nevison et al., 1995; Prather et al., 2001). The potential of the oceanic feedback to global warming through N_2O is substantial: a 50% increase in oceanic emissions of N_2O would be equivalent to ~230 TgC yr^{-1}, roughly 7% of the present rate of CO_2 build-up in the atmosphere – based on the assumed lifetime of 100 years for N_2O in the atmosphere and a global warming potential of N_2O of 300 times that of CO_2.

Priority Questions

What are the spatial and temporal scales of CO_2 storage in the ocean interior?

Long time-series and repeat transects over recent decades have shown an increase in the total DIC in the upper ocean (Gruber and Sarmiento, 2002). In addition, methods have been developed to evaluate changes of anthropogenic CO_2 inventories where direct time-series observations are not available (Sabine et al., 2004). These methods will require continued improvement and the testing of some of their critical assumptions; for example, existence of a steady-state natural carbon cycle.

In addition to the direct geochemical response of the marine carbon cycle, the Anthropocene is characterised by significant human-driven changes in physical forcing of the Earth System, more of which are likely to become detectable during the next decade. Modelling has illustrated the feedback potential of the ocean carbon cycle under global change (Friedlingstein et al., 2001; Plattner et al., 2001). The role of ocean circulation in the meridional and zonal transport of carbon is starting to be assessed directly using interior ocean measurements of carbon and related tracers (Holfort et al., 1998; Schlitzer, 2000). These oceanic transports of carbon, together with measured gradients in atmospheric CO_2, provide independent information on the overall source, sink, storage and transport behaviour of the land-atmosphere-ocean system (Sarmiento et al., 2000; Wallace, 2001). It remains to be demonstrated how expected changes in intermediate and deep-water ventilation and the meridional overturning circulation will affect the passive uptake and interior transport of anthropogenic CO_2 by the ocean.

^{13}C (Quay et al., 1992) and $^{18}O_2$ have proven to be very useful in the interpretation of long-term trends of atmospheric CO_2. Changes in the carbon cycle may be better understood by observing the ocean's oxygen reservoir, which is one order of magnitude smaller than the carbon reservoir but is tightly coupled to biological and hydrographic processes. There is growing evidence that the ocean's oxygen reservoir has been decreasing during recent decades in intermediate waters (Emerson et al., 2001; Keller et al., 2002). Only one-fifth of these changes can be explained by ocean warming (Bopp et al., 2002; Keller et al., 2002), with the remainder attributed to changes in the ventilation of these waters and/or the efficiency of the soft tissue biological pump (Keller et al., 2002). Jointly, oxygen and CO_2 may therefore be the best parameters to measure for detecting Anthropocene trends of the ocean's storage of natural and anthropogenic CO_2.

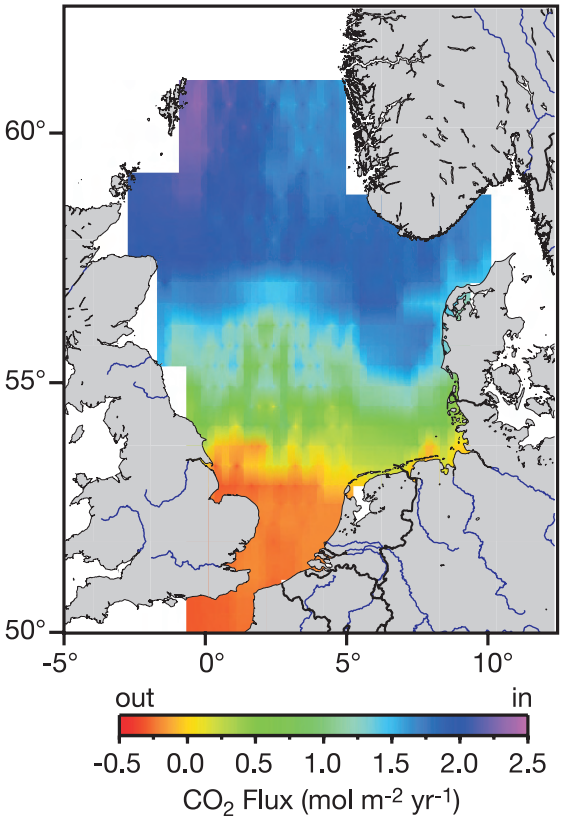
What is the role of the continental margins in ocean carbon storage under global change?

Coastal and marginal seas play a key role in the global carbon cycle by linking the terrestrial, oceanic and atmospheric carbon reservoirs. Current global ocean biogeochemistry models do not resolve ocean margins,

nor do they appropriately include the exchange between the coastal and open oceans. Inclusion of this zone in carbon models is necessary because the outer coastal zone is likely to be net autotrophic, taking up CO_2 (due to upwelling along the ocean margin) and fuelling – after lateral exchange – heterotrophic processes in the open ocean (Thomas et al., 2004). The postulated "continental shelf pump" mechanism (Tsunogai et al., 1999) may constitute an effective mechanism of carbon transfer from the shelf into the ocean's interior (Figure 16).

Since coastal and shelf zones are characterised by strong biological signals, but also exhibit large anthropogenic impacts (e.g. global warming, eutrophication), they are likely to be the most vulnerable to global change. IMBER will address this vulnerability, as well as how the impacts of global change in the continental margin may propagate into the open ocean and thus affect the oceanic carbon cycle as a whole.

Figure 16. Net annual CO_2 uptake of the North Sea, which is thought to be almost entirely exported into the North Atlantic Ocean. Adapted from Thomas et al. (2004); reprinted with permission from the American Association for the Advancement of Science.



Issue 3.2: Ecosystem Feedback to Ocean Physics and Climate

Ecosystem feedbacks to ocean physics and climate include direct feedbacks through changes in the ocean's heat budget, and indirect effects such as changes in the carbon cycle (discussed earlier) and changes in oxygen minimum zones and their impacts on the nitrogen cycle.

Marine organisms may modify global temperature since heat absorption by chlorophyll and related phytoplankton pigments will lead to heating of the upper ocean. These pigments absorb approximately half the incoming solar radiation in the spectral range 350–700 nm. The effect of this absorption on ocean temperature is dependent on the relative depth of radiation attenuation and on the depth of the mixed layer. If the mixed layer is shallow, absorption is particularly sensitive to changes in phytoplankton biomass.

Existing coupled physical-biological models have become relatively sophisticated, as shown in important contributions of Fasham et al. (1993) and Sarmiento et al. (1993) and more recently by Moore et al. (2002). However, the intrinsic non-linearities of the ocean system often make it difficult to distinguish the feedbacks between biological and physical processes (Miller et al., 2003). It has been known for decades that marine biota affect the penetration of incident radiation, and thus have the potential to affect water column temperature (Denman, 1973). This feedback has been well studied (Lewis et al., 1990; Sathyendranath et al., 1991), but the traditional approach to its inclusion in state-of-the-art coupled climate models has been rather simplistic, with a constant attenuation depth (Schneider and Zhu, 1998). This may have been partly due to one-dimensional ocean studies (Simpson and Dickey, 1981a, b), which failed to capture the dynamic feedbacks that can result from ecosystem-related radiative feedbacks. With the availability of remotely sensed global surface-chlorophyll concentrations, the impact of ecosystems on radiative attenuation is being readdressed in ocean general circulation models (Nakamoto et al., 2001; Murtugudde et al., 2002).

Priority Questions

How do marine food web structure and variability affect ocean and ice physics and large-scale climate and its variability, via the upper-ocean heat budget?

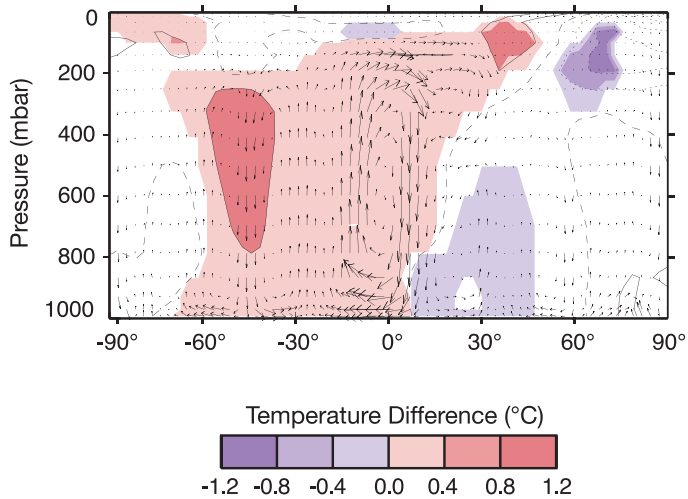
The vertical distribution of phytoplankton species not only depends on a supply of macro- and micronutrients, but also on the availability of light. The distribution of light is modified by the vertical distribution of light absorbing/reflecting species and, in turn, feeds back to ocean physics through conversion of light to heat. The impact of such a conversion will occur locally as stratification changes, which will cascade into dynamic feedbacks on local and regional scales. This two-way interaction which operates in the context of marine food web structures and ocean physics, has the additional aspect of the impact of global change on both ocean physics and food web structure.

Dynamic feedbacks in the ocean do impact sea surface temperatures – a key driver of atmospheric temperatures. In the eastern tropical Pacific Ocean sunlight increases during spring, winds are at their weakest and mixed layers in the cold-tongue tend to be shallow with weak entrainment from below. The thermocline relaxes from strong upwelling of the previous season, with both the thermocline and the nutricline still in the euphotic zone. This leads to a subsurface chlorophyll bloom and a heat source just below the mixed layer. Existing ocean circulation models do not include this heat source, and simulate colder-than-observed temperatures below the mixed layer and excessive surface cooling due to entrainment of cold water. Accurate representation of the radiative penetration leads to nearly 70% reduction of the SST errors (Murtugudde et al., 2002). Even if it is not yet proven that climatically significant biological effects on ocean physics occur outside of the eastern equatorial Pacific Ocean, preliminary studies using coupled ocean-atmosphere models indicate that biologically mediated SST warming amplifies the seasonal cycle of the lowest atmospheric layer temperatures (an average magnitude of 0.3°C, but reaching over 1°C locally (Shell, 2003)),

thus indicating a broad influence on climate via atmospheric teleconnections from affected regions to other regions (Figure 17).

The impacts of changes in light attenuation within the mixed layer due to chlorophyll have been reported to affect El Niño and La Niña in an asymmetric way (Timmermann and Jin, 2002), and Nakamoto et al. (2001) show significant impacts of changes in light attenuation in the Arabian Sea. These results must be studied, and ultimately, model ensembles should be run to provide estimates of the robustness of such direct biological feedback on the climate.
In high latitudes sea ice dynamics could be important in propagating feedbacks to the climate through the capacity of sea ice to affect exchange or storage of CO_2 (Stephens and Keeling, 2000; Bopp et al., 2003). Additionally the biology of high latitudes affects solar heat penetration and ocean dynamics: preliminary results show that phytoplankton at high latitudes can reduce summer sea ice cover by up to 6%, and increase winter cover by up to 2% (Manizza et al., 2005). These changes will lead to further feedbacks on vertical mixing and heat fluxes, as well as amplification of the seasonal cycle.

Figure 17. Differences (significance level 95%) in longitudinally averaged air temperatures for January between "phytoplankton" and "control" model runs for different latitudes and atmospheric pressures (i.e. heights above sea level). Solid contours indicate positive differences, dotted contours indicate negative differences and the dashed contour indicates a zero difference. Circulation patterns are indicated by arrows. From Shell (2003).



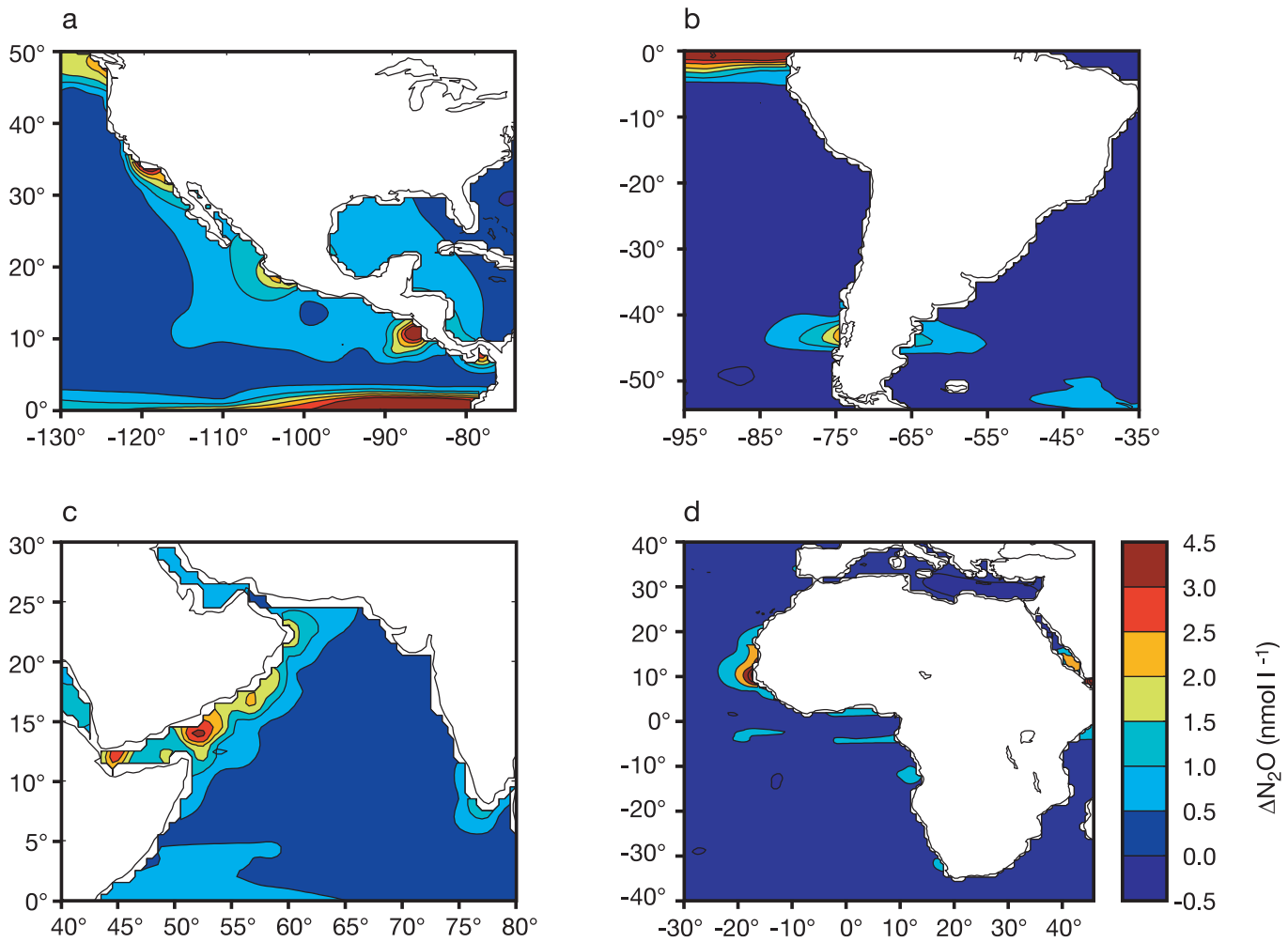
What will be the effect of global changes in oxygen minimum zones on sources, transport and outgassing of N_2O?

N_2O emissions are not uniformly distributed over the sea surface: the tropical upwelling zones containing O_2-deficient mesopelagic waters make a disproportionately large contribution (Codispoti and Christensen, 1985; Suntharalingam et al., 2000; Nevison et al., 2004) (Figure 18). This is because the O_2-deficient conditions promote production of N_2O through nitrification as well as denitrification. Denitrification also involves the consumption of N_2O, which serves as an intermediate during bacterial conversion of NO_3^- to N_2. Whether or not N_2O accumulates during the process depends on the balance between production and consumption. This balance will most likely be affected by global change, but the processes that regulate it appear to be complicated and are currently not well understood.

It is believed that human activities will impact the oceanic nitrogen cycle, especially the transformations involving N_2O and ultimately its efflux to the atmosphere, by altering the distribution of O_2 in the ocean (Codispoti et al., 2001). Changes in physical forcing (e.g. circulation and stratification) are directly linked to global warming, whereas biogeochemical forcings are mostly in the form of enhanced inputs of nutrients from the land. While the former are expected to be dominant in the open ocean, the latter may be more important in coastal areas and land-locked seas.

Increased stratification of the upper ocean (Sarmiento et al., 1998) and a reduction in the strength of the thermohaline circulation (Houghton et al., 2001) are predicted to occur with global change. In a more stratified ocean characterised by lower export production, primary producers are likely to be adapted to a more regenerative system (Bopp et al., 2001; Karl et al., 2001a). However, the sea-air flux of O_2 is expected to increase at the cost of its supply to the subsurface waters, leading to an expansion of the mesopelagic O_2 minimum zones in the open ocean (Bopp et al., 2002; Joos et al., 2003). Also, the increased nutrient runoff observed in semi-enclosed seas and open-ocean shelves affects eutrophication, near-bottom anoxia and algal blooms (Rabalais and Nixon, 2002). In the context of direct feedbacks to global warming, the impact on N_2O cycling needs to be investigated in detail, particularly in coastal areas where O_2-deficient conditions have developed in the last few decades (Malakoff, 1998).

Figure 18. Annual composite maps at the sea surface of ΔN_2O (excess concentration of seawater over the corresponding saturation value; nmol l^{-1}) for (a) Pacific Northwest and Central American coast, (b) western coast of South America, (c) perimeter of the Arabian Sea, and (d) west coast of Africa. The model-derived anomalies are the highest in coastal upwelling zones. These account for a minimum of 5% of the global N_2O emissions from the sea surface. From Nevison et al. (2004)



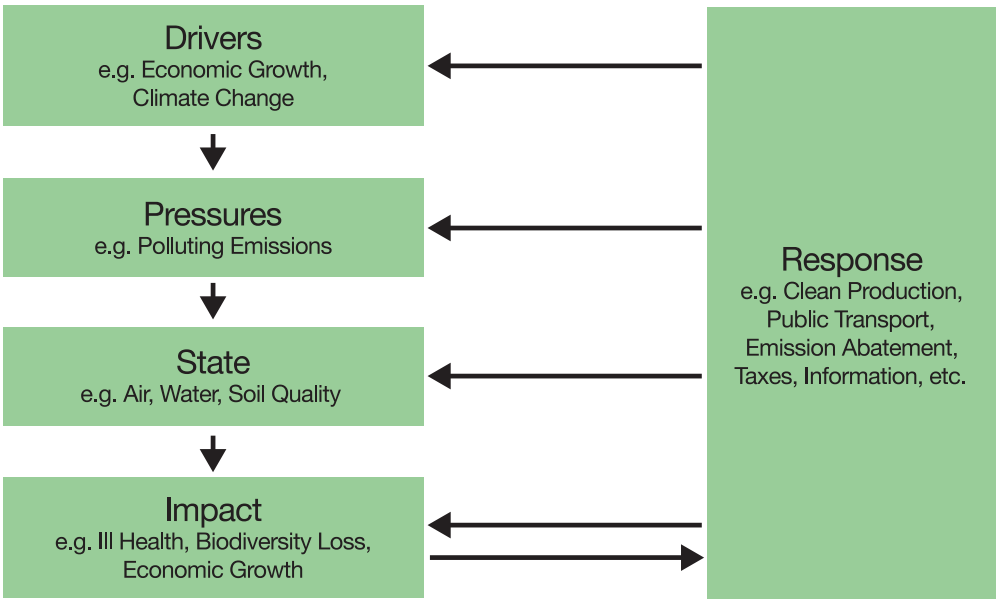
Theme 4: Responses of Society

What are the relationships between marine biogeochemical cycles, ecosystems and human society?

This theme focuses on interactions between human and open ocean systems; its motivation lies in recognition that humans not only influence ocean systems, but also depend on ocean systems for goods (e.g. oil, gas and minerals) and services (e.g. weather mediation, regulation of local and regional water quality, transportation, waste assimilation and global regulation of atmospheric concentrations of CO_2). Several interactions between humans and natural systems are considered in the previous three themes, including addressing the human system as a cause of change in the ocean system (e.g. marine harvesting and as a source of nutrients and contaminants) and considering the role of the ocean in human-induced climate change. The possible implications of changes in the open ocean system for human society (e.g. loss of biodiversity, decreased productivity, introduction of new plankton and fish species and reduced CO_2 buffering) are also important.

The goals of this theme are to promote understanding of the multiple feedbacks between human and open ocean systems, and to clarify what human institutions can do either to mitigate human-caused perturbations in the ocean system or to adapt to system changes. Achievement of these goals will depend on inputs from the natural and social sciences; a major challenge is therefore to bring together scientists from a wide range of disciplines to identify areas of joint concern and interest, and to build an ongoing collaborative natural-social science research community. These scientists must be capable of, and strongly committed to, communicating not only within their own specialist disciplines, but also across disciplines and with policy makers. This theme is not as fully developed as the previous themes, and additional steps will need to be taken prior to implementation.

Figure 19. The DPSIR framework. Adapted from org.eea.eu.int/documents/brochure/brochure_reason.html.



The first tasks in bringing a range of disciplines together are identification of common issues of interest and concern and development of a common language and concepts. Current multi-disciplinary, interdisciplinary and perhaps even transdisciplinary research is slowly building a common language. This theme can expect to benefit from these efforts, and to contribute to them. The Driver-Pressure-State-Impact-Response (DPSIR) framework may be useful for developing this research theme and for helping scientists categorise their contributions (Figure 19). The DPSIR framework describes the interactions between society and the environment and has been adopted by the European Environment Agency (EEA) as a basis for analysing the inter-related factors impacting the environment. It is an extension of the Pressure-State-Response model developed by the Organisation for Economic Cooperation and Development.

Examples of drivers include consumer preferences, economic growth, the effects of globalisation, transportation and energy production. Pressures are typically sources of nutrients and contaminants, but also include the effects of harvesting and use of the marine environment in general. "State" relates to the quantity and quality of various environmental components, for example, chlorophyll concentration, stocks of fish and biodiversity. Changes to environmental states can lead to impacts, which may be positive for people or ecosystems, but are more often negative. For example, environmental quality targets may not be met, fish stocks may decline below levels needed to support those dependent on them, or the relative abundance of stocks may be altered towards less valuable species (Pauly et al., 1998).

The severity of negative impacts determines whether or not a response is required. Responses may include attempts to mitigate adverse environmental impacts, usually by reducing pressures either directly (e.g. emission abatement) or indirectly (e.g. influencing drivers such as consumer preferences). Responses may also include attempts to restore environmental states (e.g. dredging to remove stocks of nutrients in lake sediments) and even ecosystems (e.g. mangrove reforestation and wetland creation). Responses may also involve adaptation – helping humans accommodate, and perhaps even benefit from, changes in state. Implementation of this framework by the EEA has focused on the development of indicators, particularly for the driver, pressure and state components. This framework has been used in environmental analysis (Turner et al., 1999; Kannen et al., 2003).

Application of the DPSIR framework requires close cooperation between natural and social scientists as well as between science and policy. Research being undertaken within other IMBER themes will provide information and data for Theme 4, however, it is within Theme 4 that cooperation between natural and social scientists will be stimulated. The aim in the first phase of IMBER is to make small but important steps towards developing multidisciplinary science to address the question "what are the relationships between marine biogeochemical cycles, ecosystems and human society?"

Key to the success of the implementation of this theme will be identifying and engaging a core group of natural scientists (representing studies of biogeochemical cycles and end-to-end food webs) and social scientists (representing studies such as sociology, anthropology, economics, political science, law and geography). These scientists are likely to be already literate in, or open to, and interested in the methods, insights and approaches of scientists on the other side of the natural/social science divide. They will also be comfortable with the issues raised by research that attempts to study and engage the policy world, while maintaining an analytical distance from policy development. Co-chairs will be identified to develop this theme: one representing the natural sciences and one representing the social sciences. Efforts will be made to identify – amongst the natural scientists involved in the other three IMBER themes – those who are interested in participating in Theme 4 research. These efforts will also target social scientists who are engaged in research on ocean-related issues, and who recognise the value of, and seek to foster, ongoing engagement with natural scientists.

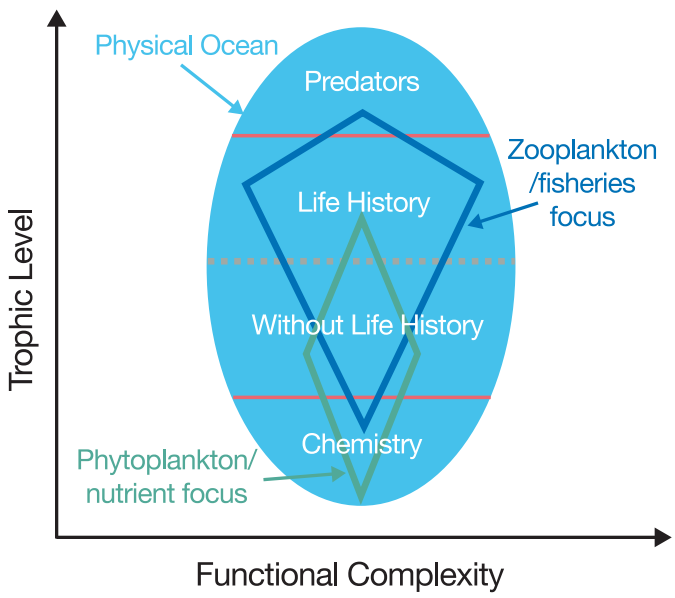
IMBER will seek funding for a workshop (to be held in 2006) to bring natural and social scientists together to identify key issues to be developed under this theme. It is intended that the research identified will build on, and complement, the work of other initiatives, including those of IDGEC, GLOBEC and LOICZ. IHDP will be an important partner in the development of this theme. After the key issues have been identified, an implementation plan for this theme will be developed; this may involve the development of a pilot project to progress the theme.

Integrated Modelling

IMBER will use numerical models to examine the sensitivity of marine biogeochemical cycles and ecosystems to global change, and to examine how the ocean impacts other components of the Earth System. Models will be used to study the impacts (at all trophic levels) of changes in ocean physics and chemistry (bottom-up) and changes in higher trophic levels (top-down); the latter in collaboration with GLOBEC. Study of the impacts of the various perturbations driven by global change, and the feedbacks to the atmosphere and land, requires integration of physical, biogeochemical and food web models. To date, models of different complexity have been developed separately and models are only beginning to be coupled. For example, global-scale physical and biogeochemical models have been coupled (Le Quéré et al., in review), and local-scale models of the physical system and of pelagic fish communities have been coupled (Huggett et al., 2003). The inclusion of feedbacks between all components, from physics to higher trophic levels and vice versa, has not been achieved. For IMBER to accomplish its scientific goals greater integration amongst modelling disciplines will be required.

Different approaches are necessary for modelling the different components of the marine ecosystem. Firstly, individual variability and life-history details become increasingly important at higher levels of the food web; incorporating important details at higher trophic levels requires structured population models and even individual-based models. Availability of data constrains the complexity of these models, but increased complexity is required to include organism behaviour and species adaptiveness. Secondly, the time scales and details of the processes being studied constrain the complexity of the models. Eddy-resolving models are used for short-term integrations and their output can be used to study rapid processes. However, to study decadal variability at basin scales will require coarse-resolution models in which high-frequency and small-scale processes are parameterised. This diversity of models suggests a hierarchy of models should be developed, in which the knowledge obtained from more complex models is incorporated in more generalised models in an integrated manner.

Figure 20. Conceptualisation of the relationship between trophic level and functional complexity in marine ecosystem models. The dark blue rhomboid represents models that focus on the complex life-history development of zooplankton, and which therefore include detailed representations of ontogenetic development. The green rhomboid represents models that focus on phytoplankton and biogeochemical cycles, but which also include coarse representations of zooplankton life-history. The light blue oval represents the physical ocean which affects all trophic levels. From deYoung et al. (2004); reprinted with permission from the American Association for the Advancement of Science.



Physical, biogeochemical and ecosystem models vary vastly in complexity and structure. It is not always clear what kinds of questions can be addressed through fully integrated models, and what questions might require new approaches. New strategies to couple different components need to be developed in IMBER to construct integrated marine biogeochemical and ecosystem models and to facilitate information transfer among models. An approach that can be followed to achieve this goal is illustrated in Figure 20.

Integrated modelling will be used in a wide range of applications in IMBER research. Firstly, evaluation of annual-to-decadal variability needs to be conducted systematically in hindcast mode at the scale of major basins – where consolidated datasets exist ranging from physics to marine ecosystems (Beaugrand et al., 2003; Chavez et al., 2003; deYoung et al., 2004). Secondly, the sensitivity of models to different climate and environmental conditions should be explored, including scenarios for the future and the past. Sensitivity analyses should (i) identify particularly important processes that could propagate significant perturbations throughout entire marine ecosystems, (ii) analyse mechanisms under various hypotheses, and (iii) stimulate research to improve the parameterisation of key processes or to design new relevant research. Thirdly, imbedding integrated models of biogeochemistry and ecosystems in advanced oceanographic circulation models, would allow nowcast and even weekly forecast modes. This capability may make it possible to optimise research campaigns as well as to provide a continuous real-time analysis of marine biogeochemical and ecosystem states at basin scale. For hindcast, nowcast and forecast modes, integrated models need to be developed closely with the Climate Variability and Prediction (CLIVAR) and Global Ocean Data Assimilation Experiment (GODAE) communities. Because IMBER will focus on time scales of years to decades, large basin-scales need to be taken into account. However, due to cascading impacts from large scales to key regional or coastal areas, where rich, dynamic ecosystems are found, high-resolution models need to be nested into basin-scale models, and downscaling methods need to be developed.

Earth System models are developed by coupling sophisticated general circulation models of the physical climate system to detailed chemistry and biology modules. Development of Earth System modules will be undertaken in IGBP's AIMES project and in the WCRP. AIMES will focus on Earth System models of intermediate complexity which are useful for long simulations and explorative research, while WCRP is developing comprehensive high-resolution Earth System models. New developments include atmospheric chemistry modules, dynamic vegetation modules and fully interactive marine ecosystem modules. The latter are particularly important for feedbacks between the physical climate and the global carbon cycle. IMBER will develop, test and validate new modules that integrate marine biogeochemical cycles and ecosystems such as those described above. These will serve as components for the Earth System models developed by AIMES and WCRP. Ideally, this should be undertaken using a common model infrastructure that supports model development, model component exchange and multi-model experiments.

Model parameter values, initial and boundary conditions are often uncertain due to limited data; furthermore, models cannot include all processes: some are excluded and others are parameterised. This implies that a "deterministic" approach, in which only one model realisation is made, is inappropriate. Instead, a more probabilistic approach is necessary, in which ensembles of simulations are made using different parameterisations. IMBER will use multi-model ensembles to deal with the inherent uncertainties. Finally, combinations of simulations and observations could constrain model trajectories via assimilation procedures (to be developed), and should lead to new products focussed on biogeochemical and marine ecosystem dynamics while reanalysis of data from recent decades is undertaken. This approach is similar to those used in the meteorological community: by assimilating the point measurements, hydrographic data and satellite data into basin-scale models, observations will be put in a basin-scale perspective leading to improved estimates of the ocean state. IMBER will draw from the experience in CLIVAR and GODAE when it develops appropriate synthesis techniques.

Implementation Strategy

This Implementation Strategy describes the project structure, the mechanisms for research implementation, the pathways for engaging scientists worldwide and the process for forming effective collaborative links with relevant projects and programmes. The Implementation Strategy will be used as the basis for the development of implementation plans for IMBER research by its working groups. A mid-term review of this strategy and implementation plans will be undertaken to ensure that the project builds on the research undertaken in this and other projects, and to ensure that new science results and innovations are incorporated into the project.

Research Approaches

Key aspects of IMBER research will be the seamless integration of biogeochemical and ecosystem research in a truly interdisciplinary approach, and the incorporation of social science research to enable the investigation of options for mitigating or adapting to the impacts of global change. Bringing together these science communities will be a significant challenge, and will need to start with the development of common terminologies that can be understood by all participants.

Marine biogeochemical and ecosystem responses to global change are complex and diverse, and can only be evaluated through integrated multidisciplinary studies that allow observation and analysis of the target process in the context of the system and its feedbacks. Such studies will include targeted field-based process studies, *in situ* mesocosm studies and laboratory experiments, and comprehensive observation and modelling of biological, chemical and physical processes.

The field research fostered by IMBER will require advances in the networks of sustained observations, using both *in situ* and remotely sensed observations in key domains. This strategy will require close collaboration between IMBER and GOOS to ensure effective development, coordination and use of GOOS data.

Extrapolation to the global scale will require integration of data from standard transects (e.g. repeat hydrography lines) in close collaboration with CLIVAR and other basin-wide global surveys, such as those planned by GEOTRACES to investigate the global marine biogeochemical cycles of trace elements and their isotopes. IMBER will also foster the development of innovative techniques for interpretation of palaeoceanographic records in collaboration with PAGES (including IMAGES) to enable synthesis and development of a predictive capability based on historical observations. Understanding and modelling the complex system of biogeochemical and ecosystem feedbacks will be an important integrating activity across IMBER. This will involve coupling life history models developed by GLOBEC with generic primary production and biogeochemical cycling models developed by JGOFS. This approach requires the development of nested suites of models and expansion of ecosystem models to basin scales. This nested approach will also link regional understanding to the global scale, providing the framework on which to build a predictive capability for the ocean system and its subsystems.

IMBER will take advantage of new and innovative approaches to conducting marine research, including the

use of stable isotopes for unravelling food web dynamics, biomarkers for identifying functional groups and new molecular techniques for detecting biological diversity. Past studies have focused on bulk biological processes and measurements rather than on the roles of key species or functional groups. The understanding of the distribution and functioning of microbial communities, their dynamics and their role in cycling materials in the ocean remain at a rudimentary level. Yet this knowledge is key to predicting ecosystem and biogeochemical responses to global change. Novel techniques must be applied, including enzymological and molecular methods that are targeted directly at the genome of plankton at the level of individuals, to allow direct quantification of specific functional groups of organisms and key species, and to understand their role under changing environmental conditions.

Process Studies

Process studies will be required to address specific research questions, focusing on mechanisms, interactions, fates and sources. These studies should encompass observational efforts, experimental and perturbation approaches. Whenever possible, these studies should be integrated with the sustained observation programmes, to ensure that measurements are comparable and that the data can be integrated for more comprehensive understanding. Process studies can also be used to extend the limited spatial scales that can be captured by time-series efforts to ocean basin-scale dimensions. Shipboard process studies should also be integrated as far as possible with hydrographic survey efforts.

Small-scale manipulation experiments, such as predator exclusions, have been an important approach in recent decades for testing various hypotheses regarding the structure and function of marine food webs. Many early insights in marine ecology were gained through manipulations of inter-tidal benthic marine ecosystems (Paine, 1994). An important development of the past decade was the implementation of large-scale manipulation experiments to test hypotheses on the role of iron in marine ecosystems (e.g. IronEx, EisenEx and SOIREE). The success of these experiments suggest that this approach might be useful for studying other aspects of ocean biogeochemistry and ecosystems. Additional experiments are still needed to study the effects of iron on carbon export from different ecosystem types, the ecosystem effects of iron (e.g. species successions and biodiversity effects) and how iron-enrichment feeds back to the atmosphere – an area of particular interest to SOLAS. Similar approaches with other limiting micronutrients (e.g. Zn, Mn, Cu and Mo) could help in understanding the role of these elements in marine systems.

Process studies could also be used to assess:

- how macronutrient concentrations and ratios change the abundance of individual species and functioning of marine ecosystems;
- the effects of low oxygen on ocean biogeochemical cycles and ecosystems;
- complex action and interaction of pH effects;
- the effects of CO_2 enrichment, for example, by using a marine analogue to the Free Air CO_2 Enrichment experiments carried out by the terrestrial research community;
- top-down, bottom-up and wasp-waist controls in ecosystems; there may be opportunities to combine nutrient addition and predator exclusion studies in mesocosms or large enclosed ocean areas to study these control factors; and
- triggers of blooms of specific types of phytoplankton and zooplankton species.

Such process studies will be very useful for testing and improving the level of understanding about how biogeochemical cycles and ecosystems function and interact. This in turn will enable the impacts of global change to be understood and predicted.

Sustained Observations

In situ sustained observations are required to capture the unpredictable, extreme and episodic events that have significant impacts on biogeochemistry and ecosystems. Sustained observations will also provide new insight into potential effects of longer-term global change on marine biogeochemical cycles and ecosystems. The JGOFS strategy of sustained observations (i.e. time-series studies) significantly increased understanding of the links between biogeochemistry and ecosystems (Steinberg et al., 2000). IMBER requires similar long-term observations of physical, chemical and biological variables to monitor and interpret variability in biogeochemical cycles and ecosystems, and to enable development of a predictive capability. Such observations should include time-series observations extending over several decades, augmented by comprehensive data mining and reanalysis. Sustained observation sites will act as central components

around which other investigations, such as process and experimental studies, will be clustered. New, additional sustained observation sites in areas such as the continental margins, high-latitude and polar ocean areas, and within the mesopelagic layer, should be developed with due consideration of relevant time and space scales, nesting of sites and transect designs. Properly designed sustained observations will capture variability on time scales from hours (e.g. sensors on moorings), through events (e.g. salp or diazotroph blooms) and seasons (e.g. monsoons), to interannual and longer (e.g. variability associated with climate modes such as ENSO and NAO). IMBER will encourage the use of a wide range of measurement platforms, such as floats, autonomous underwater vehicles (AUV), moorings, volunteer ships of opportunity, repeat hydrographic lines and new platforms, as these technologies develop. Long-term, cost-effective sustained observations of the ocean, particularly for biogeochemical and biological variables, are in an early stage of development. IMBER must play an active role and take advantage of developments as they occur. IMBER will form close collaborative links with ongoing sustained observation programmes at international, regional and national levels, including with GOOS, the International Ocean Carbon Coordination Project (IOCCP), current time-series stations such as Hawaii Ocean Time-series station, Bermuda Atlantic Time-series Study, the Kyodo North Pacific Ocean Time-series station, global plankton repeat surveys such as the Continuous Plankton Recorder and the Ocean Sustained Interdisciplinary Time-series Environment Observations System.

Satellite observations are obtained from sensors that measure scattered, reflected or emitted electromagnetic radiation that carries information about the sea surface and upper mixed layer. Once calibrated, some measurements can be transformed into biological or biogeochemical variables. For example, accurate and robust algorithms allow ocean colour to be used as a proxy for surface chlorophyll. Coordinated international activities are being sponsored by organisations such as the IOCCG, IGOS-P and national space agencies. While significant progress has been made, this process needs to continue beyond the present generation of satellites (SeaWIFS, MODIS, MERIS, OCTS, POLDER) and operational systems to obtain greater ocean coverage (60% global, over a 3–5 day time frame). To achieve this goal IMBER will work collaboratively with IGOS-P in the development of its Coastal Theme and the review of its Ocean Theme. Beyond surface chlorophyll, the development and testing of a new generation of ocean-colour remote sensing algorithms is required to cover other aspects of ecosystem structure. For example, recent developments are able to detect different phytoplankton functional groups (i.e. coccolithophorids, diatoms and cyanobacteria: Iglesias-Rodriguez et al., 2002a; Iglesias-Rodriguez et al., 2002b; Subramaniam, 2002), size spectra, dissolved organic matter and suspended matter (Loisel et al., 2002; Siegel et al., 2002). To ensure the calibration and validation of such tools, IMBER will promote the development of systematic *in situ* measurements for on-going and new satellite ocean-colour analysis. Long time series will be particularly important to quantify and merge ocean-colour products from different sensors and platforms.

Although research ships and satellites will undoubtedly remain important observing assets, the development of an ocean observing system encompassing autonomous *in situ* measurements and sampling from the wide range of available platforms is an increasingly important task. Emerging new platforms and sensors and their future potential have been discussed in detail by Dickey (2001). Given the inevitable risk of loss or failure of even the most advanced *in situ* device, real-time (or near real-time) telemetry of the data is an important feature. However, even the next decade's developments in sensors may not meet all measurement needs, hence autonomous *in situ* sampling devices (e.g. trace metal clean samplers) may help to fill the gaps.

A variety of platforms form the backbone of any ocean observation system. A nested approach is required, combining platforms of different types, such as Eulerian platforms (e.g. moorings, buoys, bottom landers and offshore platforms), Lagrangian platforms (e.g. drifters, floats and gliders) and other platforms (e.g. volunteer observing ships and AUVs). However, all these platforms can only assist IMBER research if adequate chemical and biological sensors or autonomous sampling devices are available. Clearly, the use of such platforms is more mature for physical oceanography, with biogeochemical and ecosystem studies limited to date by the availability of chemical and biological sensors of sufficient miniaturisation with sufficiently low power requirements.

Sensors suitable for the above platforms have to be developed under significant constraints in terms of response time, stability, drift, size, power requirements, durability, reliability, susceptibility to biofouling, data storage and telemetry, and cost. Often these challenging requirements cannot be met with current technology, making invest-

ment and development in this field crucial. Where simple and rugged detection techniques (e.g. optical – oxygen optode, and electrochemical – pH glass electrode) are not yet available, miniaturised systems based on more classical chemical methods have been developed (e.g. nutrients and pCO_2). The application of these systems, however, is restricted because their size, power requirements and costs are often prohibitive (e.g. for use on profiling floats). Bio-optical and bio-acoustic sensors have been widely used in studies of phytoplankton and higher trophic levels. These techniques need further development and adaptation for use on autonomous platforms.

Observation and analysis at ocean-basin scales will be essential for IMBER. Cross-basin transects will allow data collection for integrated analysis of ocean ecosystems and biogeochemical cycles (e.g. hydrography, gases, carbon system parameters, transient tracers, nutrients, primary and secondary production, phytoplankton and zooplankton community composition and trophic interactions). Selected survey lines will focus on specific aspects of IMBER including micronutrient distributions and turnover and end-to-end food web studies. Extrapolation to the global ocean of observations and research results from process studies and sustained observations at specific sites will be achieved, in part, through such surveys. Long transects will be designed for all ocean basins in the coming decade. Coordination with CLIVAR and GEOTRACES may allow ancillary observations for IMBER during planned ocean-basin surveys.

Synthesis and Modelling

Continuous synthesis of available information can only be achieved if interconnected databases are constructed, quality controlled, shared in a common format and updated in near real-time, jointly for biological, geochemical and physical variables. As IMBER covers time scales up to decades and longer, systematic data mining (including estimated uncertainties) will be strongly encouraged, with ocean biogeochemical reanalyses as one of the goals. Over millennial time scales high-density sampling and synchronised palaeo-proxies are critical, as is the development of new palaeo-proxies. The collation and quality control of data from various sources remains a daunting task that modellers must address. For new observations, clear procedures and protocols for data quality control and dissemination are at the heart of an emerging sustained observing system for marine biogeochemistry and ecosystems: these activities must be developed in close cooperation with GOOS.

Models provide a suite of tools to investigate hypotheses, analyse and extrapolate data in space and time, help gather data efficiently through observational system simulation experiments, and identify crucial gaps to be filled by new observations and research to reduce uncertainties. To achieve such interactions a synthesis and modelling framework must be active from the beginning of IMBER to integrate knowledge and to refine the implementation strategy. In the long term, reliable prognostic ocean models that are linked to models of biogeochemical cycles and ecosystems are required to predict the impact of global change on the ocean. The linkages to other Earth System components should be both implicit and explicit; ocean models are needed that provide relevant inputs and parameters for models of atmospheric and terrestrial processes. In the short term, explorative process-oriented models are needed which improve understanding of mechanisms, controls, feedbacks and interactions. Such models depend critically on the continued existence of observational data and process studies.

To accelerate the development of IMBER-relevant models, innovation in biological, geochemical and physical modelling should be encouraged. Improvements are likely to come from recent progress in:

- reconstruction and forecast of space and time variability of physical ocean states made by CLIVAR and GODAE communities;
- identifying and modelling nutrient sources and sinks, including both macro- and micronutrients, the remineralisation loop, and exchanges with continental margins, sediments and the atmosphere;
- parameterisations of organism adaptations to temperature, light, pH and other physical and chemical forcings;
- functional group representations for key microbial and phytoplankton species, allowing simulation of the quality and quantity of food, the export of organic carbon and the production of gases by organisms;
- understanding trophic-level interactions, leading to coupling of life-history GLOBEC-type models for large feeders (meso- and macrozooplankton or small fish) to generic non-life-history JGOFS-type models developed for primary producers and microbial processes;

- extending results of individual-based models, which include explicit species behaviour and characteristics, to cohort and population-level models and hence to ecosystem models; and
- stimulating the inclusion of ocean biogeochemistry in the high-resolution ocean circulation and ocean-atmosphere circulation models used by the CLIVAR and GODAE communities.

The model hierarchy will need to range from diagnostic models for hindcasts and nowcasts to prognostic models for ocean forecasting. These models will differ in the complexity of their mathematical frameworks and their biogeochemical and ecosystem representations, according to the particular questions being addressed. Their spatial coverage should range from global to regional, using various coupling and/or nesting schemes to ensure propagation of non-linear perturbations within the different components. This point is particularly important for open-ocean–ocean-margin coupling and for benthic-pelagic interactions, from synoptic events to decadal and global change time scales.

IMBER will benefit from initiatives already underway, such as the Green Ocean Modelling (plankton functional group approach for primary producers) and CLIOTOP approaches to end-to-end food web modelling. Simplified versions of first-order process-based models will play an essential role in the development of Earth System models of intermediate complexity – a cooperation with GCP and AIMES. Such models will most likely be the primary tool for assessing the impact of human activities on the Earth System, and thus for assessing the potential feedbacks to human societies. Model development and research should be an iterative process: good models will suggest what is needed from observations and good observations will help refine models.

Data assimilation into biogeochemical and ecosystem models, as has occurred for meteorology and more recently in operational oceanography (e.g. GODAE), should be encouraged and promoted. Approaches to data assimilation should ensure that there is close coupling with data systems that will provide the correct type and frequency of data. The models developed must remain flexible to make optimal use of new data streams, new parameterisations and new developments in the mathematical concepts of non-linearity and inverse/assimilation schemes. Diagnostic models will continue to play a major role in addressing research questions associated with network optimisation and parameter estimation studies. New mathematical and conceptual approaches to quantify and model biodiversity, trophic interactions and the impacts of global change on food web dynamics and human dimensions, will be important for IMBER research.

A full synthesis of IMBER research will be critical to the overall success of the project. The IMBER SSC needs to play a leading role in this synthesis. This will require the development of a synthesis framework early in the project to enable effective interaction between the SSC, the IMBER working groups and national and regional programmes. The development of this framework will be an early priority for the IMBER SSC.

Palaeoceanography

Palaeoceanographic approaches will be important for IMBER, as indicated in the theme descriptions. In the past decade the spatial and temporal resolution of studies has increased, highlighting that variations on time scales from seasonal-to-decadal up to centuries-to-millennia are characteristic of different key ocean processes. Effective use of palaeoceanographic data allows extrapolation of relatively short time series back through time to help distinguish between oscillatory and directional change, and to help distinguish natural from anthropogenic change. Such extrapolations are necessary for the development of models that predict the potential marine effects of global change. This will only be achieved if accurate and understandable proxies of important variables are available. Particularly important for IMBER will be palaeo-proxies that help elucidate how physical and chemical environments impact ocean biogeochemistry and ecosystems. Examples include palaeo-proxies for understanding:

- how physical conditions affect marine species composition;
- how oxygen levels affect species abundance and diversity and remineralisation in the mesopelagic layer and in sediments;
- how pH affects biogeochemical cycles and ecosystems;
- how marine biological diversity affects ecosystem stability;
- effects of climate modes on ocean chemistry and biology; and
- trigger points in transitions from one biogeochemical-ecological regime to another.

Multiple proxies are needed to reveal synchronous biogeochemical and ecosystem variations. Unequivocal interpretation of a proxy record requires an understanding of the processes that control its formation and its preservation in sediments; this understanding of the genesis of a proxy signal is not available for most proxies.

Development of palaeo-proxies will require field work, laboratory experiments and testing of correlations on samples from sediment cores, corals and possibly other sources. Field efforts, for example, should take a synergistic approach with the long-term goal of understanding the variability in the downward pulses of POM and its accumulation and incorporation into sediments. Field efforts should include (i) integrated trapping and environmental monitoring to study vertical fluxes at large temporal and spatial scales, (ii) integrated trapping and sediment studies in order to assess the transformation of the climate signal ("proxies") from the water column to the seafloor and its preservation in sediments; and (iii) assessment of the effect of varying oxygenation on early diagenesis of organic matter and bioturbation rates in different bottom environments.

Biologically important isotopes, trace metals and unusual remnant organic molecules ("biomarkers") should be further explored. For example, records of lattice-bound cadmium in banded corals can help reconstruct patterns of anthropogenic fertiliser flux to the ocean. If possible, new proxies should be related to existing proxies whose behaviour is well understood. Two SCOR/IMAGES working groups, on "Analysing the Links Between Present Oceanic Processes and Palaeo-records," and "Reconstruction of Past Ocean Circulation" will contribute information needed by IMBER. IMBER will work with these groups and others to advance the use of palaeo-proxies.

Molecular Genetics and Genomics

In recent years oceanographers have come to appreciate the value of subcellular investigations (including molecular biology and genomics) for identifying, quantifying, understanding and predicting biological patterns and processes at organism, population, community and ecosystem levels. DNA-based characters can define species boundaries, reveal cryptic species, accurately estimate biodiversity for marine organisms from microbes to whales (Hebert et al., 2003), and identify prey species in digestive system contents. DNA can provide a means of documenting trophic relationships in complex food webs, including DNA sequencing of target regions for species identification (e.g. "Barcode of Life" and "Fluorescent *In Situ* Hybridisation"). Molecular genetic analysis can reveal underlying population dynamics (i.e. patterns of recruitment, dispersal and mortality) as well as species' evolutionary histories and responses to climatic variability; for example, recent studies using microsatellite DNA markers for Atlantic cod have linked individual fish to their population of origin (Nielsen et al., 2001). Mitochondrial DNA (mtDNA) sequence variation can be used to infer historical fluctuations in population sizes for marine organisms (Bucklin and Wiebe, 1998; Grant and Bowen, 1998; Nielsen et al., 2001).

Rapid advances in genomics (i.e. study of genes and their functions) and analysis of gene expression (i.e. creation of proteins from genes) are being used to detect the occurrence of specific metabolic traits and to study recently discovered metabolic pathways in marine animals. Such techniques allow identification of groups of organisms that perform certain functions within food webs, for example, nitrogen fixation and calcification. Biological oceanographers can examine environmental effects on gene expression and are developing molecular indicators of complex biological processes, including physiological condition, growth and reproduction, and likelihood of survival. Miniaturisation and automation are becoming standard in molecular laboratories. "Lab-on-a-chip" technologies will increasingly make it possible to conduct molecular assays remotely using equipment on moored or autonomous instrumentation deployed in the ocean. At the ecosystem level, random "shotgun" sequencing of DNA purified from ocean environments is being used to identify biodiversity hot spots and concentrations of unknown organisms – especially microbes that cannot be cultured. It may soon be possible to assemble and sequence whole genomes of microorganisms from natural samples, and to discover novel genes and their functions in biogeochemical cycles.

Data Management and Mining

The collective value of data is greater than the dispersed value, hence the development of an appropriate data management plan is fundamental and critical for the ultimate success of IMBER. Data management and exchange are important components of IMBER research and should be addressed by each proposed activity.

To ensure effective data management within IMBER a small Data Management working group will be formed. The first task for this group will be to develop a data management policy and plan for IMBER based on the recommendations of the SCOR/IGBP Meeting on Data Management for International Marine Research Projects (Appendix II), which drew on the experience of several marine research projects including JGOFS and WOCE. The Data Management working group will work closely with data management teams from other marine projects to ensure interoperability of datasets between research projects and with GOOS. The working group will have an ongoing role in assisting IMBER activities and assisting the IPO with data management.

IMBER's years-to-decades focus makes the creation and rescue of long time series necessary; for example, Continuous Plankton Recorder (CPR) records for the north-eastern Atlantic Ocean since the 1950s (Reid et al., 1998) are a unique source of information about the changing state of these ecosystems. However, deconvolution of possible environmental effects and harvesting effects in CPR records is a daunting challenge for IMBER. Another challenge will be to take advantage of the numerous datasets available worldwide from scattered research institutions, commercial ventures (fisheries, oil and gas companies, and ocean mining groups) and government agencies that collect marine data for a variety of uses. These data may be difficult to access if they are only available in hard copy form or on outdated electronic storage devices, or if they are embargoed for commercial or national security reasons. To discover and gather relevant observations acquired during the past century, IMBER will encourage the rescue of historical datasets by proposing a plan for data discovery, quality control, aggregation and analysis. Significant value could be added to historical data by sharing it among nations and different parts of the ocean science community. IMBER will work with ongoing initiatives at national and regional levels, such as the Global Oceanographic Data Archaeology and Rescue project and the World Data Centre for Marine Environmental Sciences, to create a coherent and distributed online database facility on biogeochemical and ecosystem measurements.

Project Organisation and Management

Scientific Steering Committee

In the proposed project organisational structure (Figure 21) the Scientific Steering Committee (SSC) is responsible for providing scientific guidance and overseeing the development, planning and implementation of IMBER. The SSC will facilitate the publication of IMBER findings and will encourage active communication among IMBER activities. The SSC will encourage national governments and regional and international funding agencies to support IMBER research, and in conjunction with project sponsors will seek funding to support IMBER infrastructure. The SSC will facilitate active collaboration with relevant projects and programmes to ensure that the IMBER goals are met. An Executive Committee comprising the Chair, two Vice Chairs and 2–3 SSC members will be formed, and will be responsible for decisions between SSC meetings.

Working Groups

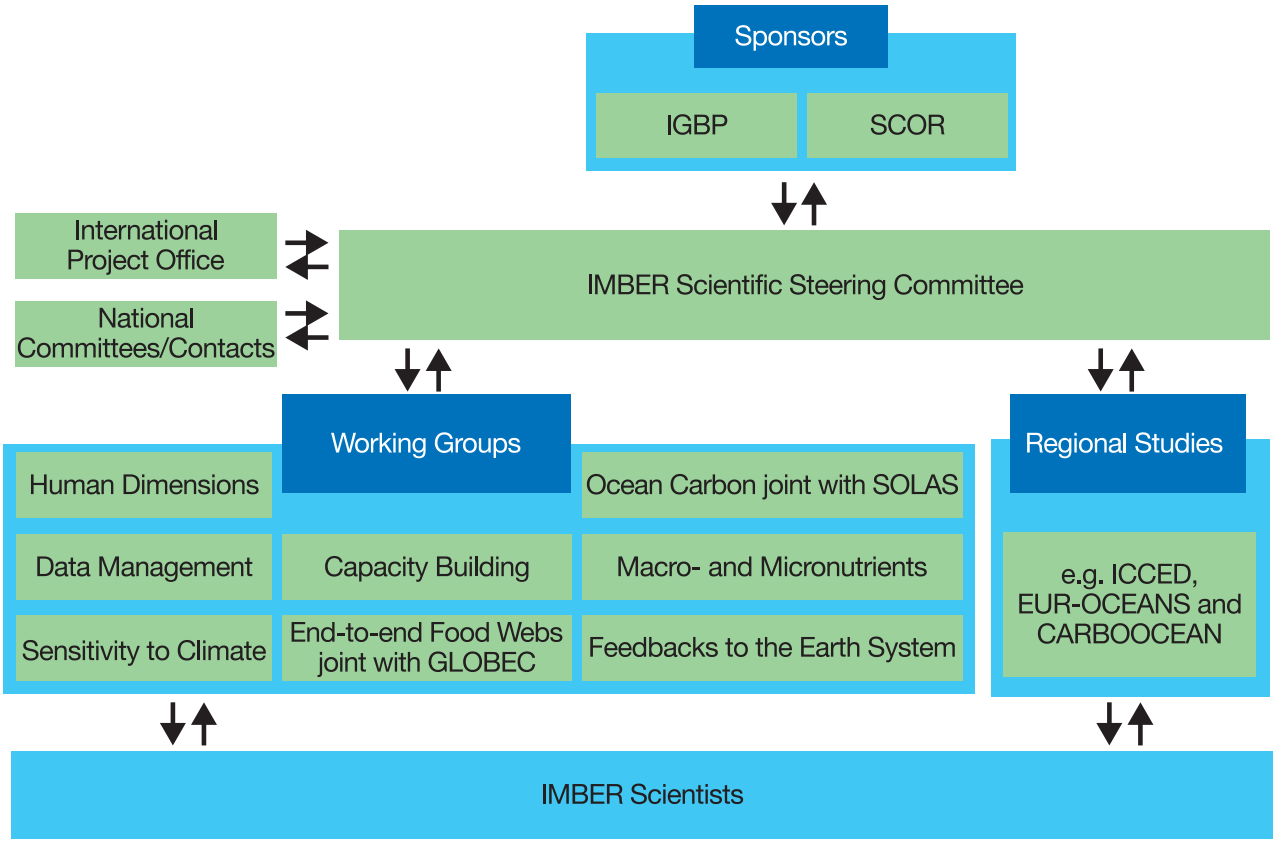
The implementation of IMBER will be facilitated by the development by working groups of implementation plans for specific research topics. Some working groups will cut across the themes and issues of the Science Plan, while others will be closely aligned with individual themes. Eight working groups (described below) have been identified for development, with the first five being of high priority for development in the first year.

A cross-cutting *End-to-end Food Webs* (Material and Energy Flow) working group will focus on the development of an implementation plan for end-to-end food web studies. The group will be conducted jointly with GLOBEC, with co-chairs from each project. The plan will be developed to guide studies of integrated marine food webs extending from viruses to whales, and the impacts of harvesting on end-to-end food webs and biogeochemical cycles. The implementation plan will ensure a coordinated focus on biogeochemical processes, integrated food web and ecosystem modelling, functional biodiversity and impacts of global change (as they relate to marine food webs). The planned studies will involve collaborative research between IMBER and GLOBEC.

An *Ocean Carbon* working group (formed jointly with SOLAS) is already working toward seamless implementation of ocean carbon research in SOLAS and IMBER. Two major scientific emphases have been identified: (i) carbon inventories, fluxes and transports; and (ii) sensitivities of carbon-relevant processes to changes occurring in the ocean. After development of the implementation plan the group will work to encourage the development of requisite research activities at national and international levels. This group will work in coordination with IOCCP.

A *Human Dimensions* working group will focus on the development and implementation of Theme 4. The first task will be to bring together natural and social scientists to collaboratively plan a workshop to identify theme issues; the second task will be to develop a theme implementation plan.

Figure 21. IMBER organisational structure.



A small *Capacity Building* working group will be established very early to develop – by correspondence – a capacity-building strategy. This strategy will then be used by the other working groups to guide capacity building issues, including school based education.

A small *Data Management* working group of data gatherers, data users and data management specialists will be established to develop a project data management policy and to ensure consistency and interoperability with other marine research projects and with GOOS.

A *Macro- and Micronutrients* working group will focus on development of an implementation plan for research on the impacts of changing macro- and micronutrient inputs on biogeochemical cycles and ecosystems. The group will work closely with LOICZ, SOLAS and GEOTRACES.

A *Sensitivity to Climate* (from Variability to Change) working group will focus on sensitivity studies with models that are forced by changes in atmospheric composition (using IPCC scenarios). Specific attention will be paid to the impact of changes in extreme events on biogeochemical cycles and ecosystems. The group will also stimulate the inclusion of biogeochemical components in reanalysis of ocean data as undertaken by CLIVAR and GODAE, and will advise on down-scaling strategies (such as nesting or statistical methods) to determine the implications of basin-scale climate change simulated by global models for regional and coastal areas. The implementation plan should be prepared in cooperation with CLIVAR, GODAE and PAGES.

A *Feedbacks to the Earth System* working group will stimulate interactions between the climate, biogeochemistry and marine ecosystems modelling communities and hydrographic and palaeoceanographic field scientists. The group will identify feedbacks between physical climate, biogeochemistry and marine ecosystems, and their spatial and temporal scales of variation. The group will identify how these processes affect or interact with natural climate variability and how they affect anthropogenic climate change. It will recommend how to use models and observational data to identify feedbacks and to validate models. The group will stimulate research in relation to identified feedbacks, coordinate modelling activities and organise synergistic activities to achieve their goals. The group will work closely with AIMES and CLIVAR.

All IMBER working groups will all be expected to further the IMBER vision and goal and to serve in an advisory capacity to the SSC. Working group chairs will meet with SSC members and project managers at regular intervals and will prepare written summaries of each meeting. Working groups will be expected to make substantive recommendations in their implementation plans regarding:

- achieving the IMBER goal of integrating biogeochemistry and ecosystem research;
- specifying standards and protocols for IMBER research;
- addressing research questions in priority domains;
- defining the role of integrated modelling activities, including integrating diverse data types across time/space scales of interest;
- planning for integration and synthesis activities; and
- defining strategies and approaches for building new research capacity, especially in developing nations.

Regional Projects

The development of regional projects, including time-series and process studies (i.e. EUR-OCEANS, CARBOOCEAN and ICCED) will be encouraged as a mechanism for regional implementation of IMBER research. Regional projects and organisations will be encouraged to develop implementation plans that facilitate collaboration and communication between individual and national projects. The SSC will encourage the participation of regional bodies (e.g. European Union, International Council for the Exploration of the Seas and North Pacific Marine Science Organisation) in the development and implementation of IMBER-relevant activities. These regional organisations will be encouraged to have all or parts of their projects endorsed as IMBER activities. The chairs of regional projects will be responsible for reporting on the activities of their projects to the SSC.

International Project Office

The IPO will provide day-to-day administrative support for IMBER and will support all SSC activities. The IPO will have a major role in seeking financial support for IMBER activities, facilitating communication both

within and outside the project, and ensuring effective data management and information archiving. The IPO will be responsible for working with the SSC to ensure that IMBER provides a wide range of products to the science community, and will keep a record of these products. Products are likely to include books, special journal issues, synthesis papers and open science conference proceedings. The production of outreach materials aimed at the wider community will also be important, and will include books, brochures, science highlight articles, newsletter articles and an effective web site. The IPO will be based at the Institut Universitaire Européen de la Mer, in Brest, France for 2005–2008, funded by the Centre National de la Recherche Scientifique, the Institut de Recherche pour le Développement, the Université de Bretagne Occidentale and the Brittany Region.

National Committees and Contacts

There is broad worldwide interest in IMBER demonstrated by participation from 36 countries at the 2003 OCEANS Open Science Conference. To ensure broad international participation the SSC will encourage the formation of national committees to support the development and coordination of IMBER. National committees will be encouraged to promote and seek funding for IMBER research, and will help coordinate research and communication within countries. National committees will be requested to evaluate projects for IMBER endorsement and provide recommendations to the IPO for consideration by the SSC. National committees will be asked to have clear links with IGBP and SCOR National Committees in countries where they exist, as in many cases these committees will be instrumental in setting up and supporting the IMBER National Committees. In countries without an IMBER National Committee, the SSC will seek a national contact person to facilitate communication with the scientific community, and may invite this person to form an IMBER National Committee if appropriate. Strong and effective National Committees will be crucial for IMBER as virtually all research and observation systems are implemented using national funding.

Recognition of IMBER Research

The aim of this Science Plan and Implementation Strategy is to provide a framework that encourages participation of regional, national and individual research efforts in IMBER. Research efforts can be submitted for recognition as IMBER activities. This will ensure that (i) the IMBER SSC is aware of what research is being conducted under the IMBER label, (ii) research carrying the IMBER label falls within the identified science themes, (iii) such research conforms to the agreed scientific approaches, and (iv) a data management sharing plan is in place for the activity.

International/regional research groups can submit their project for recognition by the SSC via the IMBER website. National groups and individual principle investigators (PIs) should first work through their IMBER National Committee or representative, who will in turn present the application to the SSC. If the PI or group is from a nation without an IMBER National Committee or other formal representation, they may apply directly to the SSC. Projects seeking recognition from multiple IGBP/SCOR projects are welcome, as the SSC recognises that many national/regional activities will potentially contain research objectives relevant to more than one project. The information requirements for endorsement are given in Appendix III and on the web site.

The benefits for IMBER-endorsed projects are:

- enhanced scientific value of planned research by provision of complementary information, for example, a widened range of studies and extended spatial and temporal coverage, or co-authorship of synthesis articles;
- more rapid communication of ideas and results through workshops, conferences and project publications;
- closer working links with other relevant international programmes and projects including sharing of berths on research cruises;
- development and testing of standard methods and protocols for measurement thereby facilitating quality control and meaningful data sharing;
- access to datasets collected in component studies and development of a common data management strategy;
- opportunities for participation in the development, planning, and implementation of a collaborative, internationally recognised programme;
- strengthening of national funding proposals by links to IMBER and its science plan and other IMBER-endorsed projects;
- an international training forum for younger scientists via IMBER training schools;
- opportunities for younger scientists to network with their peers and with senior scientists;
- access to the IMBER website for posting and obtaining job vacancies; and
- access to the public outreach documentation provided by the IMBER International Project Office.

The responsibilities of IMBER-endorsed projects are:

- acceptance of the general IMBER principles and goals;
- conducting project research in general accordance with the relevant aspects of the IMBER Science Plan and Implementation Strategy;
- participation in IMBER management bodies and in IMBER planning and development;
- provision to the IPO (six months in advance) of any cruise details including cruise track, process study locations, date, focus of research, contact person and if berths are available;
- provision of metadata to the IPO within six months;
- provision of data to the community within two years (except where constrained by funding agency data policy);
- provision of relevant model output and source code to the IPO within three months of publication (except where constrained by institutional or funding agency policies); and
- acknowledgement of IMBER in project products including scientific papers.

Capacity Building

Capacity building is an important objective of the Implementation Strategy and a Capacity Building working group will be established (see description earlier) to develop a capacity building strategy. The success of IMBER will depend on substantial contributions from a wide range of scientific disciplines; a high level of participation will require mechanisms for effective interaction and communication amongst scientists from around the world, and mechanisms for knowledge and skills transfer from IMBER to marine resource managers.

Education and training should assist both the new generation (e.g. university students and young researchers) and existing practitioners to develop the skills necessary to undertake IMBER research. IMBER will encourage training by providing opportunities for young scientists to participate in international research programmes that are relevant to marine biogeochemical-ecosystem interactions. IMBER will also seek funding for specific training workshops and web-based training initiatives, and will encourage the exchange of scientists and students between institutions, the development of summer schools and the provision of berths on cruises for developing country scientists, university students and teachers. IMBER will work also with Global Change System for Analysis, Research and Training (START) to develop appropriate training activities in developing regions.

Scientific networking and effective resource coordination will improve comparability of methods and techniques across IMBER. The SSC will hold meetings and workshops in different regions to encourage and facilitate this networking and coordination, and to encourage and facilitate broad national and regional participation. The SSC will assess the ability of community groups to contribute data to IMBER, and will investigate networking with national bodies that coordinate research resources relevant to IMBER research to add value to ongoing and/or planned projects.

Communication

Clear and effective communication will be important for successful project implementation, including amongst national/regional activities, the SSC, working groups and the IPO, and with the science and policy communities beyond IMBER.

The IMBER web site will be a central source of information, including key planning documents, contact information, and reports of scientific highlights and research activities. It will provide links to working groups and national/regional activities, and act as a portal to IMBER datasets. Scientific conferences, working groups and workshops will all be important platforms by which scientific communication is established, and will also help consolidate the identity of IMBER. Newsletters and email bulletins will also be used to communicate with the IMBER science community and other interested scientists.

The detailed results of IMBER research will primarily be published in scientific journals. However, it will also be important to ensure that results are accessible to a broad audience including policy makers, resource managers, teachers and the public. The SSC will therefore facilitate the production of appropriate synthesis documents for this broad audience and will encourage IMBER researchers to make their findings available in widely accessible forms. The SSC will work in partnership with school teachers to make results available for classroom use.

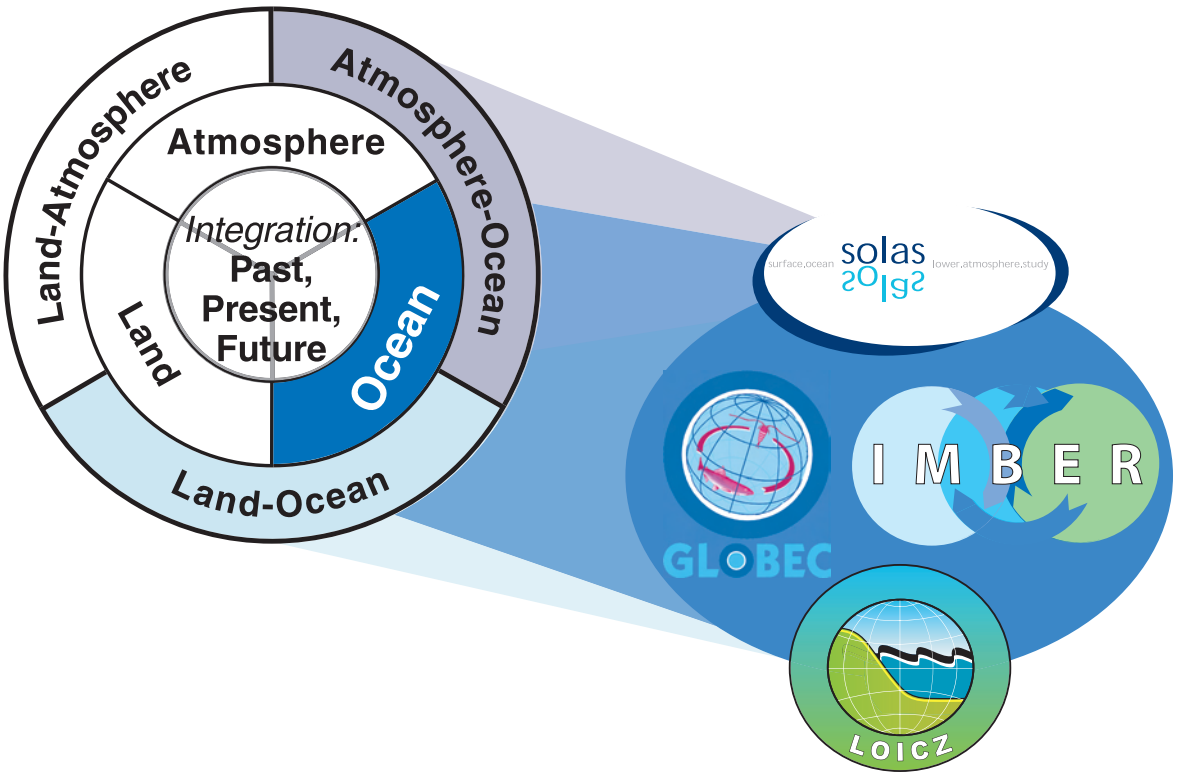
Linkages with Other Projects and Programmes

IMBER will build on the approaches taken and the knowledge gained in prior projects such as JGOFS and WOCE, as well as the approaches being developed in new and ongoing projects sponsored by IGBP, SCOR, IOC and other organisations. IMBER will develop collaborative activities that draw on the expertise of these projects and programmes and will avoid duplication of effort. The relationships with IGBP projects (Figure 22) and other projects and programmes are detailed below.

Global Ocean Ecosystem Dynamics (GLOBEC) Project

GLOBEC (www.globec.org) is co-sponsored by IGBP, SCOR and IOC. The scientific approaches of IMBER and GLOBEC will cover a wide range of marine trophic levels, with a view to integrating the food web from end-to-end. Studying end-to-end food webs will be a joint activity, with IMBER concentrating on trophic levels up to zooplankton, and GLOBEC focusing on zooplankton to top predators. After GLOBEC's completion in 2010 these interface activities will continue; the collaborative activities of the two projects will address the interactions between phytoplankton and zooplankton, and how these interactions are influenced by physical processes and biogeochemical cycles. This research has not been pursued systematically in the past, nor is it currently being pursued by any other large-scale marine research project. GLOBEC and IMBER will also work together in the study of the impacts of harvesting on food webs and the feedbacks to society (GLOBEC's Focus 4 Working Group) and biogeochemical cycling. IMBER will address biogeochemical cycling, including remineralisation processes, in relation to the entire spectrum of trophic levels.

Figure 22. Relationships between IMBER and other IGBP projects with marine components.



IMBER and GLOBEC use somewhat different measurements, measurement techniques, and spatio-temporal measurement intervals and modelling, because of the different sizes and life cycles of the organisms of primary interest. Future collaborations should emphasise process-oriented field and mesocosm studies. An important modelling focus in GLOBEC uses spatially explicit individual-based models embedded in realistic circulation models to study the growth, transport and survival of zooplankton and larval fish. Individual-based models for single and multi-zooplankton species, as well as for fish early life stages, are actively being developed. However, additional work is needed to develop integrated trophodynamic models from phytoplankton to fish. This significant research challenge requires joint effort by both communities, which has already begun (deYoung et al., 2004). GLOBEC (through its existing ESSAS and Southern Ocean GLOBEC regional programmes) and IMBER both have high-latitude and polar ocean areas as regional foci, and joint work is already underway and being planned for the Southern Ocean. In the tropical oceans, a recently approved GLOBEC Regional Programme – CLIOTOP (linking phytoplankton, physics and fish in the tropical oceans) – offers additional opportunities for GLOBEC and IMBER collaboration.

In summary, GLOBEC and IMBER will collaborate in some regions, in research focussed on end-to-end integration of marine food webs, on the impacts of harvesting on food webs and biogeochemical cycling, and on ecosystem modelling. The IMBER and GLOBEC SSCs will form a joint working group to plan integration in areas of shared scientific interest, and will develop a joint implementation plan for research on end-to-end food webs. To facilitate IMBER-GLOBEC interactions the Executive Committees will hold back-to-back co-located meetings, and the Chair of each project will be an *ex officio* member of the other project's SSC. A mid-term review of the IMBER Science Plan and Implementation Strategy will ensure that the GLOBEC synthesis activities are taken into account.

Surface Ocean–Lower Atmosphere Study (SOLAS)

SOLAS (www.solas-int.org) is co-sponsored by IGBP, SCOR, WCRP and CACGP. Close collaboration between IMBER and SOLAS is important, particularly in regard to SOLAS Foci 1 and 3 and IMBER Issue 2.2 and Issue 3.1. To ensure a close and effective collaboration in the area of oceanic carbon cycle research, IMBER and SOLAS are developing a joint ocean carbon research implementation plan. SOLAS will focus on the flux of CO_2 between the ocean and atmosphere and the processes in the euphotic zone that control this flux, and IMBER will focus on the ocean carbon cycle in the euphotic zone, looking downward into the water column (Table 1). The two projects will jointly study N_2O, with SOLAS focussing on surface-ocean production, air-sea exchange and climatic impacts, and IMBER focussing on the sediment-water interface, deep production and transport into the surface ocean.

Land-Ocean Interactions in the Coastal Zone (LOICZ)

LOICZ (www.loicz.org) is co-sponsored by IGBP and IHDP, and its Theme 4 (Biogeochemical cycles of coastal and shelf waters) is relevant to IMBER: IMBER should collaborate with LOICZ in continental margin research. The Chair, or other representative of the LOICZ SSC, will be an *ex officio* member of the IMBER SSC, and LOICZ representation will be critical in the Ocean Carbon, Macro- and Micronutrient, and Human Dimensions working groups. In 2006 IMBER and LOICZ will hold a workshop to develop collaborative research activities in the continental margins.

Past Global Changes (PAGES)

PAGES (www.pages-igbp.org) is an integration project of IGBP; there is great potential for collaboration between IMBER and the palaeoceanographic activities of PAGES – in particular those of IMAGES which focuses on high-resolution palaeoceanographic studies of rapidly deposited marine sediments.

Palaeoceanographic information and long-term observations provide key information on different biogeochemical states of the ocean and their temporal and spatial scales of variability. IMBER-PAGES linkages provide an opportunity to study the dynamics of ocean biochemistry and ecosystem changes of past environmental transitions that far exceed the amplitude of what can be observed in the modern ocean. Integrating IMBER and PAGES datasets and modelling efforts may identify key mechanisms that are driving changes. Furthermore, the proxy-based approach of palaeoenvironmental research requires quantitative calibration against direct observations, thus symbiotic integration of palaeoceanography and ocean biogeochemistry will help to refine palaeoceanographic proxies, which will increase the usefulness of palaeoceanographic reconstructions to IMBER

research. Collaborative activities will be identified, including integration of observations and reconstructions, identifying potential new proxies, improving proxy calibration and establishing useful chronometers. Participation by the major international projects concerned with obtaining and studying marine sediment cores is expected – in particular IMAGES and to a lesser degree the Integrated Ocean Drilling Programme. Combining the insights from observations and modelling will be a vital part of this collaboration.

Analysis, Integration and Modelling of the Earth System (AIMES)

AIMES (www.aimes.ucar.edu) is an IGBP integration project with which IMBER will collaborate on future modelling frameworks that treat the Earth as a system in which biogeochemical and ecosystem interactions and their feedbacks are considered. Common interests in evolving computer technologies and computational techniques will be used by IMBER and AIMES to examine the role of the ocean in defining the relations between global climate variability/predictions, biogeochemistry and ecosystem feedbacks. IMBER will actively participate in the development of the AIMES Science Plan to ensure effective collaborative linkages.

Climate Variability and Predictability (CLIVAR)

CLIVAR (www.clivar.org) is a WCRP project with an extensive organisational structure in place and many observational and modelling/synthesis activities in progress. As IMBER research evolves, specific efforts will be made to develop linkages into CLIVAR's Global Ocean-Atmosphere-Land System activity, its Decadal-to-Centennial activity and its Anthropogenic Climate Change activity. This needs to occur, in particular, through interaction with CLIVAR's Ocean Basin Panels, its Global Synthesis and Observation Panel, the joint CLIVAR-PAGES panel and the CLIVAR modelling

Table 1. IMBER's role in ocean carbon research in relation to other projects considering oceanic carbon.

Topic	IMBER Role	Project Links
Vertical and horizontal fluxes in the ocean	Major	SOLAS
Continental shelf/open ocean exchange	Major	LOICZ
Benthic/pelagic coupling	Major	LOICZ
Continental margin carbon cycling	Shared	LOICZ, SOLAS
Carbon fixation/respiration and vertical transport	Major	SOLAS
Food web dynamics	Major	GLOBEC
Anthropogenic carbon accumulation	Shared	LOICZ
pH and ecosystems	Shared	SOLAS
Temperature effects on photosynthesis and respiration	Major	SOLAS
Impact of macro/micronutrient relationships on vertical export and ecosystems	Major	GLOBEC, SOLAS, LOICZ, GEOTRACES

panels, so that activities can be merged or interact to avoid duplication of organisational and planning efforts.

IMBER must collaborate closely with CLIVAR on its Repeat Hydrography/CO_2 Lines (Sabine and Hood, 2003), and IMBER will therefore take responsibility for coordinating the biogeochemical measurements on these Repeat Hydrography Lines. This coordination will be implemented through appropriate membership on the CLIVAR Basin Panels in association with the joint SOLAS-IMBER Carbon Implementation working group and IOCCP.

Various modelling activities in CLIVAR must be considered in detail to identify the commonalities that allow the physical, biogeochemical and ecosystem modelling needs of IMBER to be addressed in ways that avoid duplication. Common interests in evolving computer technologies and computational techniques should be used by IMBER and CLIVAR to translate climate variability/change predictions into biogeochemistry and ecosystem responses and feedbacks. There is strong interest in both CLIVAR and IMBER to use data, techniques and output from operational oceanography (in particular GODAE) to enable the common definition of ongoing analyses and reanalyses of the climate system. IMBER will consider coordinated activities in regions and processes that CLIVAR is investigating so that the best possible use of the limited resources available for sustained observations can be made (e.g. time-series stations and repeat hydrography lines). The interdisciplinary nature of IMBER science necessitates that its organisational structure involve members and representatives of the CLIVAR community where appropriate.

DIVERSITAS

DIVERSITAS (www.diversitas-international.org) is an international programme of biodiversity science, and one of the global environmental change programmes of ICSU. IMBER will coordinate with DIVERSITAS planning and implementation through a variety of mechanisms. Opportunities will be sought to link IMBER biodiversity research to the broader framework of mainstream ecology in association with DIVERSITAS. IMBER and DIVERSITAS will seek to share expertise for microbial systems with respect to ecosystem functioning, and to share networks of interdisciplinary researchers committed to understanding the feedbacks between society and biodiversity change.

Programmatic overlap exists between IMBER and DIVERSITAS in the area of ecosystem functioning, in particular between IMBER Issue 1.3 which considers functional biodiversity and the DIVERSITAS eco-Services project which assesses impacts of biodiversity changes on ecosystem functioning and services. The DIVERSITAS bioSustainability area which develops the science of conservation and sustainable use of biodiversity overlaps with IMBER Theme 4 (human dimensions). IMBER will actively encourage selected DIVERSITAS projects to seek endorsement from IMBER and will encourage reciprocal consideration from DIVERSITAS.

International Human Dimensions Programme on Global Environmental Change (IHDP)

IHDP (www.ihdp.org) is co-sponsored by ISCU and the International Social Science Council (ISSC). IMBER Theme 4 is of interest to IHDP and effective links with IHDP (in particular IDGEC) and the wider social science community will be critical in the development of this theme. Initially, IHDP can assist by identifying social scientists interested in the interactions and relationships between marine biogeochemical cycles, ecosystems and human systems.

Global Carbon Project (GCP)

GCP (www.globalcarbonproject.org) is one of the joint projects of the Earth System Science Partnership (ESSP) of the four international global environmental change programmes. GCP has developed a research framework for the synthesis of global carbon cycle data and models. It assists in the coordination of national programmes for global scale carbon research and facilitates the coupling of carbon research between the natural sciences and the social sciences. It is important that there is effective collaboration and communication between IMBER and GCP to ensure that IMBER data and research results are integrated into the GCP synthesis.

Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB)

GEOHAB (www.geohab.info) is a joint SCOR-IOC project with which IMBER shares common interests in biogeochemical cycles and ecosystem interactions – particularly in the continental margins, as well as in how ocean physics, chemistry and biology control phytoplankton population dynamics. IMBER and GEOHAB will share data and scientific results through various collaborations and including the development of

a common data management strategy for IGBP-SCOR marine projects and research into the controls of phytoplankton population dynamics. GEOHAB's project on Harmful Algal Blooms in Upwelling Systems could be particularly fruitful for joint work.

International Ocean Carbon Coordination Project (IOCCP)

Many national and international programmes conduct or have a direct interest in observations and research related to the global ocean carbon cycle. There is an immediate need for a global forum for coordination of ocean carbon studies including data collection, large-scale synthesis efforts, model-data integration and the development of a sustained ocean carbon observing system. Coordination is central to the achievement of the carbon-related goals of SOLAS and IMBER.

IOCCP (ioc.unesco.org/ioccp) is a joint SCOR-IOC project that helps meet these needs: it will help conduct coordination activities including the development of the observing system and permanent data archiving. IOCCP will:

- implement a central information centre for programme planning (for example, compiling information on current and planned repeat hydrographic sections, volunteer observing ship carbon measurements, time-series networks measuring carbon and process studies);
- develop international agreements on standards, best practices, data and meta-data standards; and
- monitor implementation of the global ocean carbon observing systems and liaise with the larger global ocean/climate observing system.

The joint SOLAS-IMBER Ocean Carbon working group will be an active cooperating partner with IOCCP to avoid duplications and to highlight areas for potential collaboration with other ocean carbon research projects. The two groups will work together to ensure compatibility of ocean carbon data management activities and to encourage data sharing.

GEOTRACES

GEOTRACES (www.geotraces.org) is a SCOR project, data from which will be important in addressing IMBER research on understanding biogeochemical cycles and basin-scale trace element distributions. In particular, GEOTRACES research will be a critical contribution to IMBER Issue 1.1. IMBER and GEOTRACES will investigate the development of joint studies and field activities. To ensure effective communication between IMBER and GEOTRACES, the Chair/Co-Chair of the GEOTRACES SSC will be an *ex officio* member of the IMBER SSC.

The Census of Marine Life (CoML)

CoML (www.coml.org) is a SCOR-affiliated international marine biodiversity programme with national and regional implementation committees, targeted special-issue panels, three component projects, 14 field projects and diverse programmatic elements (e.g. education and communication). IMBER will coordinate with CoML by encouraging participation of CoML researchers in IMBER working groups and field projects in order to provide critical taxonomic expertise for IMBER research. Several CoML field projects, including the International Census of Marine Microbes (icomm.mbl.edu) and the Census of Marine Zooplankton (plankton.unh.edu), are particularly relevant. IMBER will seek opportunities for joint planning and implementation activities with CoML. IMBER will seek participation in and coordination with a new SCOR Panel on New Technologies for Observing Marine Life, which was developed to serve both the CoML community and, more generally, other marine biology projects. IMBER will also coordinate with selected national and regional implementation committees in areas where IMBER-endorsed research will be conducted.

Other SCOR Affiliated Projects

Three other projects affiliated with SCOR will seek to involve their scientists in IMBER activities: the International Ocean Colour Coordinating Group, the International Antarctic Zone Programme, and the International RIDGE Studies. Specific interactions with these projects have not been identified as yet.

Global Ocean Observing System (GOOS) and Global Climate Observing System (GCOS)

GOOS (ioc.unesco.org/goos) and GCOS (193.135.216.2/web/gcos/gcoshome.html) are global observing programmes which share many data and data system needs with IMBER. Best use should be made of standards, procedures and protocols developed by the international ocean community to ensure data interoperability between research projects and GOOS. Routinely generated ocean products may assist IMBER process

studies, and IMBER use of routinely collected data may lead to improvements in sustained observing systems.

IMBER and the two science panels of GOOS (OOPC and COOP) should develop mechanisms to enable effective communication and interaction between IMBER and GOOS/GCOS. This will occur primarily through direct linkages of OOPC and COOP with the IMBER Ocean Carbon, End-to-end Food Webs and Macro- and Micronutrients working groups. This interaction should ensure that new knowledge and technologies developed by IMBER are used effectively to improve operational capabilities of GOOS.

References

Anderson DM, Gilbert PM and Bulkholder JM (2002). Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuaries 25: 704–726.

Archer D, Winguth A, Lea D and Mahowald N (2000). What caused the glacial/interglacial atmospheric pCO_2 cycles? Reviews of Geophysics 38(2): 159–189.

Armstrong RA, Lee C, Hedges JI, Honjo S and Wakeham SG (2002). A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with mineral ballast. Deep-Sea Research II 49(1-3): 219–236.

Arrigo KR, Robinson DH, Worthen DL, Dunbar RB, DiTullio GR, van Woert M and Lizotte MP (1999). Phytoplankton community structure and the drawdown of nutrients and CO_2 in the Southern Ocean. Science 283: 365–367.

Baden SP and Neil DM (2003). Manganese accumulation by the antennule of the Norway lobster *Nephrops norvegicus* (L.) as a biomarker of hypoxic events. Marine Environmental Research 55: 59–71.

Bakun A (1996). Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. University of California Sea Grant, San Diego, California, USA, in cooperation with Centro de Investigaciones Biologicas de Noroeste, La Paz, Baja California Sur, Mexico.

Barange M and Harris R (Eds.) (2003). Marine Ecosystems and Global Change. International Geosphere-Biosphere Programme. IGBP Science No. 5. Stockholm.

Bates NR, Knap AH and Michaels AF (1998). Contribution of hurricanes to local and global estimates of air-sea exchange of CO_2. Nature 395: 58–61.

Bates NR, Pequignet AC, Johnson RJ and Gruber N (2002). Changes in the oceanic sink of CO_2 in subtropical mode water of the North Atlantic Ocean. Nature 420: 489–492.

Baumgartner TR, Soutar A and Ferreira-Bartrina V (1992). Reconstruction of the history of Pacific sardine and northern anchovy populations over the past two millennia from sediments of the Santa Barbara basin. California, CALCOFI Report, 33: 24–40.

Beaugrand G, Brander KM, Lindley JA, Souissi S and Reid PC (2003). Plankton effect on cod recruitment in the North Sea. Nature 426: 661–664.

Beaugrand G, Reid PC, Ibanez F, Lindley JA and Edwards M (2002). Reorganisation of North Atlantic marine copepod biodiversity and climate. Science 296: 1,692–1,694.

Beaumont KL, Nash GV and Davidson AT (2002). Ultrastructure, morphology and flux of microzooplankton faecal pellets in an east Antarctic fjord. Marine Ecology Progress Series 245: 133–148.

Bellwood DR, Hughes TP, Folke C and Nystrom M (2004). Confronting the coral reef crisis. Nature 429: 827–833.

Berelson W, McManus J, Coale K, Johnson K, Burdige, D, Kilgore T, Colodner D, Chavez F, Kudela R and Boucher J (2003). A time series of benthic flux measurements from Monterey Bay, CA. Journal of Continental Shelf Research 23: 457–482.

Bertilsson S, Berglund O, Karl DM and Chisholm SW (2003). Elemental composition of marine *Prochlorococcus* and *Synechococcus*: Implications for the ecological stoichiometry of the sea. Limnology and Oceanography 48: 1,721–1,731.

Bishop J, Davis R and Sherman J (2002). Robotic observations of dust storm enhancement of carbon biomass in the North Pacific. Science 298: 817–821.

Bopp L, Kohfeld KE, Le Quéré C and Aumont O (2003). Dust impact on marine biota and atmospheric CO_2 during glacial periods. Paleoceanography 18(1046): doi:10.1029/2002PA000,810.

Bopp L, Le Quéré C, Heimann M, Manning AC and Monfray P (2002). Climate-induced oceanic oxygen fluxes: Implications for the contemporary carbon budget. Global Biogeochemical Cycles 16(2): article no. 1,022.

Bopp L, Monfray P, Aumont O, Dufresne J-L, Le Treut H, Madec G, Terray L and Orr JC (2001). Potential impact of climate change on marine export production. Global Biogeochemical Cycles 15: 81–99.

Boucher NP and Prezelin BB (1996). An *in situ* biological weighting function for UV inhibition of phytoplankton carbon fixation in the Southern Ocean. Marine Ecology Progress Series 144: 223–236.

Bousquet P, Peylin P, Ciais P, Le Quéré C, Friedlingstein P and Tans PP (2000). Regional changes in carbon dioxide fluxes of land and oceans since 1980. Science 290: 1,342–1,346.

Boyd PW and Doney SC (2003). The impact of climate change and feedback processes on the ocean carbon cycle. In Fasham MJR (Ed.), Ocean Biogeochemistry: The Role of the Ocean Carbon Cycle in Global Change. Springer-Verlag, Berlin. Pp157–193.

Brander KM (1995). The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science 52(1): 1–10.

Bratbak G, Thingstad F and Heldal M (1994). Viruses and the microbial loop. Microbial Ecology 28(2): 209–221.

Breitburg D (2002). Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25: 767–781.

Brodeur RD, Sugisaki H and Hunt Jr GL (2002). Increases in jellyfish biomass in the Bearing Sea: implications for the ecosystem. Marine Ecology Progress Series 233: 89–103.

Bruland KW, Rue EL and Smith GJ (2001). Iron and macronutrients in California coastal upwelling regimes: Implications for diatom blooms. Limnology and Oceanography 46(7): 1,661–1,674.

Bucklin A and Wiebe PH (1998). Low mitochondrial diversity and small effective population sizes of the copepods, *Calanus finmarchicus* and *Nannocalanus minor*, possible impact of climatic variation during recent glaciation. Journal of Heredity 89: 383–392.

Burkhardt S, Zondervan I and Riebesell U (1999). Effect of CO_2 concentration on C:N:P ratio in marine phytoplankton: A species comparison. Limnology and Oceanography 44: 683–690.

Burkhart S, Amoroso G, Riebesell U and Sultemeyer D (2001). CO_2 and HCO_3^- uptake in marine diatoms acclimated to different CO_2 concentrations. Limnology and Oceanography 46: 1,378–1,391.

Butler A (1998). Acquisition and utilisation of transition metal ions by marine organisms. Science 281: 207–210.

Caldeira K and Wickett ME (2003). Anthropogenic carbon and ocean pH. Nature 425: 365–368.

Charlson RJ, Lovelock JEM, Andreae O and Warren SG (1987). Oceanic phytoplankton, atmospheric sulphur, cloud albedo and climate. Nature 326: 655–661.

Chavez FP, Ryan J, Lluch-Cota SE and Ñiquen C (2003). From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. Science 299: 217–221.

Chen C-TA, Liu KK and MacDonald R (2003). Continental margin exchanges. In: Fasham MJR (Ed.), Ocean Biogeochemistry. Berlin, Springer. Pp53–97.

Chiba S, Ono T, Tadokoro K, Midorikawa T and Saino T (2004). Increased stratification and decreased lower trophic level productivity in the Oyashio Region of the North Pacific: a 30-year retrospective study. Journal of Oceanography 60: 149–162.

Christensen V, Guénette S, Heymans JJ, Walters CJ, Watson R, Zeller D and Pauly D (2003). Hundred year decline of North Atlantic predatory fishes. Fish and Fisheries 4(1): 1–24.

Codispoti LA, Brandes JA, Christensen JP, Devol AH, Naqvi SWA, Paerl HW and Yoshinari T (2001). The oceanic fixed nitrogen and nitrous oxide budgets: moving targets as we enter the Anthropocene? Scientia Marina 65: (Supplement 2) 85–105.

Codispoti LA and Christensen JP (1985). Nitrification, denitrification and nitrous oxide cycling in the eastern tropical South Pacific Ocean. Marine Chemistry 16: 277–300.

Cooper RU, Clough LM, Farwell MA and West TL (2002). Hypoxia-induced metabolic and antioxidant enzymatic activities in the estuarine fish *Leiostomus xanthurus*. Journal of Experimental Marine Biological Ecology 279: 1–20.

Cowen JP, Giovannoni SJ, Kenig F, Johnson HP, Butterfield D, Rappe MS, Hutnak M and Lam P (2003). Fluids from aging ocean crust that support microbial life. Science 299: 120–123.

Crawford DW, Lipsen MS, Purdie DA, Lohan MC, Statham PJ, Whitney FA, Putland JN, Johnson WK, Sutherland N, Peterson TD, Harrison PJ and Wong CS (2003). Influence of zinc and iron enrichments on phytoplankton growth in the northeastern subarctic Pacific. Limnology and Oceanography 48(4): 1,583–1,600.

Cury P, Shannon L and Shin YJ (2003). The Functioning of Marine Ecosystems: a Fisheries Perspective. In: Sinclair M and Valdimarsson G (Eds.), Responsible Fisheries in the Marine Ecosystem. FAO.

Danard M, Munro A and Murty T (2003). Storm surge hazard in Canada. Natural Hazards 28(2-3): 407–431.

Dayton PK (1985). Ecology of kelp communities. Annual Reviews of Ecology and Systematics 16: 215–245.

de Baar HJW, Boyd PW, Coale K, Buesseler K, Bakker D, Bozec Y, Boye M, Croot P, Laan P, Lancelot C, Levasseur M, Nishioka J, Nojiri Y, van Oijen T, Takeda S, Timmermans KA, Tsuda A and Veldhuis MJW (in press). Synthesis of eight *in-situ* iron fertilisations in high nutrient low chlorophyll waters confirms the control by wind mixed layer depth of phytoplankton blooms in the oceans. Journal of Geophysical Research.

Debernard J, Saetra O and Roed LP (2002). Future wind, wave and storm surge climate in the North Atlantic. Climate Research 23(1): 39–49.

DeMaster DJ (2002). The accumulation and cycling of biogenic silica in the Southern Ocean: revisiting the marine silica budget. Deep-Sea Research II 49(16): 3,155–3,167.

Denman K (1973). A time-dependent model of the upper ocean. Journal of Physical Oceanography 3: 173–184.

de Young B, Heath M, Werner F, Chai F, Megrey B and Monfray P (2004). Challenges of modelling ocean basin ecosystems. Science 304: 1,463–1,464.

Diaz RJ and Rosenburg R (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses on benthic macrofauna. Oceanography Marine Biology Annual Review 33: 245–303.

Dickey TD (2001). The role of new technology in advancing ocean biogeochemical research. Oceanography 14(4): 108–120.

DIVERSITAS (2002). Science Plan. DIVERSITAS, Paris, France.

Dugdale RC and Wilkerson FP (1998). Silicate regulation of new production in the equatorial Pacific upwelling. Nature 391: 270–273.

Edwards M and Richardson AJ (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430: 881–884.

Elrod VA, Berelson WM, Coale KH and Johnson KS (2004). The flux of iron from continental shelf sediments: a missing source for global budgets. Geophysical Research Letters 31(12): article no. L12,307.

Emerson S, Mecking S and Abell J (2001). The biological pump in the subtropical North Pacific Ocean: nutrient sources, Redfield ratios and recent changes. Global Biogeochemical Cycling 15: 535–554.

Engel A, Thoms S, Riebesell U, Rochelle-Newall E and Zondervan I (2004). Polysaccharide aggregation as a potential sink of marine dissolved organic carbon. Nature 428: 929–932.

FAO (2000). The State of World Fisheries and Aquaculture – 2000. Pp142.

Fasham MJR, Baliño BM and Bowles MC (Eds.) (2001). A new vision of ocean biogeochemistry after a decade of the Joint Global Ocean Flux Study (JGOFS). Ambio (Special Report 10): 4–31.

Fasham MJR, Sarmiento JL, Slater RD, Ducklow HW and Williams RA (1993). A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone: a comparison of the model results with observations from Bermuda Station S and OWS India. Global Biogeochemical Cycles 7: 379–416.

Feely RA, Boutin J, Cosca CE, Dandonneau Y, Etcheto J, Inoue HY, Ishii M, Le Quéré C, Mackey DJ, McPhaden M, Metzl N, Poisson A and Wanninkhof R (2002). Seasonal and interannual variability of CO_2 in the equatorial Pacific. Deep-Sea Research II 49(13–14): 2,443–2,469.

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas JA, Fabry VJ and Millero FJ (2004). Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science 305: 362–367.

Fiksen Ø, Utne ACW, Aksnes DL, Eiane K, Helvik JV and Sundby S (1998). Modelling the influence of light, turbulence and ontogeny on ingestion rates in larval cod and herring. Fisheries Oceanography 7: 355–363.

Fonseca CR and Ganade G (2001). Species functional redundancy, random extinctions and the stability of ecosystems. Journal of Ecology 89(1): 118–125, doi: 10.1046/j.1365–2745.2001.00528.x.

Friedlingstein P, Bopp L, Ciais P, Dufresne J-L, Fairhead L, LeTreut H, Monfray P and Orr J (2001). Positive feedback between future climate change and the carbon cycle. Geophysical Research Letters 28(8): 1,543–1,546.

Gallego A, Mardaljevic J, Heath MR, Hainbucher D and Slagstad D (1999). A model of the spring migration into the North Sea by *Calanus finmarchicus* overwintering off the Scottish continental shelf. Fisheries Oceanography Supplement 1: 107–125.

GLOBEC (1999). GLOBEC Implementation Plan. IGBP Secretariat, Stockholm, Sweden. IGBP Report Series No. 47.

Goddard L and Graham NE (1999). Importance of Indian Ocean for simulating rainfall anomalies over eastern and southern Africa. Journal of Geophysical Research 104: 19,099–19,016.

Grad G, Williamson CE and Karapelou DM (2001). Zooplankton survival and reproduction responses to damaging UV radiation: a test of reciprocity and photoenzymatic repair. Limnology and Oceanography 46: 584–591.

Granéli E and Haraldsson C (1993). Can increased leaching of trace-metals from acidified areas influence phytoplankton growth in coastal waters. Ambio 22: 308–311.

Granger J and Ward BB (2003). Accumulation of nitrogen oxides in copper-limited cultures of denitrifying bacteria. Limnology and Oceanography 48: 313–318.

Grant WS and Bowen BW (1998). Shallow population histories in deep evolutionary lineages of marine fishes: insights from sardines and anchovies and lessons for conservation. Journal of Heredity 89: 415–426.

Grantham BA, Chan F, Nielsen KJ, Fox DS, Barth JA, Huyer A, Lubchenco J and Menge BA (2004). Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. Nature 429: 749–754.

Greene CH, Pershing AJ, Conversi A, Planque B, Hannah C, Sameoto D, Head E, Smith PC, Reid PC, Jossi J, Mountain D, Benfield MC, Wiebe PH and Durbin E (2003). Trans-Atlantic responses of *Calanus finmarchicus* populations to basin-scale forcing associated with the North Atlantic Oscillation. Progress in Oceanography 58: 301–312.

Greve W, Lange U, Reiners F and Nast J (Eds.) (2001). Predicting the seasonality of North Sea zooplankton. In: Burning Issues of North Sea Ecology, Proceedings of the 14th International Senckenberg Conference, North Sea, 2000. Senckenbergiana marit., Frankfurt.

Grosholz E (2002). Ecological and evolutionary consequences of coastal invasions. Trends in Ecological Evolution 17: 22–27.

Gruber N and Sarmiento JL (2002). Biogeochemical–physical interactions in elemental cycles. In: Robinson AR, McCarthy JJ and Rothschild BJ (Eds.) The Sea Volume 12: Biological–Physical Interactions in the Oceans. John Wiley and Sons. Pp337–399.

Hare SR and Mantua NJ (2000). Empirical evidences for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47: 103–145.

Hearn CJ and Robinson BJ (2001). Inter-annual variability of bottom hypoxia in shallow Mediterranean estuaries. Estuarine and Costal Shelf Science 52: 643–657.

Hebert PDN, Cywinska A, Ball SL and deWaard JR (2003). Biological identifications through DNA barcodes. Proceedings of the Royal Society of London B 270: 313–322.

Hedges JI and Keil RG (1995). Sedimentary organic matter preservation: an assessment and speculative synthesis. Marine Chemistry 49: 81–115.

Hein M and Sand-Jensen K (1997). CO_2 increases oceanic primary production. Nature 388: 526–527.

Helbling EW, Buma AGJ, De Boer MK and Villafane VE (2001). *In situ* impact of solar ultraviolet radiation on photosynthesis and DNA in temperate marine phytoplankton. Marine Ecology Progress Series 211: 43–49.

Hinga KR (2002). Effect of pH on coastal marine phytoplankton. Marine Ecology Progress Series 238: 281–300.

Hoffmeyer MS (2004). Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species. Journal of Plankton Research 26: 181–189.

Holfort J, Johnson KM, Schneider B, Siedler G and Wallace DWR (1998). Meridional transport of dissolved inorganic carbon in the South Atlantic Ocean. Global Biogeochemical Cycles 14: 479–499.

Holland HD (1984). The Chemical Evolution of the Atmosphere and Oceans. Princeton University Press, Princeton.

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ and Xiaosu D (2001). Climate Change 2001: The Scientific Basis – Contribution of Working Group I to the Third Assessment Report of IPCC. Intergovernmental Panel on Climate Change. Cambridge Univserity Press, UK. Pp944.

Huggett J, Fréon P, Mullon C and Penven P (2003). Modelling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: the effect of spatio-temporal spawning patterns. Marine Ecology Progress Series 250: 247–262.

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JB, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B and Roughgarden J (2003). Climate change, human impacts, and the resilience of coral reefs. Science 301: 929–933.

Huse I (1994). Feeding at different illumination levels in larvae of three marine teleost species: Cod, *Gadus morhua* L., plaice, *Pleuronectes platessa* L., and turbot, *Scophthalmus maximus* L. Aquaculture Fisheries Management 25: 687–695.

Hutchins DA and Bruland KW (1998). Iron-limited diatom growth and Si:N uptake ratios in a coastal upwelling regime. Nature 393: 561–564.

Hutchins DA, Hare CE, Weaver RS, Zhang Y, Firme GF, DiTullio GR, Alm MB, Riseman SF, Maucher JM, Geesey ME, Trick CG, Smith GJ, Rue EL, Conn J and Bruland KW (2002). Phytoplankton iron limitation in the Humboldt Current and Peru Upwelling. Limnology and Oceanography 47: 997–1,011.

ICES (2003). Report of the Working Group on Ecosystem Effects of Fishing Activities. ICES Head Quarters Copenhagen, Denmark, ICES CM 2003/ACE: 05. Pp193.

IGBP/SCOR (2002). Framework for Future Research on Biological and Chemical Aspects of Global Change in the Ocean: an IGBP/SCOR Collaboration. www.igbp.net//uploads/FW-Final-2002.pdf.

Iglesias-Rodriguez MD, Brown CW, Doney SC, Kleypas JA, Kolber D, Kolber Z, Hayes PK and Falkowski PG (2002a). Representing key phytoplankton functional groups in ocean carbon cycle models: Coccolithophorids. Global Biogeochemical Cycles 16(4): 1,100.

Iglesias-Rodriguez MD, Saez AG, Groben R, Edwards KJ, Batley J, Medlin LK and Hayes PK (2002b). Polymorphic microsatellite loci in global populations of the marine coccolithophorid *Emiliania huxleyi*. Molecular Ecology Notes 2(4): 495–497.

IHDP (1999). Global Environmental Change and Human Security: Science Plan. Lonergan S et al. (Eds.) IHDP Report Series No. 11. Bonn.

Indermühle A, Stocker TF, Joos F, Fischer H, Smith HJ, Wahlen M, Deck B, Mastroianni D, Tschumi J, Blunier T, Meyer R and Stauffer B (1999). Holocene carbon-cycle dynamics on CO_2 trapped in ice at Taylor Dome, Antarctica. Nature 398: 121–126.

Irigoien Z, Huisman J and Harris RP (2004). Global biodiversity levels of marine phytoplankton and zooplankton. Nature 429: 863–867.

Ittekkot V, Humborg C and Schafer P (2000). Hydrological alterations on land and marine biogeochemistry: a silicate issue? BioScience 50: 776–782.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke RG, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ and Warner RR (2001). Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–638.

Jahnke RA (1996). The global ocean flux of particulate organic carbon: areal distribution and magnitude. Global Biogeochemical Cycles 10: 71–88.

Jahnke RA, Nelson JR, Marinelli RL and Eckman JE (2000). Benthic flux of biogenic elements on the southeastern U.S. continental shelf: influence of pore water advective transport and benthic micro-algae. Continental Shelf Research 20: 109–127.

Jones G P, McCormick MI, Srinivasan M and Eagle JV (2004). Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences of the United States of America 101(21): 8,251–8,253.

Joos F, Plattner G-K, Stocker TF, Körtzinger A and Wallace DWR (2003). Trends in marine dissolved oxygen: implications for ocean circulation changes and the carbon budget. EOS – Transactions of the American Geophysical Union 84(21): 197–201.

Justic D, Rabalais NN and Turner RE (1997). Impacts of climate change on net productivity of coastal waters: implications for carbon budget and hypoxia. Climate Research 8: 225–237.

Justic D, Turner RE and Rabalais NN (2003). Climatic influences on riverine nitrate flux: implications for coastal marine eutrophication and hypoxia. Estuaries 26: 1–11.

Kannen A, Windhorst W and Colijn F (2003). The use of indicators in the EUROCAT project. Book of Abstracts. European Conference of Coastal Zone Research: an ELOISE Approach, Jointly organised by the European Commission-DG Research. The Norwegian Institute for Air Research, and the Gdansk University of Technology, 24–27 March 2003.

Karl DM (1999). A sea of change: biogeochemical variability in the North Pacific subtropical gyre. Ecosystems 2: 181–214.

Karl DM (2002). Nutrient dynamics in the deep blue sea. Trends in Microbiology 10: 410–418.

Karl DM, Bates NR, Emerson S, Harrison PJ, Jeandel C, Llinás O, Liu KK, Marty JC, Michaels AF, Miquel JC, Neuer S, Nojiri Y and Wong CS (2003). Temporal studies of biogeochemical processes determined from ocean time-series observations during the JGOFS era. In Fasham MJR (Ed.), Ocean Biogeochemistry: The Role of the Ocean Carbon Cycle in Global Change. Springer-Verlag, Berlin. Pp239–267.

Karl DM, Bidigare RR and Letelier RM (2001a). Long-term changes in plankton community structure and productivity in the North Pacific Subtropical Gyre: the domain shift hypothesis. Deep-Sea Research II 48: 1,449–1,470.

Karl DM, Björkman KM, Dore JE, Fujieki L, Hebel DV, Houlihan T, Letelier RM and Tupas LM (2001b). Ecological nitrogen-to-phosphorus stoichiometry at station ALOHA. Deep Sea Research Part II: Topical Studies in Oceanography 48(8–9): 1,529–1,566.

Karl D, Letelier R, Tupas L, Dore J, Christian J and Hebel D (1997). The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. Nature 388: 533–538.

Keeling CD, Whorf TP, Wahlen M and Vanderplicht J (1995). Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. Nature 375: 666–670.

Keller K, Slater RD and Bates NR (2002). Possible biological or physical explanation for decadal scale trends in North Pacific nutrient concentrations and oxygen utilisation. Deep-Sea Research II 49: 345–362.

Kester DR (1986). Equilibrium models in seawater: applications and limitations. In: Bernhard M, Brinckman FE and Sadler PJ (Eds.), The Importance of Chemical 'Speciation' in Environmental Processes. Springer-Verlag, Berlin. Pp337–363.

Kideys AE (2002). Rise and fall of the Black Sea ecosystem. Science 297: 1,482–1,484.

Klaas C and Archer DE (2002). Association of sinking organic matter with various types of mineral ballast in the deep sea: implications for the rain ratio. Global Biogeochemical Cycles 16(4): article no. 1,116.

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

Klyashtorin LB (1998). Long-term climate change and main commercial fish production in the Atlantic and Pacific. Fisheries Research 37(1–3): 115–125.

Knutti R and Stocker TF (2002). Limited predictability of the future thermohaline circulation close to an instability threshold. Journal of Climate 15: 179–186.

Kustka A, Sañudo-Wilhelmy S, Carpenter EJ, Capone DG and Raven JA (2003). A revised estimate of the iron use efficiency of nitrogen fixation, with special reference to the marine cyanobacterium *Trichodesmium* spp. (Cyanophyta). Journal of Phycology 39: 12–25.

Köster FW, Hinrichsen HH, St. John MA, Schnack D, MacKenzie B and Plikshs M (2001). Developing Baltic cod recruitment models II: incorporation of environmental variability and species interaction. Canadian Journal of Fisheries and Aquatic Science 58: 1,534–1,556.

Labeyrie L, Cole J, Alverson K and Stocker T (2002). The history of climate dynamics in the late Quaternary. In: Alverson K, Bradley RS and Pederson T (Eds.), Paleoclimate, Global Change and the Future. IGBP Book Series. Springer Verlag, Heidelberg. Pp33–61.

Langdon C, Broecker WS, Hammond DE, Glenn E, Fitzsimmons K, Nelson SG, Peng T-H, Hajdas I and Bonani G (2003). Effect of elevated CO_2 on the community metabolism of an experimental coral reef. Global Biogeochemical Cycles 17: article no. 1,011.

Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J, Marubini F, Aceves H, Barnett H and Atkinson MJ (2000). Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. Global Biogeochemical Cycles 14: 639–654.

Laws EA, Falkowski PG, Smith WO Jr, Ducklow H and McCarthy JJ (2000). Temperature effects on export production in the open ocean. Global Biogeochemical Cycles 14(4): 1,231–1,246.

Legendre L and Rivkin RB (2002). Fluxes of carbon in the upper ocean: regulation by food-web control nodes. Marine Ecology Progress Series 242: 95–109.

Lehodey P (2001). The pelagic ecosystem of the tropical Pacific Ocean: dynamic spatial modelling and biological consequences of ENSO. Progress in Oceanography 49: 439–468.

Le Quéré C, Harrison SP, Prentice IC, Buitenhuis ET, Aumont O, Bopp L, Claustre H, Cotrim da Cunha L, Geider RJ, Giraud X, Klaas C, Kohfeld KE, Legendre L, Manizza M, Platt T, Rivkin RB, Sathyendranath S, Uitz J, Watson AJ and Wolf-Gladrow DA (in review). Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. Global Change Biology.

Le Quéré C, Orr JC, Monfray P, Aumont O and Madec G (2000). Interannual variability of the oceanic sink of CO_2 from 1979 through 1997. Global Biogeochemical Cycles 14(4): 1,247–1,265.

Levitus S, Antonov JI and Boyer TP (2005). Warming of the world ocean, 1955–2003. Geophysical Research Letters 32 L02604, doi:10.1029/2004GL021592.

Lewis M, Carr M, Feldmann G, Essias W and McClain C (1990). Influence of penetrating solar radiation on the heat budget of the equatorial Pacific Ocean. Nature 347: 543–545.

Lewitus AJ, Kawaguchi T, DiTullio GR and Keesee JDM (2004). Iron limitation of phytoplankton in an urbanised vs. forested southeastern U.S. salt marsh estuary. Journal of Experimental Marine Biology and Ecology 298(2): 233–254.

Li DJ, Zhang J, Huang DJ, Wu Y and Liang J (2002). Depletion of dissolved oxygen off the Chagjiang Eastuary. Science China 32(D): 686–694.

Loisel H, Nicolas JM, Deschamps PY and Frouin R (2002). Seasonal and inter-annual variability of the particulate matter in the global ocean. Geophysical Research letters 29: 2,996.

Longhurst A (1995). Seasonal cycles of pelagic production and consumption. Progress In Oceanography 36(2 SU): 77–167.

Loreau M and Oliveri I (1999). DIVERSITAS: an international programme on biodiversity science. Trends in Ecology and Evolution 14(1): 5.

Lynam CP, Hay SJ and Brierley AS (2004). Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnology and Oceanography(3): 637–643.

Mackas DL and Tsuda A (1999). Mesozooplankton in the eastern and western subarctic Pacific: community structure, seasonal life histories, and interannual variability. Progress in Oceanography 43: 35–363.

Macy WK, Sutherland SJ and Durbin EG (1998). Effects of zooplankton size and concentration and light intensity on the feeding behaviour of Atlantic mackerel *Scomber scombrus*. Marine Ecology Progress Series 172: 89–100.

Madin LP, Horgan EF and Steinberg DK (2001). Zooplankton at the Bermuda Atlantic Time-series Study (BATS) station: diel, seasonal and inerannual variation in biomass, 1994–1998. Deep-Sea Research II 48(8-9): 2,063–2,082.

Malakoff D (1998). Death by suffocation in the Gulf of Mexico. Science 281: 190–192.

Malone TC, Pike SE and Conley DJ (1993). Transient variations in phytoplankton productivity at the JGOFS Bermuda time-series station. Deep-Sea Research I 40: 903–924.

Manizza M, Le Quéré C, Watson AJ and Buitenhuis ET (2005). Bio-optical feedbacks among phytoplankton, upper ocean physics and sea-ice in a global model. Geophysical Research Letters 32(5): L05603 10.1029/2004GL020778.

Mann EL, Ahlgren N, Moffett JW and Chisholm SW (2001). Copper toxicity and cyanobacteria ecology in the Sargasso Sea. Limnology and Oceanography 47: 976–988.

Marshall CT (1999). Total lipid energy as a proxy for total egg production by fish stocks. Nature 402(6759): 288–290.

McGowan JA (1990). Climate and change in oceanic ecosystems: the value of time-series data. Trends in Ecological Evolution 5: 293–295.

McGowan JA, Bograd SJ, Lynn RJ and Miller AJ (2003). The biological response to the 1977 regime shift in the California Current. Deep-Sea Research II 50: 2,567–2,582.

Michaels A and Silver M (1988). Primary production, sinking fluxes and the microbial food web. Deep-Sea Research I 35(4): 473–490.

Micheli F (1999). Eutrophication, fisheries and consumer-resource dynamics in marine pelagic ecosystems. Science 285: 1,396–1,398.

Middelburg JJ, Soetaert K, Herman PMJ and Heip CHR (1996). Denitrification in marine sediments: a model study. Global Biogeochemical Cycles 10: 661–673.

Miller AJ, Alexander MA, Boer GJ, Chai F, Denman K, Erickson DJ III, Frouin R, Gabric AJ, Laws EA, Lewis MR, Liu Z, Murtugudde R, Nakamoto S, Neilson DJ, Norris JR, Ohlmann JC, Perry RI, Schneider N, Shell KM and Timmermann A (2003). Potential feedbacks between the Pacific Ocean ecosystems and interdecadal climate variations. Bulletin American Meterology Society 84(5): 617–633.

Moffett JW (1995). Temporal and spatial variability of strong copper complexing ligands in the Sargasso Sea. Deep-Sea Research I 42(8): 1,273–1,295.

Moffett JW and Brand LE (1996). The production of strong, extracellular Cu chelators by marine cyanobacteria in response to Cu stress. Limnology and Oceanography 41: 288–293.

Mohtadi M and Hebbeln D (2004). Mechanisms and variations of the paleoproductivity off northern Chile (24°S–33°S) during the last 40,000 years. Palaeoceanography 19: PA2023, doi:10.1029/2004PA001003.

Molenaar FJ and Breeman AM (1997). Latitudinal trends in the growth and reproductive seasonality of *Delesseria sanguinea*, *Membranoptera alata*, and *Phycodrys rubens* (Rhodophyta). Journal of Phycology 33: 330–343.

Moore JK, Doney SC, Kleypas JA, Glover DM and Fung IY (2002). An intermediate complexity marine ecosystem model for the global domain. Deep-Sea Research II 49: 403–462.

Murtugudde R, Beauchamp J, McClain CR, Lewis M and Busalacchi AJ (2002). Effects of penetrative radiation on the upper tropical ocean circulation. Journal of Climate 15(5): 470–486.

Myers N (1995). Environmental unknowns. Science 269: 358–360.

Myers RA and Worm B (2003). Rapid worldwide depletion of predatory fish communities. Nature 423: 280–283.

Möllmann C, Kornilovs G, Fetter M, Köster FW and Hinrichsen H-H (2003). The marine copepod, *Pseudocalanus elongatus*, as a mediator between climate variability and fisheries in the central Baltic Sea. Fisheries Oceanography 12(4/5): 360–368.

Nakamoto S, Prasanna Kumar S, Oberhuber JM, Ishizaka J, Muneyama K and Frouin R (2001). Response of the equatorial Pacific to chlorophyll pigment in a mixed layer isopycnal ocean general circulation model. Geophysical Research Letters 28: 2,021–2,024.

Nakken O and Raknes A (1987). The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the Barents Sea 1978–1984. Fisheries Research 5(2/3): 243–252.

Napp JM and Hunt GL (2001). Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean and biology. Fisheries Oceanography 10: 61–68.

Naqvi SWA, Sarma VVSS and Jayakumar DA (2002). Carbon cycling in the northern Arabian Sea during the northeast monsoon: significance of salps. Marine Ecology Progress Series 226: 35–44.

Nevison CD, Lueker TJ and Weiss RF (2004). Quantifying the nitrous oxide source from coastal upwelling. Global Biogeochemical Cycles 18: GB1018, doi: 10.1029/2003GB002110.

Nevison CD, Weiss RF and Erickson DJ (1995). Global oceanic emissions of nitrous oxide. Journal of Geophysical Research 100: 15,809–15,820.

Nielsen EE, Hansen MM, Schmidt C, Meldrup D and Grønkjær P (2001). Population of origin of Atlantic cod. Nature 413: 272.

Nozaki Y (1997). Vertical profiles of elements in the North Pacific Ocean. EOS – Transactions of the American Geophysical Union 78: 221.

Officer CB, Biggs RB, Taft JL, Cronin LE, Tyler MA and Boynton WR (1984). Chesapeake Bay anoxia: origin, development and significance. Science 223: 22–27.

Ohman MD and Wood SN (1995). The inevitability of mortality. ICES Journal of Marine Science 52: 517–522.

Ono T, Tadokoro K, Midorikawa T, Nishioka J and Saino T (2002). Multi-decadal decrease of net community production in western subarctic North Pacific. Geophysical Research Letters 29(10).

Pace LP, Cole JJ, Carpenter SR and Kitchell JF (1999). Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14(12): 483–488.

Pagani M, Arthur MA and Freeman KH (1999). Miocene evolution of atmospheric carbon dioxide. Palaeoceanography 14: 273–292.

Paine RT (1994). Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective. In: Kinne O (Ed.), Excellence in Ecology, Book 4. Germany, International Ecology Institute, Oldendorf/Luhe: 152.

Parmesan C and Yohe G (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.

Patten BC, Jørgensen SE and Auerbach SI (Eds.) (1995). Complex Ecology: The Part-whole Relation in Ecosystems. Englewood Cliffs, Prentice-Hall.

Pauly D, Christensen V, Dalsgaard J, Froese R and Torres F (1998). Fishing down marine food webs. Science 279: 860–863.

Pavia EG and Badan A (1998). ENSO modulates rainfall in the Mediterranean Californias. Geophysical Research Letters 25: 3,855–3,858.

Pearson PN and Palmer MR (1999). Middle Eocene seawater pH and atmospheric carbon dioxide concentrations. Science 284: 1,824–1,826.

Perry I and Ommer R (2003). Scale issues in marine ecosystems and human interactions. Fisheries Oceanography 12(45): 513–522.

Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola JM, Basile I, Bender M, Chappellaz J, Davis M, Delaygue G, Delmotte M, Kotlyakov VM, Legrand M, Lipenkov VY, Lorius C, Pepin L, Ritz C, Saltzman E and Stievenard M (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nature 399: 429–436.

Plattner G-K, Joos F, Stocker TF and Marchal O (2001). Feedback mechanisms and sensitivities of the ocean carbon uptake under global warming. Tellus B 53: 564–592.

Prather M, Ehhalt D, Dentener F, Derwent R, Dlugokencky E, Holland E, Isaksen I, Katima J, Kirchhoff V, Matson P, Midgley P and Wang M (2001). Atmospheric chemistry and greenhouse gases. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K and Johnson CA (Eds.), Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, UK. Pp239–287.

Prospero JM (1999). Long-range transport of mineral dust in the global atmosphere: impact of African dust on the environment of the southeastern United States. Proceedings of the National Academy of Sciences 96: 3,396–3,403.

Quay PD, Tilbrook B and Wong CS (1992). Oceanic uptake of fossil fuel CO_2: carbon-13 evidence. Science 256: 74–79.

Quigg A, Finkel ZV, Irwin AJ, Rosenthal Y, Ho TY, Reinfelder JA, Schofield O, Morel FMM and Falkowski PG (2003). The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. Nature 425: 291–294.

Quiñones RA, Serra R, Nuñez S, Arancibia H, Córdova J and Bustos F (1997). Relación Espacial Entre el Jurel y sus Presas en la Zona Centro-Sur de Chile. In: Tarifen E (Ed.) Gestión de Sistemas Oceanográphicos del Pacífico Oriental. Comissión Oceanográfica Intergubernamental de la UNESCO IOC/INF. Pp187–202.

Rabalais N and Nixon S (2002). Nutrient over-enrichment in coastal waters: global patterns of cause and effect. Estuaries 25(4B): 639–900.

Rabalais NN and Turner RE (2001). Coastal Hypoxia: Consequences for Living Resources and Ecosystems. Coastal and Estuarine Studies. American Geophysical Union, Washington, DC. Pp58.

Raven JA (1997). Inorganic carbon acquisition by marine autotrophs. Advances in Botanical Research 27: 85–209.

Raven JA and Lucas WJ (1985). Energy costs of carbon acquisition. In: Lucas WJ and Berry JA (Eds.), Inorganic Carbon Uptake by Aquatic Photosynthetic Organisms. American Society of Plant Physiologists, Rockville, MD. Pp305–324.

Redfield AC (1934). On the proportions of organic derivatives in seawater and their relation to the composition of plankton. In: Daniel R (Ed.), James Johnstone Memorial Volume. University Press of Liverpool, UK. Pp176–192.

Reid PC, de Borges MF and Svendsen E (2001). A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. Fisheries Research 50: 163–171.

Reid PC, Edward M, Hunt H and Warner AJ (1998). Phytoplankton change in the North Atlantic. Nature 391: 546.

Reimers C, Friedrichs C, Bebout B, Howd P, Huettel M, Jahnke RA, MacCready P, Ruttenberg K, Sanford L and Towbridge J (2004). Coastal Benthic Exchange Dynamics – Report on the CoOP CBED Workshop. Skidaway Institute of Oceanography Technical Report TR-04-01.

Rice J (2001). Implications of variability on many time scales for scientific advice on sustainable management of living marine resources. Progress in Oceanography 49: 189–209.

Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE and Morel FMM (2000). Reduced calcification of marine plankton in response to increased atmospheric CO_2. Nature 407: 364–367.

Roman MR, Dam HG, Gauzens Al and Napp JM (1993). Zooplankton biomass and grazing at the JGOFS Sargasso Sea time series station. Deep-Sea Research I 40: 883–901.

Ross SW, Dalton DA, Kramer S and Christensen BL (2001). Physiological (antioxidant) responses of estuarine fishes to variability in dissolved oxygen. Comparitive Biogeochemistry and Physiology 130C: 289–303.

Rost B, Riebesell U, Burkhardt S and Sultemeyer D (2003). Carbon acquisition of bloom-forming marine phytoplankton. Limnology and Oceanography 48(1): 55–67.

Rothschild BJ and Osborn TR (1988). Small-scale turbulence and plankton contact rates. Journal of Plankton Research 10(3): 465–474.

Sabine C and Hood M (2003). Ocean Carbon scientists organise to achieve better coordination, cooperation. EOS – Transactions of the American Geophysical Union 84: 218.

Sabine CL, Feely RA, Gruber N, Key RM, Lee K, Bullister JL, Wanninkhof R, Wong CS, Wallace DWR, Tilbrook B, Millero FJ, Peng T-H, Kozyr A, Ono T and Rios AF (2004). The oceanic sink for anthropogenic CO_2. Science 305: 367–371.

Saiz E and Kiørboe T (1995). Suspension and predatory feeding of the copepod *Acartia tonsa* in turbulent environments. Marine Ecology Progress Series 122: 147–158.

Sañudo-Wilhelmy SA, Tovar-Sanchez A, Fisher NS and Flegal AR (2004). Examining dissolved toxic metals in U.S. estuaries. Environmental Science Technology 38(2): 34A–38A.

Sarmiento JL, Slater RD, Fasham MJR, Ducklow HW, Toggweiler JR and Evans GT (1993). A seasonal three-dimensional ecosystem model of nitrogen cycling in the North Atlantic euphotic zone. Global Biogeochemical Cycles 7: 417–450.

Sarmiento JL, Hughes TMC, Stouffer RJ and Manabe S (1998). Simulated response of the ocean carbon cycle to anthropogenic climate warming. Nature 393: 245–249.

Sarmiento JL, Monfray P, Maier-Remier E, Aumont O, Murnane R and Orr JC (2000). Sea–air CO_2 fluxes and carbon transport: a comparison of three ocean general circulation models. Global Biogeochemical Cycles 14: 1,267–1,281.

Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, Hirst AC, Kleypas J, Matear R, Mikolajewicz U, Monfray P, Orr J, Soldatov V, Spall SA and Stouffer R (2004). Response of ocean ecosystems to climate warming. Global Biogeochemical Cycles 18 GB3003, doi:10.1029/2003GB002134.

Sarmiento JL and Toggweiler JR (1984). A new model for the role of oceans in determining atmospheric pCO_2. Nature 308: 621–624.

Sathyendranath S, Gouveia AD, Shetye SR, Ravindran P and Platt T (1991). Biological control of surface temperature in the Arabian Sea. Nature 349: 54–56.

Schlitzer R (2000). Electronic atlas of WOCE hydrographic and tracer data now available. EOS – Transactions of the American Geophysical Union 81(5): 45.

Schneider EK and Zhu Z (1998). Sensitivity of the simulated annual cycle of sea surface temperature in the equatorial Pacific to sunlight penetration. Journal of Climate 11: 1,932–1,950.

Schultz KG, Zondervan I, Gerringa LJA, Timmermans KR, Veldhuis MJW and Riebesell U (2004). Effect of trace metal availability on coccolithophorid calcification. Nature 430: 673–676.

Schwartzlose RA, Alheit J, Bakun A, Baumgartner TR, Cloete R, Crawford RJM, Fletcher WJ, Green-Ruiz Y, Hagen E, Kawasaki T, Lluch-Belda D, Lluch-Cota SE, MacCall AD, Matsuura Y, Nevarez-Martinez MO, Parrish RH, Roy C, Serra R, Shust KV, Ward MN and Zuzunaga JZ (1999). Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science 21: 289–347.

Seitzinger SP, Kroeze C, Bouwman AF, Caraco N, Dentener F and Styles RV (2002). Global patterns of dissolved inorganic and particulate nitrogen inputs to coastal systems: recent conditions and future projections. Estuaries 25(4B): 640–655.

Shell KM, Frouin R, Nakamoto S and Somerville RCJ (2003). Atmospheric response to solar radiation absorbed by phytoplankton. Journal of Geophysical Research 108(D15): 4,445.

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

Siedler G, Church J and Gould J (2001). Ocean Circulation and Climate: Observing and Modelling the Global Ocean. London, Academic Press.

Siegel DA, Maritorena S, Nelson NB, Hansell DA and Lorenzi-Kayzer M (2002). Global distribution and dynamics of coloured dissolved and detrital organic materials. Journal of Geophysical Research 107: 3,228.

Simpson JJ and Dickey TD (1981a). Alternative parameterisation of downward irradiance and their dynamical significance. Journal of Physical Oceanography 11: 876–882.

Simpson JJ and Dickey TD (1981b). The relationship between downward irradiance and their dynamical significance. Journal of Physical Oceanography 11: 309–323.

Snyder MA, Sloan LC, Diffenbaugh NS and Bell JL (2003). Future climate change and upwelling in the California Current. Geophysical Research Letters 30(15).

Southward AJ, Hawkins SJ and Burrows MT (1995). Seventy years observations of changes in distribution and abundance of zooplankton and inter-tidal organisms in the western English Channel in relation to rising sea temperature. Journal of Thermal Biology 1–2: 127–155.

Speekmann CL, Bollens SM and Avent SR (2000). The effect of ultraviolet radiation on the vertical distribution and mortality of estuarine zooplankton. Journal of Plankton Research 22: 2,325–2,350.

Spencer PD and Collie JS (1997). Effect of nonlinear predation rates on rebuilding the Georges Bank Haddock (*Melanogrammus aeglefinus*) stock. Canadian Journal of Fisheries and Aquatic Science 54: 2,920–2,929.

Steffen W, Sanderson A, Tyson P, Jäger J, Matson P, Moore B III, Oldfield F, Richardson K, Schellnhuber H-J, Turner BJ II and Wasson R (2004). Global Change and the Earth System: A Planet Under Pressure. Springer-Verlag, Heidelberg, Germany. Pp336.

Steinberg DK, Carlson CA, Bates NR, Goldthwait SA, Madin LP and Michaels AF (2000). Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. Deep-Sea Research I 47: 137–158.

Steinberg DK, Carlson CA, Bates NR, Johnson RJ, Michaels AF and Knap AF (2001). Overview of the U.S. JGOFS Bermuda Atlantic Time-series Study (BATS): A decade-scale look at ocean biology and biogeochemistry. Deep-Sea Research II 48: 1,405–1,447.

Stenseth NC, Ottersen G, Hurrell JW and Belgrado A (2004). Marine Ecosystems and Climate Variation. Oxford University Press, Oxford, UK.

Stephens BB and RF Keeling (2000). The influence of Antarctic sea ice on glacial–interglacial CO_2 variations. Nature 404: 171–175.

Sterner RW and Elser JJ (2002). Ecological Stoichiometry: The Biology of Elements from Molecules to Biosphere. Princeton University Press, New York.

Stocker TF (1999). Climate changes: from the past to the future – a review. International Journal of Earth Science 88: 365–374.

Stockwell DA, Whitledge TE, Zeeman SI, Coyle KO, Napp JM, Brodeur RD, Pinchuk AI and Hunt GL (2001). Anomalous conditions in the south-eastern Bering Sea, 1997: nutrients, phytoplankton and zooplankton. Fisheries Oceanography 10: 99–116.

Stoecker DK, Li A, Wayne Coats D, Gustafson DE and Nannen MK (1997). Mixotrophy in the dinoflagellate *Prorocentrum minimum*. Marine Ecology Progress Series 152: 1–12.

Subramaniam A, Brown CW, Hood RR, Carpenter EJ and Capone DJ (2002). Detecting *Trichodesmium* blooms in SeaWiFS imagery. Deep-Sea Research II 49(1-3): 107–121.

Sukhanova IN and Flint MV (1998). Anomalous coccolithophorid bloom over the eastern Bering Sea shelf. Okeanologiya 38: 557–260.

Sundby S (2000). Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. Sarsia 85(4): 277–298.

Suntharalingam P, Sarmiento JL and Toggweiler JR (2000). Global significance of nitrous-oxide production and transport from oceanic low-oxygen zones: a modelling study. Global Biogeochemical Cycles 14: 1,353–1,370.

Svensen C, Nejstgaard JC, Egge JK and Wassmann P (2002). Pulsing versus constant supply of nutrients (N, P, and Si): effect on phytoplankton, mesozooplankton, and vertical flux of organic matter. Scientia Marina 66: 189–203.

Takeda S (1998). Influence of iron availability on nutrient consumption ratio of diatoms in oceanic waters. Nature 393: 774–777.

Thomas H, Bozec Y, Elkalay K and de Baar HJW (2004). Enhanced open ocean storage of CO_2 from shelf sea pumping. Science 304: 1,005–1,008.

Thompson PM and Ollason JC (2001). Lagged effects of ocean climate change on fulmar population dynamics. Nature 413: 417–420.

Thrush SF (1991). Spatial patterns in soft-bottom communities. Trends in Ecology and Evolution 6: 75–79.

Timmermann A and Jin F (2002). Phytoplankton influences on tropical climate. Geophysical Research Letters 29: 2,104.

Tortell PD, DiTullio GR, Sigman DM and Morel FMM (2002). CO_2 effects on species composition and nutrient utilisation in an Equatorial Pacific phytoplankton community. Marine Ecology Progress Series 236: 37–43.

Tsuda A, Takeda S, Saito H, Nishioka J, Nojiri Y, Kudo I, Kiyosawa H, Shiomoto A, Imai K, Ono T, Shimamoto A, Tsumune D, Yoshomura T, Aono T, Hinuma

A, Kinugasa M, Suzuki K, Sohrin Y, Noiri Y, Tani H, Deguchi Y, Tsurushima N, Ogawa H, Fukami K, Kuma K and Saino T (2003). A mesoscale iron enrichment in the western subarctic Pacific induces large centric diatom bloom. Science 300: 958–961.

Tsunogai S, Watanabe S, Nakamura T, Ono T and Sato T (1999). Is there a continental shelf pump for the adsorption of atmospheric CO_2? Tellus Series. B 51: 701–712.

Turk D, McPhaden MJ, Busalacchi AJ and Lewis MR (2001). Remotely sensed biological production in the Equatorial Pacific. Science 293: 471–474.

Turner DR and Hunter KA (Eds.) (2001). The Biogeochemistry of Iron in Seawater. IUPAC Series on Analytical and Physical Chemistry of Environmental Systems. John Wiley and Sons, New York.

Turner RE (2002). Elemental ratios and aquatic food webs. Estuaries 25: 694–703.

Turner RK, Georgiou S, Gren I, Wulff F, Barrett S, Söderqvist T, Bateman IJ, Folke C, Langaas S, Zylicz T, Mäler K and Markowsk A (1999). Managing nutrient fluxes and pollution in the Baltic: an interdisciplinary simulation study. Ecological Economics 30: 333–352.

van Weering TCE, de Stigter HC, Balzer W, Epping EHG, Graf G, Hall IR, Helder W, Khripounoff A, Lohse L, McCave IN, Thomsen L and Vangriesheim A (2001). Benthic dynamics and carbon fluxes on the NW European continental margin. Deep-Sea Research II 48: 3,191–3,222.

Veccione M, Young RE, Guerra A, Lindsay DJ, Clague DA, Bernhard JM, Sager WW, Gonzalez AF, Rocha FJ and Segonzac M (2001). World-wide observations of remarkable deep-sea squids. Science 294: 2,505–2,506.

Venter JC, Remington K, Heidelberg JF, Halpern AL, Rusch D, Eisen JA, Wu D, Paulsen I, Nelson KE, Nelson W, Fouts DE, Levy S, Knap AH, Lomas MW, Nealson K, White O, Peterson J, Hoffman J, Parsons R, Baden-Tillson H, Pfannkoch C, Rogers YH and Smith HO (2004). Environmental genome shotgun sequencing of the Sargasso Sea. Science 304: 66–74.

Wada S, Oishi M and Yamada T-K (2003). A newly discovered species of living baleen whale. Nature 426: 278–281.

Wallace DWR (2001). Storage and transport of excess CO_2 in the oceans: the JGOFS/WOCE Global CO_2 Survey. In: Church J, Siedler G and Gould J (Eds.), Ocean Circulation and Climate. Academic Press, London. Pp489–521.

Weeks SJ, Currie B and Bakun A (2002). Satellite imaging: massive emissions of toxic gas in the Atlantic. Nature 415: 493–494.

Wolf-Gladrow DA, Riebesell U, Burkhardt S and Bijma J (1999). Direct effects of CO_2 concentration on growth and isotopic compositions of marine plankton. Tellus 51B: 461–476.

Wollast R and Chou L (2001a). The carbon cycle at the ocean margin in the northern Gulf of Biscay. Deep-Sea Research II 48: 3,265–3,293.

Wollast R and Chou L (2001b). Ocean Margin EXchange in the Northern Gulf of Biscay: OMEX I. An Introduction. Deep-Sea Research II 48: 2,971–2,978.

Wong CS and Matear RJ (1999). Sporadic silicate limitation of phytoplankton productivity in the subarctic NE Pacific. Deep-Sea Research II 46(11/12): 2,539–2,555.

Yool A and Fasham MJR (2001). An examination of the continental shelf pump in the open ocean general circulation model. Global Biogeochemical Cycles 15: 831–844.

Zhang J, Zhang ZF, Liu SM, Wu Y, Xiong H and Chen HT (1999). Human impacts on the large world rivers: would the Changjiang (Yangtze River) be an illustration? Global Biogeochemical Cycles 13: 1,099–1,105.

Zondervan I, Zeebe RE, Rost B and Riebesell U (2001). Decreasing marine biogenic calcification: a negative feedback on rising atmospheric pCO_2. Global Biogeochemical Cycles 15: 507–516.

Appendices

Appendix I: Acronym List

AIMES	Analysis, Integration and Modelling of the Earth System
AUV	autonomous underwater vehicle
CACGP	Commission on Atmospheric Chemistry and Global Pollution
CLIOTOP	Climate Impacts on Oceanic Top Predators
CLIVAR	Climate Variability and Prediction
CoML	Census of Marine Life
COOP	Coastal Ocean Observing Panel
CPR	Continuous Plankton Recorder
DIC	dissolved inorganic carbon
DMS	dimethylsulphide
DOC	dissolved organic carbon
DPSIR	Driver-Pressure-State-Impact-Response
EEA	European Environment Agency
EisenEx	Southern Ocean Iron Fertilisation Experiments
ENSO	El Niño-Southern Oscillation
GAIM	Global Analysis, Integration and Modelling
GCOS	Global Climate Observing System
GCP	Global Carbon Project
GEOHAB	Global Ecology and Oceanography of Harmful Algal Blooms
GEOTRACES	A collaborative multi-national programme to investigate the global marine biogeochemical cycles of trace elements and their isotopes
GLOBEC	Global Ocean Ecosystem Dynamics
GODAE	Global Ocean Data Assimilation Experiment
GOOS	Global Ocean Observing System
HNLC	high-nutrient low-chlorophyll
ICSU	International Council for Science
IDGEC	Institutional Dimensions of Global Environmental Change Project
IGBP	International Geosphere-Biosphere Programme

IGOS-P	Integrated Global Observing Strategy Partnership
IHDP	International Human Dimensions Programme on Global Environmental Change
IMAGES	International Marine Past Global Changes Study
IMBER	Integrated Marine Biogeochemistry and Ecosystem Research
IOC	Intergovernmental Oceanographic Commission
IOCCG	International Ocean Colour Coordinating Group
IOCCP	International Ocean Carbon Coordination Project
IPCC	Intergovernmental Panel on Climate Change
IPO	International Project Office
IronEx	Iron Addition Experiment
ISSC	International Social Science Council
JGOFS	Joint Global Ocean Flux Study
LOICZ	Land-Ocean Interactions in the Coastal Zone
MERIS	Medium Resolution Imaging Spectrometer
MODIS	Moderate Resolution Imaging Spectroradiameter
NAO	North Atlantic Oscillation
NIWA	National Institute of Water and Atmospheric Research (New Zealand)
OCEANS	Ocean Biogeochemistry and Ecosystems Analysis
OCTS	Ocean Colour and Temperature Scanner
OOPC	Ocean Observing Panel for Climate
PAGES	Past Global Changes
PDO	Pacific Decadal Oscillation
POC	particulate organic carbon
POLDER	Polarisation and Directionality of the Earth's Reflectances
POM	particulate organic matter
SCOR	Scientific Committee on Oceanic Research
SeaWIFS	Sea-viewing Wide Field-of-view Sensor
SOIREE	South Ocean Iron Release Experiment
SOLAS	Surface Ocean–Lower Atmosphere Study
SSC	Scientific Steering Committee
SST	sea surface temperature
TEP	transparent exopolymer particles
WCRP	World Climate Research Programme
WOCE	World Ocean Circulation Experiment

Appendix II: Data Policy Template for IGBP and SCOR Large-Scale Ocean Research Projects

The following data policy template for IGBP and SCOR marine projects was recommended by the SCOR/IGBP Meeting on Data Management for International Marine Research Projects held in Liverpool, December 2003.

Scientific data and information derived from large-scale research projects with oceanic components are critical to project success and are an important legacy of these projects. Project data should be available for assessment and use by independent scientists, including, initially, other project scientists and later by external scientists. To ensure long-term survival, integrity, and availability of project data and models, a workable plan, policy, and associated infrastructure must be established early in the life of a project. Project data, as well as model code and model output, must be made available to the community.

A data management policy and plan should (i) encourage rapid dissemination of project results; (ii) ensure long-term security of key project data, as well as model-related information; (iii) protect the rights of the individual scientists; (iv) treat all involved researchers equitably; and (5) reward openness. IGBP and SCOR affirm the data policy of their parent organisation, the International Council for Science (ICSU):

"ICSU recommends as a general policy the fundamental principle of full and open exchange of data and information for scientific and educational purposes" (ICSU General Assembly Resolution 1996).

Participants at the December 2003 meeting on Data Management for International Marine Research Projects recommend that all IGBP/SCOR large-scale marine research projects adopt the following essential elements in their data policies. Also listed are additional considerations for the development of project data management systems.

Essential Data Policy Elements

- Project endorsement requires a credible commitment to the timely submission of data to a project-approved database to ensure long-term archiving of the data.
- Discovery Metadata (what was collected where, when and by whom) should be submitted by project scientists to the International Project Office on the shortest feasible time scales. Failure to do should be considered reason to remove project endorsement.
- Model code and documentation, initialisation, boundary conditions, forcing and output resulting in published results ("definitive runs") must be submitted to project-approved databases in forms which allow assessment of key findings.
- Timelines for data and model sharing, as well as protocols associated with intellectual property rights of different data types and models, should be defined. Currently accepted guidelines are that data should enter the public domain after a maximum of two years after data become available to the principal investigator.
- Quality control of metadata[1], data and model output needs to be addressed.
- Each project should form and support a Data Management Committee. The three primary functions of Data Management Committees are to:

  (i) make sure that data are available for project scientific purposes and ensure that data management meets the scientific need;

  (ii) oversee the compilation of data from individual principal investigators and national projects into a long-term data set; and

  (iii) address the involvement of scientists without access to effective data management infrastructure.

- Projects must adopt or establish a credible data management infrastructure.
- Projects should adopt metadata standards (content and controlled vocabularies [2]) and agreed data formats both within and among projects to facilitate data interoperability.
- Project Data Management Committees should consider how to get appropriate project data into operational data streams[3] and appropriate operational data streams into the project domain.

Additional Considerations

Project SSCs and Data Management Committees should create their project data policy, considering the following issues.

The project SSC should:

- Create a Data Management Committee with adequate representation of project science, a balance between project scientists (including modellers), national and international project data managers, and consideration of outreach functions to countries without data centres.
- Consider providing access to project-related publications through a publication database, such as that used by GLOBEC.

The project Data Management Committee[4] should:

- Develop a process to ensure that metadata and data are submitted, monitor the compliance of project scientists to the policies, and refer failure in compliance to the project SSC.
- Specify how project data will be quality controlled.
- Specify incentives to encourage project scientists to submit metadata and data to the IPO and a long-term data repository, respectively. ("One carrot is worth ten sticks.") These incentives may include citation of data in a peer-reviewed journal, access to other project data during "an embargo period" before public access, tools for use of data in the data archive (e.g., data merging, plotting, spatial visualisation and modelling tools), and help from international data managers in submitting data, accessing data, and using analysis tools. Proper incentives will reduce the efforts needed by data managers to get data into project data systems and increase participation in the project.
- Determine the variables most likely to be measured and the expected data volumes, and specify project data products.
- Address how non-geo-referenced, socioeconomic, and other non-conventional data will be handled.
- Consider setting up a Data Assembly Centre (DAC), either project-specific or shared among projects, for data that can be handled in this way. The DAC may be set up along the lines of project data streams (e.g. conductivity-temperature-depth data, bottle data) and/or the more traditional single parameter DAC (i.e. the DACs used by WOCE and CLIVAR).
- Consider whether to submit data interchange formats to the Global Change Master Directory as a means to provide access to project metadata.
- Consider making species-specific data available through Ocean Biogeographic Information System.
- Create a mechanism to interact regularly with representatives of related project Data Management Committees to develop common approaches and procedures to share data.

Project SSCs and Data Management Committees should work together to:

- Specify how project models and data will be made available both to scientists with leading-edge technology and with unreliable access to even basic access methods. The project should also present plans for training developing country scientists in techniques for data access and use.
- Develop plans to bring together data providers and data managers, considering how "project data management" principles could be applied to each project.

1 Metadata are information about data, including information that allows data sets to be located (discovery metadata: what was measured, when and where), information that enhances human understanding of the data and the uses to which it can be put (semantic metadata) and information that allows software agents to access the data (technical metadata).

2 Metadata vocabularies are controlled lists of words or phrases that are used to populate metadata fields in place of free text to ensure computer searches are not compromised by problems such as spelling variations.

3 Operational data streams are data that are available on a regular basis from routine observing systems, such as Argo floats, sea level networks, and telemetered data buoys.

4 Where modelling committees exist, these should be consulted in relation to model-specific aspects of data policy.

Appendix III: Application Process for IMBER-Endorsement

Applications for endorsement will need to include the following information and should be submitted on the IMBER endoresement form, available from www.imber.info.

1. TITLE AND DURATION

2. APPLICANTS

Lead applicant name, contact details and short CV with up to six relevant publications.

Other participants names and affiliations.

3. PROJECT SUMMARY (ONE PAGE)

Including objectives, strategy and implementation timetable.

4. OUTPUTS

Scientific:

(i) Data to be delivered.

(ii) Planned dissemination including international/national journals and conference papers.

(iii) Provisions/plans for data management, archiving, and distribution and curation of samples.

(iv) Training to be provided including graduate, undergraduate and technical training.

5. LINKS TO IMBER SCIENCE PLAN

Specify the IMBER Themes and Issues that will be addressed, and how the activity will contribute to the IMBER comparative research strategy.

6. BENEFITS FROM IMBER ENDORSEMENT

Specify how the activity would benefit from endorsement, and how the SSC could assist?

7. SCOPE FOR INTERNATIONAL PARTICIPATION AND CONTRIBUTION

Indicate whether the activity will involve international participation.

8. LINKAGES WITH OTHER PROGRAMMES

Specify whether the project is part of a national programme, and/or part of, or affiliated with, any international/regional programmes, and provide programme titles.

9. SUPPORTING INFRASTRUCTURE AND FACILITIES

Specify the infrastructure and facilities available to participants.

10. FUNDING

Indicate what funding has been obtained and/or indicate potential funding source(s).

IMBER

The Integrated Marine Biogeochemistry and Ecosystem Research project is a multidisciplinary project of the International Geosphere-Biosphere Programme (IGBP) and the Scientific Committee on Oceanic Research (SCOR). Both IGBP and SCOR are interdisciplinary bodies of the International Council for Science (ICSU).

More information on the project sponsors can be obtained from:

IGBP: www.igbp.net

SCOR: www.jhu.edu/scor

ICSU: www.icsu.org

ICSU

International Council for Science