
Springer

Berlin

Heidelberg

New York

Hong Kong

London

Milan

Paris

Tokyo

Michael J. R. Fasham (Ed.)

Ocean Biogeochemistry

The Role of the Ocean Carbon Cycle
in Global Change

With 130 Figures



Springer

Editor

Michael J. R. Fasham

Southampton Oceanography Centre
Waterfront Campus, Southampton, SO14 3ZH, UK
mjf@soc.soton.ac.uk

ISSN 1619-2435
ISBN 3-540-42398-2 Springer-Verlag Berlin Heidelberg New York

Library of Congress Cataloging-in-Publication Data

Ocean biogeochemistry : a synthesis of the Joint Global Ocean Flux Study (JGOFS) /
Michael J.R. Fasham (ed.).
p.cm. -- (Global change--the IGBP series, ISSN 1619-2435)
Includes bibliographical references.
ISBN 3-540-42398-2 (alk. paper)
1. Carbon cycle (Biogeochemistry) 2. Chemical oceanography.
I. Fasham, M. J. R. II. Joint Global Ocean Flux Study. III. Series.

QH344.025 2003
551.46'01--dc21

2002044503

Bibliographic information published by Die Deutsche Bibliothek
Die Deutsche Bibliothek lists this publication in the Deutsche Nationalbibliografie;
detailed bibliographic data is available in the Internet at <http://dnb.ddb.de>

Photos courtesy of U.S. JGOFS Planning Office.
RVIB Nathaniel B. Palmer docks at McMurdo Station, Antarctica, at start of final U.S. JGOFS cruise.
Photo by Mardi Bowles.
Launching moored instruments from RV Atlantis II. Photo by Craig Dickson.
El Niño-Southern Oscillation effects on equatorial Pacific chlorophyll *a* concentrations during January
(El Niño, left) and July (La Niña, right) of 1998. (Image courtesy of the SeaWiFS Project, NASA Goddard
Space Flight Center and ORBIMAGE.)
The copepod photo is courtesy of Southampton Oceanography Centre.

This work is subject to copyright. All rights are reserved, whether the whole or part of the material
is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation,
broadcasting, reproduction on microfilms or in any other way, and storage in data banks. Duplication
of this publication or parts thereof is permitted only under the provisions of the German Copyright
Law of September 9, 1965, in its current version, and permission for use must always be obtained from
Springer-Verlag. Violations are liable for prosecution under the German Copyright Law.

Springer-Verlag Berlin Heidelberg New York
a member of BertelsmannSpringer Science+Business Media GmbH
<http://www.springer.de>
© Springer-Verlag Berlin Heidelberg 2003
Printed in Germany

The use of general descriptive names, registered names, trademarks, etc. in this publication does not
imply, even in the absence of a specific statement, that such names are exempt from the relevant pro-
tective laws and regulations and therefore free for general use.

Cover Design: Erich Kirchner, Heidelberg
Dataconversion: Büro Stasch, Bayreuth

Printed on acid-free paper – 3140 – 5 4 3 2 1 0

Foreword

Peter G. Brewer, Monterey Bay Aquarium Research Institute, Moss Landing, USA

Pre-History

The development of the field of 'Ocean Biogeochemistry' is a remarkable story, and one in which the JGOFS program, and the researchers whose work is presented here, have played critical leadership roles. The term 'biogeochemical cycles' became familiar in the mid 1980s when scientists first tried to describe to the policy world the complex set of interlocking processes involved in global change. Before then almost wholly physical descriptions were given, of radiative balances, heat fluxes, transport processes etc., and a few simple ocean or land CO₂ terms were added. However when attempts were then made to add the real effects and feedback terms of land and oceans a view of amazing complexity appeared. The first attempts to communicate this are fondly remembered in the 'horrendograms' produced by Francis Bretherton – wiring diagrams of computer chip complexity showing simultaneous links between warming and respiration, photosynthesis and CO₂, ocean circulation and productivity, energy balances and chlorophyll, ocean gas releases and clouds. The problem was that no one knew how to handle all this, and, since real knowledge was lacking, all kinds of claims were made for rates, reservoirs and mechanisms, with no idea as to which one was dominant or even important. It was messy, clamorous, essential, and wide open. Today it is a powerful discipline, with measured rates, innovative experiments, complex models, and vigorous testing of ideas.

The use of biogeochemical cycles as a term to describe diagenetic reactions in sediments had arisen earlier, but it was a total shock to hear in about 1986 that NASA had formally reorganized its earth science programs to highlight the new discipline. No one really knew how to react, since well-entrenched physics, chemistry, and biology programs were suddenly cast adrift. I well recall a corridor conversation with a distinguished physical oceanographer the day the news broke. It seemed incomprehensible. Today the AGU journal 'Global Biogeochemical Cycles' ranks third out of 117 titles in the Geosciences in the 2000 Journal Citation Reports.

The JGOFS program, or more accurately the scientists whose energy, dedication, and creativity are represented by that acronym, arose almost simultaneously with this transition, and its success is unassailable. How that happened is a remarkable story, and one worth telling.

A U.S. Initiative

In the US in the early 1980s the set of ocean observing programs deriving from the large scale International Decade of Ocean Exploration programs were winding down. Only the geochemical tracer efforts were truly active on a global scale, and here the first powerful measurements of the chlorofluorocarbon tracers were made. In ocean biology a program examining the processes associated with warm core rings, spun off from the Gulf Stream, occupied center stage. The first glimpses of ocean color data from space appeared from the Coastal Zone Color Scanner (CZCS) on Nimbus 7, but this was a struggle compounded not only by the technical challenge, but also by problems within the NASA team responsible for the data. The sensor was exceeding its design life, and beginning to fail. Frankly, it wasn't an impressive picture. And discussions of plans for more of the same for the future were received by NASA with little enthusiasm.

Yet there were opportunities. The unease over global change was being translated, by Presidential Science Advisor D. Allan Bromley, into a 'U.S. Global Change Program' that offered the promise of political support. There were advances being made in trace metal clean techniques that yielded new insights into ocean biogeochemical processes. Lively and assertive individuals outside NASA were pressing forward with innovative CZCS results, and extending observations into blue water far beyond the coastal zones. New sediment trap techniques were capturing rhythmic fluctuations in the rain of particles to the sea floor. And the first ice core records of large scale CO₂ fluctuations associated with glaciations, and attributed to linked changes in ocean circulation and productivity, were appearing.

The leadership to capture these opportunities came first undeniably from John Steele. John was frustrated by seeing plans emerge within the ocean physics community for a major observing program, allied to an altimetric satellite, without equivalent planning for biological and geochemical programs. His own background in marine ecosystem modeling had not previously exposed him to serious ocean geochemistry, but he sensed that alone the ocean biology community would not be able to seize the opportunity. A set of planning meetings of an 'Ad Hoc Group on Ocean Flux Experiments' (John Steele, Jim Baker, Wally Broecker, Jim McCarthy, and Carl Wunsch) took place in 1983–1984 under the auspices of the US National Academy Ocean Sciences Board on Ocean Science and Policy, and this led to a major workshop at the NAS Woods Hole Center in September 1984. The 'Global Ocean Flux Study' (GOFs) report from that workshop provided the impetus for what is now the JGOFS program.

The preface for that report emphasized the need for study of "the physical, chemical, and biological processes governing the production and fate of biogenic materials in the sea ... well enough to predict their influences on, and responses to, global scale perturbations, whether natural or anthropogenic ...". It went on to draw analogies between the Pleistocene fluctuations in climate, and "the beginning of a fossil-fuel CO₂-induced super-interglacial period."

I attended that meeting, and was soon perplexed. Few attendees knew anything of the assumed linkage to satellite ocean color, and widespread skepticism prevailed (the language alone of this community was foreign to most, and to me). The failing CZCS was apparently to be replaced by an Ocean Color Imager in 1985 or so – in practice it took 15 years of hard work for SeaWiFS to be launched! The busy sediment trap community were convinced that their technique was central; but trapping particles close to the euphotic zone was fraught with problems of technique, and mixed layer modeling was scarcely understood. The reference to paleo-climates ensured that the sediment record had to be included, but the scale mismatch of those studies with upper water column chemistry and biology was obvious. And persistent large discrepancies between productivity estimates from the oxygen balance and ¹⁴C uptake, were aggressively debated. It was an interesting mess. Ocean physics was tacitly assumed to be taken care of somewhere else, most likely through WOCE. And in spite of the strong reference to the anthropogenic CO₂ signals, no one had thought to schedule any CO₂ papers into the meeting.

Building a U.S. Program

The lack of CO₂ papers in the GOFs meeting report was fixed very simply by a committee charged with editing the proceedings of the meeting. Some manuscripts were simply added. I was asked by Neil Andersen to join that editorial committee (with Ken Bruland, Peter Jumars, Jim McCarthy) and we met about a week later in Washington, D.C. It at once became clear that we were to be charged with not simply editing, but with program creation. We were briefed by Jim Baker that the most urgent item was a pitch to NASA headquarters for support of an ocean color satellite. None of us knew how to proceed with turning such a wide-ranging report into a viable and coherent research program. To break the impasse I suggested we go home, each with an editing

assignment, and meet a week later to finish the report. We also had homework to do in the nature of drafting some outline or scheme for pulling the material together into a comprehensible program. This did not work as I had hoped, for when we reconvened I was the only one of the group to have prepared any semi-formal material. These were some results from a very crude North Atlantic mixed layer model comparing physical and biological forcing of CO₂, and comments on extending a similar calculation to the basin scale with some sense of what could be measured and tested. This was enough, and I was asked to Chair the group.

A very difficult period then followed. Since the constituency was broad a large committee was formed, few of whom had any prior collegial contact. But we worked at it, and I formed a 'Planning Office' of one. We had meetings and produced some reports. After some wrangling a broad plan to implement a strategy of carrying out a global survey of CO₂ and related properties, implementing time series stations, and executing a set of sophisticated process studies was set in place. It took, and it allowed for multiple roles for remote sensing on many space and time scales.

In the fall of 1986 a set of key events took place in rapid succession. Planning for WOCE had reached the point where a large-scale hydrographic program was forming. A meeting at the U.S. National Academy framed the debate; I had independently discussed with Carl Wunsch the issue of CO₂ measurements, and he felt that these were not part of the WOCE observing package. But he asked if I would present the case at the NAS meeting. This went very well, and a compromise was proposed whereby 'GOFs' would provide funding, oversight, people and tools, and WOCE would provide bunks on their cruises and access to samples and supporting data. A handshake sealed the deal, which was proposed and accepted in about 30 seconds. We could go global.

Secondly Gene Feldman, new at NASA had created the first basin scale chlorophyll image from CZCS data. It had flaws: dubbed by some as 'the ocean on fire' from the garish orange for high pseudo-chlorophyll levels, or the 'Pac-Man' image from an oddly shaped data gap in Hudson Bay, it nonetheless broke new ground. This image appeared on the cover of the November 4, 1986 issue of EOS, with the AGU Fall Meeting abstracts and brief papers by the GOFs committee, and the NASA team. It was a coveted slot, and it had great impact.

And since the WOCE connection had been made, and WOCE was formally international, we had the impetus to move beyond the U.S. This had always been intended, but without a formal opening or partially defined plan to propose, real progress had not been made. Within an hour or two of the WOCE handshake deal a letter to SCOR was drafted, and hand carried to Tasmania the next day. The letter requested that SCOR take up the challenge of sponsoring a major new initiative on an Ocean Flux Program, and cited the progress made. It was well received, and work began at once on an enabling meeting.

Creation of JGOFs

The first SCOR-sponsored meeting was held in Paris, at ICSU House, February 17–20, 1987. Gerold Siedler, as President of SCOR, kept a careful eye on proceedings, Jim Baker acted as Chair, and Elizabeth Gross facilitated. Roger Chesselet helped secure the superb location. We had all learned some hard lessons about preparation: Gene Feldman had now created the first global chlorophyll image, and this was first shown to me in dim dawn light at the luggage carousel in De Gaulle airport by Jim Baker the day before the meeting. It was superb. I had written a discussion paper especially for the meeting on the comparative North Atlantic heat, CO₂, and nutrient budgets, with David Dyrssen. It illustrated what we might gain from a survey, and an abbreviated version was later backed up by some measurements and published in *Science*.

There was no real understanding of how international logistics might work, but as we went round the room it was clear that the desire to create a novel and important program was strong. Jim Baker proposed a 'J' for the program; everyone said yes. Gerold Siedler nominated Bernt Zeitschel as the Chair, and this was agreed upon. It all happened quickly,

and the real work began. Hugh Livingston had joined the U.S. Planning Office, and was superb in science and diplomacy in this role. Liz Gross guided the multi-national effort with grace and skill. Neil Andersen kept the thread of funding and agency sponsorship alive and well. The U.S. JGOFS Newsletter was born, and thrived. And a succession of excellent reports cataloged the evolution of scientific planning and understanding.

Fast Forward

History is fun, and important. But what did all this start up effort achieve?

There are now volumes of papers to testify to this, but perhaps I can pick on a few highlights. The 1989 multi-national North Atlantic Bloom Experiment was put together with extraordinary speed, and it combined ships and aircraft observations in new ways. U.S., German, U.K., Canadian and Dutch ships and scientists co-operated in the field. This set the tone for a whole series of successful process studies. The 1990 Fasham-Ducklow-McKelvie paper on modeling upper ocean production and the microbial loop laid the ground for a decade long renaissance in ocean biogeochemistry. The 1988 establishment of the Hawaii and Bermuda Time series Stations was essential. Critics at the time pointed to two sub-tropical locations as a deficiency: the separate signals evolving so beautifully there answer the challenge. The global CO₂ survey was a heroic effort. From that we now see the penetration of fossil fuel CO₂ to well below 1 km throughout the ocean, and the detection of sea floor carbonate dissolution from the 20th century chemical invasion. There were problems. An ocean color satellite did not fly until 1997: a full decade late, and only after endless effort. The linkage of the oceanic CO₂ problem with biogeochemical measurements and models had amazing birth pains. Most ocean chemists had no real knowledge of microbial processes; and all (so far as I could tell) ocean biologists were in disbelief that the fossil fuel CO₂ invasion was a purely inorganic/physical phenomenon. Very few people looked far to the future, say to an ocean at the end of the 21st century where the CO₂ maximum may be at the surface, and essential biogeochemical cycles may be profoundly changed. The first US JGOFS response to John Martin's proposal of an iron fertilization field experiment (at a meeting I did not attend) was to vote it down! However, funding was obtained from the DOE and the resulting iron fertilization experiments were a brilliant success.

The papers in this volume show how far we have come. Satellite ocean color images pervade the literature. Sophisticated models of biogeochemical cycles are routinely used. All participants are fluent in the CO₂ connection. Ready access to more than a decade of time series data is taken for granted. Synthesis and modeling efforts are supported, and are productive. And iron fertilization science has a strong international community.

The goals of JGOFS were carefully negotiated, and they included the need "To determine on a global scale the processes controlling the time varying fluxes of carbon and associated biogenic elements in the ocean ...", and "To develop the capability to predict on a global scale the response of oceanic biochemical processes to anthropogenic perturbations, in particular those related to climate change." This knowledge is urgently required, for mankind's influence on the carbon cycle is proceeding far faster than we usually acknowledge. In 1984, at the time of the first U.S. 'GOFS' meeting, atmospheric CO₂ levels were 344 ppm, or 64 ppm above the pre-industrial baseline. Today they are 372 ppm, or 92 ppm above the pre-industrial levels – a 43% increase while we have been planning and carrying out our research. Over these 18 years the ocean has taken up some 131 billion tons of CO₂ gas.

International ocean science of a new kind evolved with JGOFS. It is created by the efforts of individuals who do not see boundaries, only opportunities. A thriving community of students and Post Docs. emerges each year, and happily spreads across international borders seeking excellence. And they often find it in the laboratories of scientists whose work is represented here.

Contents

Introduction	1
Acknowledgements	2
References	2
1 Biogeochemical Provinces: Towards a JGOFS Synthesis	3
1.1 Plankton Community Structure and Distribution	3
1.2 Partitioning the Oceans	5
1.3 Primary Production in Ocean Domains and Provinces	8
1.3.1 Adding up Global PP Observations	11
1.4 Bacterial Production and DOC Flux	11
1.5 A Provincial Outlook	14
Acknowledgements	14
References	14
2 Physical Transport of Nutrients and the Maintenance of Biological Production	19
2.1 Introduction	19
2.2 Global Overturning Circulation and Nutrient Transport	21
2.2.1 Overturning Circulation and Water-Mass Distributions	21
2.2.2 Southern Ocean	22
2.2.3 Nutrient Supply to the Northern Basins	24
2.2.4 Summary	25
2.3 Convection	25
2.3.1 Vertical Transfer of Nutrients	25
2.3.2 Biophysical Interactions and Convection	25
2.3.3 Limited Role of Convection	28
2.3.4 Summary	28
2.4 Wind-Driven Circulations: Gyres and Boundary Currents	29
2.4.1 Wind-Induced Upwelling and Gyre Circulations	29
2.4.2 Gyre-Scale Circulations	29
2.4.3 Subduction and Fluid Transfer into the Seasonal Boundary Layer	30
2.4.4 Oligotrophic Subtropical Gyres	31
2.4.5 Western Boundary Transport of Nutrients	33
2.4.6 Summary	35
2.5 Smaller-Scale Circulations: Mesoscale Eddies, Waves and Sub-Mesoscale Fronts	35
2.5.1 Formation of Mesoscale Eddies and Sub-Mesoscale Fronts	35
2.5.2 Local Response to Planetary Waves, Eddies and Fronts	36
2.5.3 Far Field Effects: Eddy Transport and Diffusion	40
2.5.4 Summary	41
2.6 Interannual and Long-Term Variability	42
2.6.1 Coupled Atmosphere-Ocean Changes: ENSO	42
2.6.2 North Atlantic Oscillation	43
2.6.3 Changes in Overturning Circulation	45
2.6.4 Summary	46

2.7	Conclusions	46
	Acknowledgements	47
	Notes	47
	References	49
3	Continental Margin Exchanges	53
3.1	Introduction	53
3.2	Recycling Systems	56
3.3	Export Systems	59
3.4	Coastal Upwelling Systems	60
3.5	California Current System	61
3.6	Humboldt Current System	62
3.7	Benguela Current System	63
3.8	Monsoonal Upwelling Systems	63
3.9	Biogeochemical Budgeting	64
3.10	The Arctic Shelves	67
3.10.1	Introduction	67
3.10.2	The Arctic Ocean As a Mediterranean, Shelf-Dominated Sea	69
3.10.3	The Shelves of the Arctic Ocean	71
3.10.4	Barents Shelf	73
3.10.5	Kara Shelf	73
3.10.6	Laptev Shelf	74
3.10.7	East Siberian and Chukchi Shelves	74
3.10.8	Beaufort Shelf	74
3.10.9	The Mackenzie Shelf of the Beaufort Sea as a Case Study	75
3.10.10	Shelf to Basin Sediment Transport in the Arctic	76
3.10.11	CH ₄ , DMS (Dimethyl-Sulphide) Production in the Arctic	77
3.10.12	A Budget for the Arctic Shelves	77
3.10.13	Global Change; Speculation on Consequences for Arctic Shelves	78
3.11	Marginal Seas	79
3.11.1	High Latitude Marginal Seas	79
3.11.2	Semi-Enclosed Marginal Seas	80
3.11.3	Initial Synthesis	82
3.11.4	Future Research	84
3.11.5	Summary	88
	Acknowledgments	89
	References	89
	Appendix 3.1 – Continental Margins: Site Descriptions	95
4	Phytoplankton and Their Role in Primary, New, and Export Production	99
4.1	Introduction	99
4.1.1	A Brief Introduction to Phytoplankton	99
4.1.2	Photosynthesis and Primary Production	101
4.1.3	Measuring Photosynthesis and Net Primary Production in the Sea	102
4.1.4	A Brief History of the Measurement of Primary Productivity in the Oceans	102
4.1.5	Quantifying Global Net Primary Productivity in the Oceans	103
4.1.6	Export, New and ‘True New’ Production	106
4.1.7	Elemental Ratios and Constraints on New Production	107
4.1.8	New Production, Export Production, and Net Community Production	107
4.1.9	Measurement of New Production	108
4.1.10	Measurement of Net Community Production	109
4.1.11	Measurement of Export Production	109
4.1.12	Summary of Methods	111

4.2	Synthesis	112
4.2.1	Physical Controls of Export Fluxes: the Importance of Functional Groups	115
4.2.2	Calcium Carbonate Precipitation	116
4.2.3	Primary, New and Export Production and the Global Carbon Cycle on Longer Time Scales	116
	References	118
5	Carbon Dioxide Fluxes in the Global Ocean	123
5.1	Introduction	123
5.2	The Oceans' Influence on Atmospheric CO ₂	123
5.2.1	The Ocean Sets the Steady-State Atmospheric CO ₂ Concentration ..	123
5.2.2	The Pre-Industrial Steady State	125
5.2.3	Pre-Industrial North-South Transports	126
5.3	How Big is the Global Ocean Sink?	127
5.3.1	1-D Models Calibrated with ¹⁴ C	127
5.3.2	3-D Models of the Ocean Carbon Cycle	127
5.3.3	¹³ C Changes with Time in the Ocean	128
5.3.4	Atmospheric Observations	128
5.3.5	Observations of the Air-Sea Flux	129
5.3.6	Preformed Total Carbon Methods and the Ocean Inventory of CO ₂	130
5.3.7	Summary of Recent Estimates of the Ocean Sink	132
5.4	What Processes Control Air-Sea CO ₂ Flux?	132
5.4.1	Patterns in the Global Survey	132
5.4.2	Comparison Using Models	133
5.4.3	Modelled Future Uptake of Anthropogenic CO ₂	138
5.5	Variability in the CO ₂ Signal	138
5.5.1	Seasonal Variation	138
5.5.2	Inter-Annual Variation	138
5.6	The Gas Transfer Velocity	140
5.7	Conclusion: the Next Ten Years	141
	Acknowledgements	141
	References	141
6	Water Column Biogeochemistry below the Euphotic Zone	145
6.1	Introduction	145
6.2	The Twilight Zone: Biology, Biogeochemical Processes and Fluxes	146
6.2.1	Biology of the Twilight Zone	146
6.2.2	Nature of the Exported Material and Processes	147
6.2.3	Microbial Production of Nitrous Oxide	148
6.3	The Fluxes of Biogenic Matter versus Depth	149
6.3.1	The Export Flux out of the Euphotic Zone	149
6.3.2	The Export Flux towards the Ocean's Interior (>1 000 m)	150
6.4	The Variable Composition of the World Ocean Waters along the Conveyor Belt .	151
6.5	Conclusions and Perspectives	152
6.5.1	The Ventilation Depth and the ν -Ratio	153
6.5.2	The Role of Mineral Ballasts in the Export of Carbon to the Ocean Interior	153
	References	153
7	The Impact of Climate Change and Feedback Processes on the Ocean Carbon Cycle	157
7.1	Introduction	157
7.1.1	Climate and Change – Present Status	157
7.1.2	Examples of Feedbacks in the Present and the Geological Past	159
7.2	Feedbacks	159

7.2.1	Definition	159
7.2.2	Identification	159
7.2.3	Classification	160
7.2.4	Magnitude	160
7.2.5	Evolution	161
7.2.6	Interactions between Feedbacks	161
7.2.7	Scales and Response Times	161
7.2.8	Degree of Confidence – Understanding Feedbacks	162
7.3	What do Current Models Predict?	162
7.4	Status of Our Understanding of Feedbacks	164
7.5	Nutrient Dynamics	164
7.6	Phytoplankton and Carbon Limitation	164
7.6.1	Atmospheric Supply of Nutrients	164
7.6.2	Nitrogen Fixation	165
7.6.3	Changes in Nutrient Uptake Stoichiometry – the Redfield Ratio	166
7.6.4	Export Production and Remineralisation in the Deep Ocean	167
7.7	The Calcifiers	167
7.7.1	Biogeochemistry and Feedbacks	168
7.7.2	Global Distributions	168
7.7.3	Controlling Factors, Forcing and Modelling	169
7.7.4	A Case Study – the Bering Sea	169
7.8	Iron Supply to the Oceans	170
7.8.1	How Much of the Ocean Is Iron-Poor?	170
7.8.2	The Supply of Iron to the Ocean	170
7.8.3	Atmospheric Deposition of Iron versus Upwelling Supply	170
7.8.4	Dust Supply – Global Maps and Fluxes	171
7.8.5	Dust Transport – from Soil to Phytoplankton	171
7.8.6	Response by the Biota – Detection	171
7.8.7	The Future – Climate Change and Dust Deposition	172
7.8.8	A Case Study – Uncertainties in Projection	174
7.9	Dimethyl Sulphide and the Biota	174
7.9.1	The CLAW Hypothesis	174
7.9.2	What Produces DMSP/DMS?	175
7.9.3	Global Distributions of DMS	175
7.9.4	The Haptophyte Connection	176
7.10	UV-B and Ozone Depletion	176
7.10.1	Present Status of Ozone Depletion	176
7.10.2	Phytoplankton and Primary Production	177
7.10.3	Dissolved Organic Matter and Heterotrophic Bacteria	177
7.10.4	Pelagic Community Response	178
7.10.5	The Future	178
7.11	Summary of Biotic Feedbacks	178
7.12	Climate – Variability versus Change	179
7.12.1	Climate Change	179
7.12.2	Climate Variability	180
7.12.3	Regime Shifts	181
7.12.4	Unexpected Biological Responses to Climate Change	183
7.13	Modeling – Future Goals	183
7.14	The Future	185
7.14.1	Detection and Projection	185
7.14.2	Does the ‘Initial’ Condition Still Exist?	185
7.14.3	The Need for a Regional Approach	185
7.14.4	A New Definition of Biogeochemical Provinces?	186
7.15	Summary	186
	Acknowledgements	187
	References	187

8	Benthic Processes and the Burial of Carbon	195
8.1	Introduction	195
8.2	Processes of Transport and Turnover of Material in the Deep Ocean	196
8.2.1	Transfer of Organic Material from the Surface to the Deep Ocean	196
8.2.2	Benthic Carbon Turnover Processes	197
8.3	Quantitative Estimates of Carbon Deposition and Carbon Turnover	199
8.3.1	Strategies for Quantification of Benthic Fluxes	199
8.3.2	Regional Assessments of Deep-Ocean Fluxes	200
8.3.3	Global Estimates of Deep Ocean Carbon Deposition and Remineralization	201
8.4	Proxy Indicators of Paleoproductivity	204
8.4.1	Estimates Based on Organic Carbon Burial Rates	204
8.4.2	Estimates Based on Biomarker Accumulation Rates	205
8.4.3	Estimates Based on Barium Accumulation Rates	205
8.4.4	Estimates Based on Radionuclide Ratios	206
8.4.5	Estimates Based on Redox-Sensitive Trace Elements	208
8.4.6	Estimates Based on Benthic and Planktonic Foraminifera	208
8.4.7	Estimates Based on Coccolithophorids and Diatoms	209
8.4.8	Proxies of Surface Nutrient Concentration	209
8.4.9	Proxies of Surface Nutrient Utilization Efficiency	210
8.5	Conclusions	211
	References	212
9	Global Ocean Carbon Cycle Modeling	217
9.1	Introduction	217
9.2	Anthropogenic Carbon Uptake, Transient Tracers, and Physics	218
9.3	Global Biogeochemical Cycles	222
9.4	Ecosystem Dynamics	225
9.5	Other Topics	231
9.5.1	Mesoscale Physics	232
9.5.2	Climate Variability and Secular Change	232
9.5.3	Land, Coastal Ocean, and Sediment Interactions	233
9.5.4	Inverse Modeling and Data Assimilation	234
9.6	Summary	234
	Acknowledgements	235
	References	235
10	Temporal Studies of Biogeochemical Processes Determined from Ocean Time-Series Observations During the JGOFS Era	239
10.1	Introduction	239
10.2	The Oceanic Carbon Cycle and the Biological Carbon Pump	240
10.3	Global Inventory of JGOFS Time-Series Programs	244
10.3.1	Bermuda Atlantic Time-Series Study (BATS)	245
10.3.2	Dynamique des Flux Atmosphérique en Méditerranée (DYFAMED)	246
10.3.3	European Station for Time-Series in the Ocean Canary Islands (ESTOC)	247
10.3.4	Hawaii Ocean Time-Series (HOT)	247
10.3.5	Kerguelen Point Fixe (KERFIX)	248
10.3.6	Kyodo Northwest Pacific Ocean Time-Series (KNOT)	248
10.3.7	Ocean Station Papa (OSP or Sta. P)	249
10.3.8	South East Asia Time-Series Station (SEATS)	249
10.4	Some Practical Lessons Learned from the JGOFS Time-Series Programs	250
10.5	Cross Ecosystem Habitat Comparisons: Nutrient, Chlorophyll and Production-Export Relationships	251
10.5.1	Case Study 1: Estimates of the Biological Carbon Pump at Ocean Times Series Sites	255

10.5.2 Case Study 2: A 'Bermuda Triangle' Carbon Mystery with Global Implications	257
10.5.3 Case Study 3: Decade-Scale, Climate-Driven Changes in the N ₂ -Primed Prokaryote Carbon Pump	258
10.5.4 Case Study 4: OSP Ecosystem Dynamics and the Role of Iron	262
10.6 Beyond JGOFS: a Prospectus	263
Acknowledgements	264
References	265
11 JGOFS: a Retrospective View	269
11.1 The JGOFS Science Plan	269
11.2 The Process Studies	269
11.3 Iron Fertilisation Experiments	271
11.4 The Time Series Stations	271
11.5 The Global Survey	272
11.6 Remote Sensing	272
11.7 Benthic Studies	273
11.8 Continental Margins	273
11.9 Data Archiving	273
11.10 Models and Synthesis	274
11.11 Overall Conclusions	274
References	275
Index	279

Contributors

Anderson, Robert

Lamont-Doherty Earth Observatory
Columbia University
P.O. Box 1000, Palisades, NY 10964, USA

Barber, Richard T.

Nicholas School of the Environment and Earth Sciences
Duke University
135 Duke Marine Lab Road, Beaufort, NC 28516-9721, USA

Bates, Nicholas R.

Bermuda Biological Station for Research, Inc.
Ferry Reach, St. George's GE01 Bermuda

Boyd, Philip W.

National Institute of Water and Atmosphere
Centre for Chemical and Physical Oceanography
University of Otago
Dunedin, New Zealand
pboyd@alkali.otago.ac.nz

Brewer, Peter G.

Monterey Bay Aquarium Research Institute
Moss Landing CA 93923, USA

Chen, Chen-Tung Arthur

Institute of Marine Geology and Chemistry
National Sun Yat-sen University
Kaohsiung 804, Taiwan, China (Taipei)
ctchen@mail.nsysu.edu.tw

Dittert, Nicolas

Université de Bretagne Occidentale
Institut Universitaire Européen de la Mer
UMR CNRS 6539, Brest, France

Doney, Scott C.

Climate and Global Dynamics
National Center for Atmospheric Research
P.O. Box 3000, Boulder, CO 80307, USA

Ducklow, Hugh W.

School of Marine Science
The College of William & Mary
Box 1346, Gloucester Point, VA 23062-1346, USA
duck@vims.edu

Emerson, Steven

Department of Oceanography
University of Washington
Seattle, WA 98195, USA

Falkowski, Paul G.

Institute of Marine and Coastal Science and Department of Geology
Rutgers, The State University of New Jersey
New Brunswick, New Jersey 08901, USA

Fasham, Michael J. R.

Southampton Oceanography Centre
Waterfront Campus, Southampton, SO14 3ZH, UK
mjff@soc.soton.ac.uk

Follows, Michael J.

Program in Atmospheres, Oceans and Climate
Department of Earth, Atmospheric and Planetary Sciences
Massachusetts Institute of Technology
Cambridge MA 02139, USA
ric@liv.ac.uk or mick@plume.mit.edu

Francois, Roger

Woods Hole Oceanographic Institution
Woods Hole, MA 02543, USA

Harrison, Paul J.

Department of Earth and Ocean Sciences (Oceanography)
University of British Columbia
Vancouver, BC V6T 1Z4, Canada

Jahnke, Richard A.

Skidaway Institute of Oceanography
10 Ocean Science Circle, Savannah, Georgia 31411, USA

Jeandel, Catherine

Observatoire Midi-Pyrénées
14 Ave E. Belin, 31400 Toulouse, France

Karl, David M.

Department of Oceanography, SOEST
University of Hawaii, Honolulu, HI 96822, USA
dkarl@soest.hawaii.edu

Laws, Edward A.

Department of Oceanography
University of Hawaii at Manoa
Honolulu, Hawaii 96822

Legendre, Louis

Laboratoire d'Océanographie
CNRS, Villefranche-sur-mer, France

Lindsay, Keith

National Center for Atmospheric Research
Boulder, CO 80307, USA

Liu, Kon-Kee

Institute of Oceanography
National Taiwan University
Taipei 100, Taiwan 106, ROC

Llinás, Octavio

Instituto Canario de Ciencias Marinas
Telde, Gran Canaria, Spain

Lochte, Karin

Institut für Meereskunde
Düsternbrooker Weg 20
24105 Kiel, Germany
klochte@ifm.uni-kiel.de

Macdonald, Robie

Institute of Ocean Sciences
Sidney, B.C. V8L 4B2, Canada

Marty, Jean-Claude

Laboratoire d'Océanographie de Villefranche
BP 08, F-06 238 Villefranche sur mer Cedex, France

Michaels, Anthony F.

Wrigley Institute for Environmental Studies
University of Southern California
Los Angeles, CA 90089-0371, USA

Miquel, Jean C.

Marine Environment Laboratory
International Atomic Energy Agency
4 Quai Antoine Ier, BP 800, MC98000 Monaco

Moore, J. Keith

National Center for Atmospheric Research
Boulder, CO 80307, USA

Murray, James W.

School of Oceanography
University of Washington
Box 355351, Seattle, Washington, 98195-5351, USA

Neuer, Susanne

Department of Biology
Arizona State University
Tempe, AZ 85287, USA

Nojiri, Y.

National Institute for Environmental Studies
Tsukuba, Ibaraki 305-0053, Japan

Orr, James C.

Laboratoire des Sciences du Climat et de l'Environnement
Unite Mixte de Recherche CEA-CNRS, CEA Saclay
F-91191 Gif-sur-Yvette Cedex, France

Ragueneau, Olivier

Université de Bretagne Occidentale
Institut Universitaire Européen de la Mer
UMR CNRS 6539, Brest, France

Rivkin, Richard T.

Ocean Sciences Centre
Memorial University of Newfoundland
St. John's, Canada

Shimmield, Graham

Scottish Association for Marine Science
Dunstaffnage Marine Laboratory
Oban, Argyll, PA37 1QA, Scotland, UK

Tréguer, Paul

Université de Bretagne Occidentale
Institut Universitaire Européen de la Mer
UMR CNRS 6539, Brest, France
Paul.Treguer@univ-brest.fr

Vetrov, Alexander

P. P. Shirshov Institute of Oceanology
Russian Academy of Sciences
Krasikova 23, 117218 Moscow, Russia

Watson, Andrew J.

School of Environmental Sciences
University of East Anglia
Norwich NR4 7TJ, UK
a.j.watson@uea.ac.uk

Williams, Richard G.

Oceanography Laboratories
Department of Earth Sciences, University of Liverpool
Liverpool L69 7ZL, UK

Wong, Chi Shing

Climate Chemistry Laboratory, OSAP
Institute of Ocean Sciences
P.O. Box 6000, Sidney, B.C., Canada V8L 4B2

Chapter 10

Temporal Studies of Biogeochemical Processes Determined from Ocean Time-Series Observations During the JGOFS Era

David M. Karl · Nicholas R. Bates · Steven Emerson · Paul J. Harrison · Catherine Jeandel · Octavio Llinás
Kon-Keo Liu · Jean-Claude Marty · Anthony F. Michaels · Jean C. Miquel · Susanne Neuer · Y. Nojiri · Chi Shing Wong

10.1 Introduction

A comprehensive understanding of the global carbon cycle is required to address contemporary scientific issues related to the atmospheric accumulation of greenhouse gases and their cumulative effects on global environmental change. Consequently, detailed in situ investigations of terrestrial and marine ecosystems are necessary prerequisites for developing a predictive capability of future environmental variability and the effects of human-induced perturbations. These investigations need to address broad questions regarding the distribution, abundance, diversity and control of key plant, animal and microbe populations and their interactions with their habitats. They must be conducted with an explicit recognition of the interdisciplinary connections between physics, chemistry, biology and geology in each ecosystem. Ideally, these field studies should be conducted at strategic sites that are representative of large biomes or in regions that are likely to exhibit substantial interannual variability over large areas. However, it is more important that the unique features of each site elucidate representative processes that underpin the dynamics of the wider ocean. Furthermore, these field investigations should be conducted for at least several decades, in order to distinguish natural variability from that induced by human activities.

In response to a growing awareness of the ocean's role in climate and global change research and the need for comprehensive oceanic time-series measurements, the International Geosphere-Biosphere Programme: A Study of Global Change (IGBP) was established in 1986. One of the essential core components of IGBP, the Joint Global Ocean Flux Study (JGOFS) project, was established in 1987 to improve our understanding of the oceanic carbon cycle. More formally stated, "JGOFS seeks to determine and understand, on a global scale, the processes controlling the time-varying fluxes of carbon and associated biogenic elements in the ocean, to evaluate the related exchanges with the atmosphere, sea floor and continental boundaries, and to develop a capability to predict the response of oceanic biogeochemical processes to anthropogenic perturbations, in particular those related to climate change." To achieve these goals, four separate program elements were de-

defined: (1) process studies designed to capture key, regular events; (2) time-series observations at strategic sites; (3) a global inventory of carbon dioxide (CO₂) concentrations in the surface ocean; and (4) vigorous data synthesis, data assimilation and modeling efforts.

Long-term biogeochemical studies in oceanography are predicated on the relatively straightforward notion that certain processes, such as climate-driven changes in community structure and productivity, and natural or anthropogenic changes in nutrient loading and habitat changes, are long-term processes and must be studied as such. If the phenomena of greatest interest are episodic, rare, complex or characterized by thresholds or feedback control mechanisms, then long-term observations are mandatory (Risser 1991). Despite this need and strong justification, there are relatively few long-term biogeochemical studies of the world's ocean. This paucity of robust observations, especially in the remote regions of the open ocean, has led to an incomplete mechanistic understanding of the global carbon cycle, especially for key issues related to carbon sequestration in the ocean's interior. During the past two decades several ocean time-series programs have emerged and the data sets provided by these studies have collectively contributed to our increasing understanding of biogeochemical processes in the sea.

This chapter will focus on the ocean time-series components of JGOFS, especially the relationships between nutrient dynamics and productivity, and the relationships between productivity and carbon export. We will focus on the time-series program similarities, while acknowledging the important differences. Numerous papers have already been written on these topics, including at least four special issues of *Deep-Sea Research*, *Topical Studies in Oceanography* (Karl et al. 1996; Boyd and Harrison 1999a; Siegel et al. 2001; Marty et al. 2002). Our goal here is to report significant cross-ecosystem comparisons of the important processes of carbon production, export and remineralization and to investigate and understand the underlying mechanisms controlling carbon sequestration in the sea. This will be achieved by the presentation of sample data sets, and several biogeochemical 'case studies'. The structure, efficiency and controls of the ocean's various biological pumps will be a common theme in this comparative study.

10.2 The Oceanic Carbon Cycle and the Biological Carbon Pump

The large and dynamic oceanic reservoir of carbon, approximately 4×10^{19} g, is distributed unequally among dissolved and particulate constituents with various redox states and plays an important role in global biogeochemical cycles. These pools include dissolved inorganic carbon ($\text{DIC} = [\text{H}_2\text{CO}_3] + [\text{CO}_2] + [\text{HCO}_3^-] + [\text{CO}_3^{2-}]$), and the less oxidized pools of mostly uncharacterized dissolved organic carbon (DOC) and partially characterized particulate organic carbon (POC). The latter pool includes both living organisms and non-living particulate organic detritus; particulate inorganic carbon (PIC), mostly calcium carbonate (CaCO_3), is also present as a component of both living and non-living particulate matter. A chemical disequilibrium between oxidized DIC and reduced organic matter is produced and maintained by biological processes. The reversible, usually biologically-mediated, inter-conversions between dissolved and particulate carbon pools in the sea collectively define the oceanic carbon cycle.

The global distributions and movements of carbon in the sea are governed by two major processes with independent controls (Fig. 10.1). The solubility carbon pump, which transports DIC, is mediated by physical processes such as vertical mixing, advection and diffusion which are only partially understood. In particular, DIC pool dynamics in relation to mesoscale and sub-

mesoscale features and the importance of horizontal processes are not well resolved. Likewise, the air-to-sea exchange of CO_2 , especially the importance of short-term variability in wind speed, is not well constrained. Similarly, the key processes of the biological carbon pump are only partially understood.

The observed vertical distribution of DIC in the sea cannot be accurately reproduced by existing circulation models without the inclusion of biological processes. Furthermore, it is well known that the rate and efficiency of the oceanic uptake of atmospheric CO_2 can be dramatically affected by the structure and dynamics of the phytoplankton community. Because most, if not all, ecological interactions are non-linear, they are not easily studied or modeled. We consider it axiomatic that an explicit understanding of the biological carbon pump is required to understand and to model carbon dynamics in the sea. To adequately resolve the biological pump, we must know the individual mechanisms, the rates and controls, the regional and temporal variations and the sensitivities of the various biological pump components to habitat perturbations, including global environmental change. These are, we believe, the most important and as yet unresolved components of the ocean's carbon cycle.

Primary conversion of oxidized DIC to reduced organic matter (both DOC and POC) and CaCO_3 is generally restricted to the euphotic zone of the world ocean via the process of photosynthesis. The annual rate of global ocean primary production, about $90\text{--}92 \text{ Pg C yr}^{-1}$ ($1 \text{ Pg} = 10^{15} \text{ g}$), is nearly 50 times the amount of carbon entering the ocean from CO_2 build-up in the atmosphere which (estimated to be $\sim 2 \text{ Pg C yr}^{-1}$). The supply of reduced carbon and energy required to support subeuphotic zone metabolic processes is ultimately derived from the upper ocean and is transported downward by advection and diffusion of dissolved organic matter (Hansell et al. 1997), gravitational settling of particulate inorganic and organic matter (McCave 1975), and by the vertical migrations of pelagic animals (Longhurst and Harrison 1989) and phytoplankton (Villareal et al. 1993). These diverse processes collectively define the biological carbon pump.

In theory, the export flux of carbon from the euphotic zone includes both dissolved and particulate matter. However, as Margalef (1978) has so eloquently stated, "any atom is more likely to travel downwards when in a particle than in solution." This predicts a more significant role for processes that favor export of particulate matter. The ability of larger phytoplankton to aggregate (the diatom branch; Fig. 10.2) and sink out of the euphotic zone is, perhaps, the most efficient means of carbon export. As we shall see later, there are variations on this theme that can further enhance net carbon sequestration. Alternatively, when the phytoplankton assemblage is dominated by small picoplankton (the *Prochlorococcus* branch; Fig. 10.2) export is reduced. Most models of the

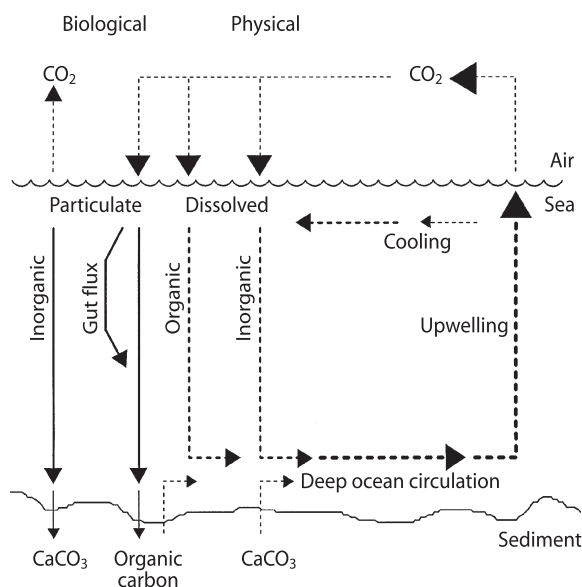
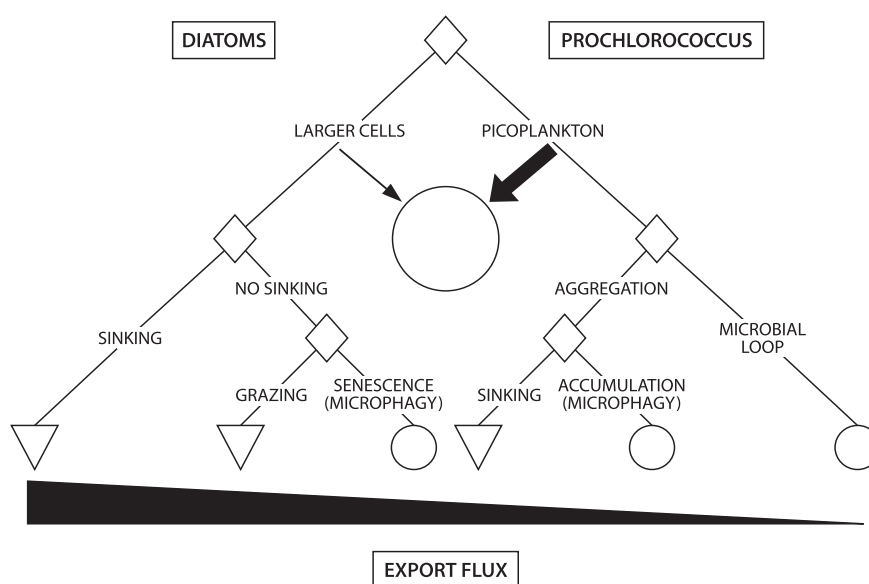


Fig. 10.1. A schematic view of the ocean's carbon pump showing the interactions between the surface ocean and the atmosphere above, and the surface ocean and the deep sea below. There are both physical and biological components of the ocean's carbon pump; the latter involve a complex set of poorly constrained ecological processes, some of which are discussed in more detail in the chapter (redrawn from SCOR (1990))

Fig. 10.2. Flows of chemical energy and materials through a hypothetical pelagic food web showing two major branches: diatom-dominated and *Prochlorococcus*-dominated biomes. Branch points, indicated by diamonds, were called 'hydrodynamic singularities' by the original authors (Legendre and Le Fèvre 1989). Branches to the left indicate a higher probability for export and branches to the right favor local regeneration and, hence, low export. The two major fates of carbon are export (triangles) or accumulation (circles) (redrawn from Cullen et al. (2002))



biological carbon pump assume that short food chains lead to high new production and high export, whereas complex microbial food webs lead to high recycling and low export.

Not all plankton carbon is created equal. The two major classes are: (1) organic carbon ($C_{org.}$), which itself is quite diverse, ranging from small lipid molecules containing only carbon and hydrogen to nucleic acids containing carbon, nitrogen, hydrogen, phosphorus and oxygen in varying proportions, and (2) inorganic carbon ($C_{inorg.}$), which is present mainly as $CaCO_3$ primarily in the skeletons of coccolithophorids, foraminifera and pteropods. The production of organic matter during photosynthesis removes CO_2 in an equimolar carbon stoichiometry ($CO_2 + H_2O \leftrightarrow CH_2O + O_2$), whereas the production of biogenic $CaCO_3$ in the pelagic realm releases CO_2 and reduces alkalinity ($Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + CO_2 + H_2O$). During massive surface blooms of coccolithophorids, the net carbon balance can swing towards net CO_2 production if the $C_{org.}:C_{inorg.}$ ratio in the exported particulate materials is <1.0 (e.g., Bates et al. 1996a). Theoretically, these two carbon-containing phases have different bulk densities, chemical behaviors including solubility, and subeuphotic zone remineralization length scales. However, in reality, the biogenic $CaCO_3$ is associated with organic carbon which affects its predicted chemical reactivity. Nevertheless, $C_{inorg.}$ is generally exported to greater depths in the water column than $C_{org.}$, so the $C_{org.}:C_{inorg.}$ ratio tends to decrease with depth. Furthermore, the ratio of Si-to-Ca or, more formally, the opal (biogenic Si) to calcium carbonate ratio in exported particulate matter, provides information on the structure of the phytoplankton assemblage in the euphotic zone. The diatom, or silicate mode, vs. the coccolithophorid, or carbonate mode is a key variable of the

biological pump. Even in low nutrient, low chlorophyll (LNLC) regions where the phytoplankton assemblage is dominated by prokaryotic picoplankton, these larger eukaryotes determine the tempo and mode of particulate export (Fig. 10.2). Among the various diatom species, maximum growth rate, iron requirements and propensity to form large blooms and subsequently aggregate are all key variables. In the Southern Ocean for example, two congeners, *Chaetoceros dichroaeta* and *C. brevis* have adopted different ecological strategies: the former has a rapid growth potential and blooms episodically in response to the pulsed atmospheric deposition of iron (Fe), whereas the latter grows best, but slowly, under the climatological Fe-deficient conditions of these high nutrient, low chlorophyll (HNLC) habitats (Timmermans et al. 2001). Community structure does matter, perhaps even down to the species level, both on the short-term and over much larger time scales.

When particulate carbon export from the euphotic zone is expressed as a proportion of contemporaneous primary production, this value is termed the export ratio or 'e-ratio' (Baines et al. 1994). Results from broad-scale, cross-ecosystem analyses suggest that the e-ratio in oceanic habitats is a positive, non-linear function of total integrated primary production (Suess 1980; Pace et al. 1987; Martin et al. 1987; Wassman 1990), with values ranging from less than 0.10 in oligotrophic waters to greater than 0.50 in productive coastal regions. It should be emphasized, however, that the field data from which the existing export production models were derived are extremely limited and that open ocean habitats, in particular, are under-represented. It is important to understand the mechanisms that control the biological carbon pump in a variety of functionally distinct biomes so that accurate and meaningful predictions of the response of the oceanic carbon cycle to glo-

bal environmental change can be made. This was a stated JGOFS goal in 1987.

Each year, the biological pump removes an estimated 7–15 Pg C from the surface waters of the world ocean, a value that is equivalent to ~10% of the annual global ocean primary production (Martin et al. 1987; Karl et al. 1996; Laws et al. 2000). Microbial transformation of sinking particles in the thermocline that gives rise to increased C:N and C:P ratios with depth can potentially drive a net atmosphere-to-ocean flux of CO₂ in the surface ocean. Episodic flux ‘events’ carry to the deep sea large amounts of ‘fresh’ organic matter (Lampitt 1985; Smith et al. 1996). These events may represent the bulk of the material reaching depths greater than 1 000 m (Anderson and Sarmiento 1994), making processes within the main thermocline also dependent upon the biological carbon pump.

After more than a decade of JGOFS research, we now realize that there are at least three fundamentally different biological carbon pumps, each with independent controls and fundamentally distinct biogeochemical consequences (Fig. 10.3):

1. ‘Redfield Ratio – Dissolved/Particulate Carbon Pump’ wherein the C:N:P stoichiometry of the exported material exactly balances the C:N:P stoichiometry of the subeuphotic zone supply of inorganic nutrients: Partitioning of the exported carbon into separate dissolved and particulate matter components is crucial because these two separate pools generally have different bulk stoichiometries, and different remineralization rates and fates. However, only particulate matter fluxes can be directly measured in the field. A characteristic of this pump is the vertical attrition of particulate matter mass, which can be modeled as a normalized power function of the form $F_z = F_{150\text{ m}}(Z/150)^b$, where Z is water depth and F and $F_{150\text{ m}}$ are fluxes at depth Z and 150 m, respectively (Martin et al. 1987; Knauer et al. 1990; Karl et al. 1996). In this model, the regeneration length scales of C vs. N and P are critical to the carbon sequestration process (Christian et al. 1997). If there is no spatial or temporal separation between C and the export of the production rate limiting nutrients N and P, there can be no net carbon sequestration. Even though the Redfield pump operates worldwide and is probably a dominant component of the ocean’s carbon cycle, it largely sustains a bi-directional reflux of bioelements, rather than net export. In other words, even though there is a measurable downward flux of carbon and associated bioelements (e.g., N and P) from the euphotic zone, there is a stoichiometrically equivalent importation of regenerated nutrients from below which over the long term (months to years) cancels out. As we shall see below, other export mechanisms may be more important for net carbon sequestration in the sea.

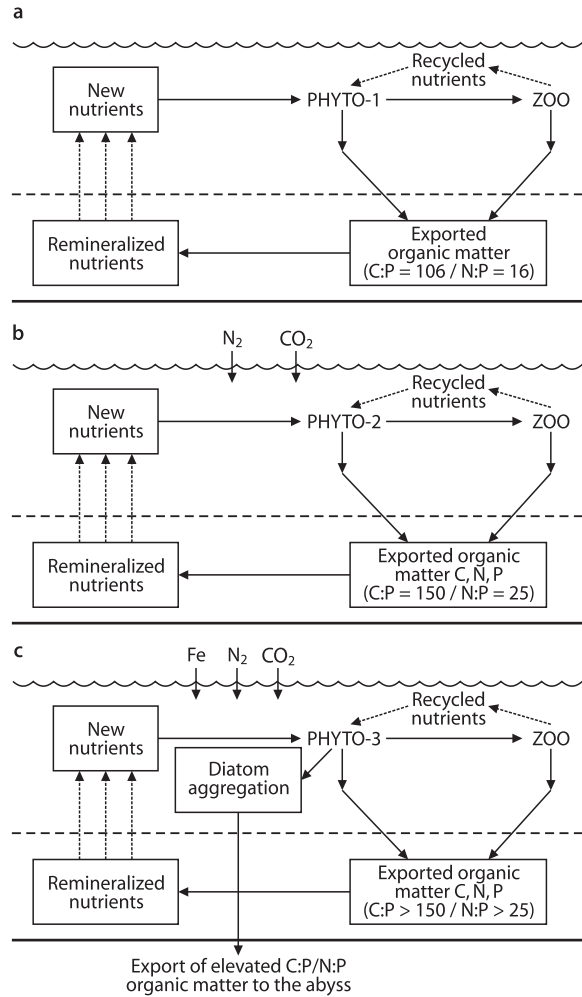


Fig. 10.3. The three major variations of the biological carbon pump in the sea. **a** The Redfield ratio – dissolved/particulate carbon pump with a balanced C:N:P stoichiometry for imported and exported materials. The PHYTO-1 assemblage is a diverse mixture of eukaryotic and prokaryotic algae and bacteria. Under these hypothetical conditions of a Redfield balanced ocean, the flux of C, N and P out of the euphotic zone is balanced by the importation of regenerated C, N and P from below, so there is no net carbon export. **b** The N₂-primed prokaryote carbon pump with a portion of the new N derived from dissolved N₂ gas. The PHYTO-2 assemblage has selected for potentially diverse free-living (unicellular and filamentous) and symbiotic N₂-fixing prokaryotes capable of surviving under conditions of fixed N depletion. Under these conditions the exported particulate matter is characteristically enriched in C and N, relative to P, and there is an imbalance between the import and export nutrient balance in favor of net C removal. **c** The event-driven, Fe-stimulated diatom aggregation carbon pump driven by the stochastic atmospheric delivery of bioavailable Fe. The PHYTO-3 assemblage has selected for large diatom species which use the Fe to assimilate nitrate or, in certain cases, to stimulate the metabolism of intracellular N₂-fixing symbiotic cyanobacteria who then manufacture fixed N for the host. The latter would be expected to occur in habitats that are both Fe- and fixed N-stressed (e.g., central gyres). Following nutrient (Fe, P or Si) exhaustion, the diatoms aggregate and sink carrying carbon to the abyss (see also diatom branch; Fig. 10.2). If N₂-fixation and Fe-stimulation co-occur, then the production stoichiometry also favors C export see **b**, above. This combined Fe-stimulated, N₂-fixing diatom pump is likely to be the most efficient means for sequestering atmospheric CO₂ in the world ocean

2. '*N₂-primed Prokaryote Carbon Pump*' wherein micro-biological fixation of N₂ temporarily relieves the ecosystem of fixed-N limitation resulting in P (or Fe) control of new and export production: Under these new habitat conditions, there is a selection for the growth of microorganisms with altered ecological stoichiometry, one which produces dissolved and particulate matter with elevated C:P ratios (>250–300:1) relative to the expected Redfield ratio (C:P = 106). Export of this non-Redfield organic matter provides a mechanism for the net, long-term (centennial to millennial) sequestration of carbon into the mesopelagic zone, or deeper (Fig. 10.3b). The time scales of this sequestration will be determined by the balance between N₂ fixation and denitrification and the time-scale for ventilation of the midwater zones where some of the denitrification occurs. Variability in this process will depend upon the stability of the climate parameters that encourage the growth of the N₂-fixing prokaryotes, and on a continued supply of bioavailable P and Fe or to the physiological limits in the non-Redfield stoichiometry. A re-supply of P and, perhaps, Fe could be satisfied by vertically-migrating, N₂-fixing microorganisms like *Trichodesmium* (Karl et al. 1992). A biogeochemical effect similar to that described here for the N₂-primed Prokaryote Carbon Pump (i.e., net removal of C from the surface water relative to N/P upwelled from depth) can also occur by the selective subeuphotic zone remineralization of N/P relative to C in the absence of N₂ fixation. However, it is unlikely that this differential remineralization process could ever result in effective C:P ratios as high as those produced by the N₂-primed prokaryote carbon pump mechanism.
3. '*Event-driven, Mass Sedimentation Carbon Pump*' wherein a specific physical or biological perturbation to the biogeochemical steady-state results in a rapid pulse of export to the sea floor. This is most often characterized by Fe-stimulated diatom aggregations where atmospheric deposition of Fe-rich dust results in the rapid growth of large chain- or aggregate-forming diatoms followed by mass export. Massive blooms of filter-feeding planktonic animals, like salps, will have the same flux impact. A characteristic feature of these rapid growth-export events is the efficient delivery of fresh organic matter to the deep sea floor (the so called phytodetritus pulse). Even if the stoichiometry of these exported materials conforms to the Redfield ratio, there is a net removal of carbon from the ocean's surface on time scales of a few decades to centuries and, hence, net carbon sequestration. Although aggregation events have been reported to occur in both coastal and open ocean habitats the physical, chemical and biological controls are poorly understood. While the diatom bloom events were once thought to be coupled to the turbulent-driven

supply of new nutrients by deep mixing events or eddy-induced upwelling, it is now evident that diatoms can propagate, aggregate and sink even from stable open ocean waters (Scharek et al. 1999b; Cullen et al. 2002). These latter, stratified open ocean blooms are likely to be manifestations of the convergence of the N₂-primed prokaryote and diatom aggregation pump processes (Fig. 10.3c), effected through endo-symbiotic associations between N₂-fixing cyanobacteria and oceanic diatoms (e.g., *Rhizosolenia-Richelia* associations; Martinez et al. 1983). In this regard, the endosymbiont-containing diatoms facilitate the utilization of diatomic N and should be called 'diatomic-diatoms' to distinguish them ecologically from the more common nitrate-utilizing diatom populations.

Of these three separate biological carbon pumps, only the first has been studied or modeled in any detail. Unfortunately, it is the most predictable of the three and, for many reasons, the least important for variations in the ocean's carbon cycle. It now appears that the non-Redfield carbon pumps may be important in many open ocean habitats. If the N₂-primed Prokaryote Carbon Pump and the Event-driven, Mass Sedimentation Carbon Pump are found to be present in other regions of the global ocean, we may need to alter our most basic dogma on nutrient biogeochemistry in the sea.

Carbon export from the upper regions of the euphotic zone can be measured directly using surface-tethered, free-drifting, particle-interceptor traps (PITs; Knauer et al. 1979), or indirectly using oxygen mass balance estimation (Jenkins 1982, and subsequent papers e.g., Emerson et al. 1991; and Michaels et al. 1994), dissolved inorganic carbon isotope mass balance estimation (Zhang and Quay 1997) or ²³⁸U-²³⁴Th disequilibrium measurements (Coale and Bruland 1987; Buesseler 1998; Benitez-Nelson et al. 2001). Each approach has fundamental advantages and limitations, and each measures a slightly different set of ecosystem processes. For example, PITs cannot assess the rates of downward diffusion of DOC or active vertical migration processes, so this approach will tend to underestimate total downward carbon flux. PITs can also suffer from hydrodynamic collection bias, especially in high turbulent regions. Net oxygen production, carbon isotope mass balance and ²³⁴Th scavenging are all indirect surrogates for carbon flux, so model assumptions must be applied. Most of these indirect methods also suffer from a general lack of distinction between particulate and dissolved organic matter export; only PITs provide a return sample for quantitative chemical, microscopic or molecular/biochemical measurement. However, taken together, this suite of carbon export techniques can provide complementary, redundant information and a robust constraint on the carbon export process.

10.3 Global Inventory of JGOFS Time-Series Programs

During the JGOFS era eight ocean time-series programs were initiated (Fig. 10.4): Bermuda Atlantic Time-series Study (BATS), European Station for Time-series in the Ocean, Canary Islands (ESTOC), Dynamique des Flux Atmosphériques Méditerranée (DYFAMED), Hawaii Ocean Time-series (HOT), Kerguelen Point Fixe (KERFIX), Kyodo Northwest Pacific Ocean Time-series (KNOT), Ocean Station Papa (OSP) and the Southeast Asia Time-series (SEATS) programs. Other JGOFS-relevant programs, some pre-dating the official commencement of JGOFS in 1987, also exist, including hydrographic and biological monitoring programs established at marine laboratories, autonomous bottom-moored sediment traps, physical-biogeochemical moorings and underway data collected during repeat transits of merchant or military vessels. This chapter will focus on the eight JGOFS-sponsored research ef-

forts (Fig. 10.5). These ecosystem-based studies include measurements of nutrient and population dynamics, primary and secondary productivity rates and controls, as well as seascape structure and variability, including climate. Each program has unique roots, experimental design, organizational structure and local-to-global connectivity. Despite these fundamental differences, they do share common JGOFS objectives and implementation procedures, including standard core measurements and protocols (Table 10.1). However, it should be pointed out that not all of the ‘recommended’ JGOFS core measurements are conducted at every site (e.g., ^{14}C primary production, ‘new production’ by ^{15}N uptake, microzoo-plankton herbivory rates are not conducted at many sites). Likewise, some of the most exciting emergent data sets from selected JGOFS time-series programs (e.g., temporal changes in the N:P stoichiometry of total dissolved and particulate organic matter, rates of N_2 fixation and atmospheric Fe deposition rates) were not even recommended as key

Fig. 10.4. The global distribution of JGOFS ocean time-series stations and related biogeochemical programs. Shown at *top* are the positions of selected study sites in relation to the surface distribution of Chl as determined from the SeaWiFS color satellite (<http://seawifs.gsfc.nasa.gov/SEAWIFS.html>). The JGOFS sites discussed in this chapter are shown as *solid circles*; the *solid triangles* and *solid rectangles* show the locations of non-JGOFS, fixed-point biogeochemical ocean time-series sites or regional surveys, respectively. Shown at the *bottom* are the potential temperature-salinity relationships for each of the JGOFS sites showing the characteristic water mass structures for each site

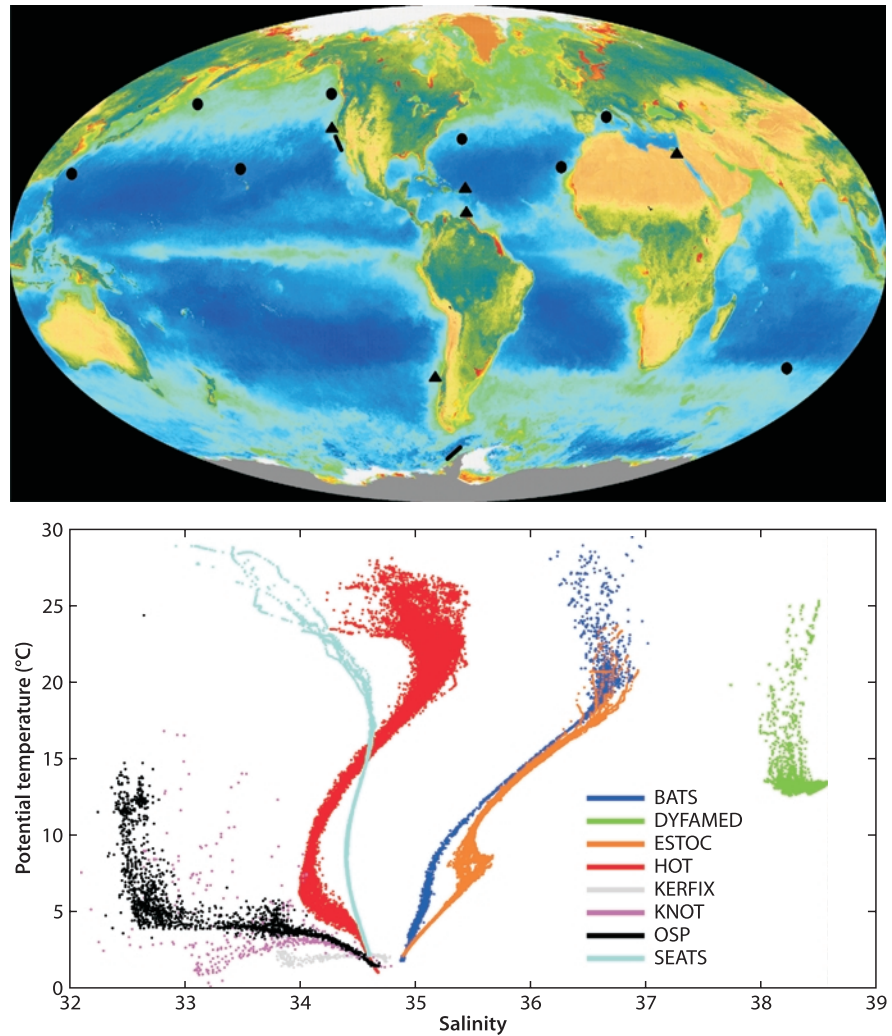
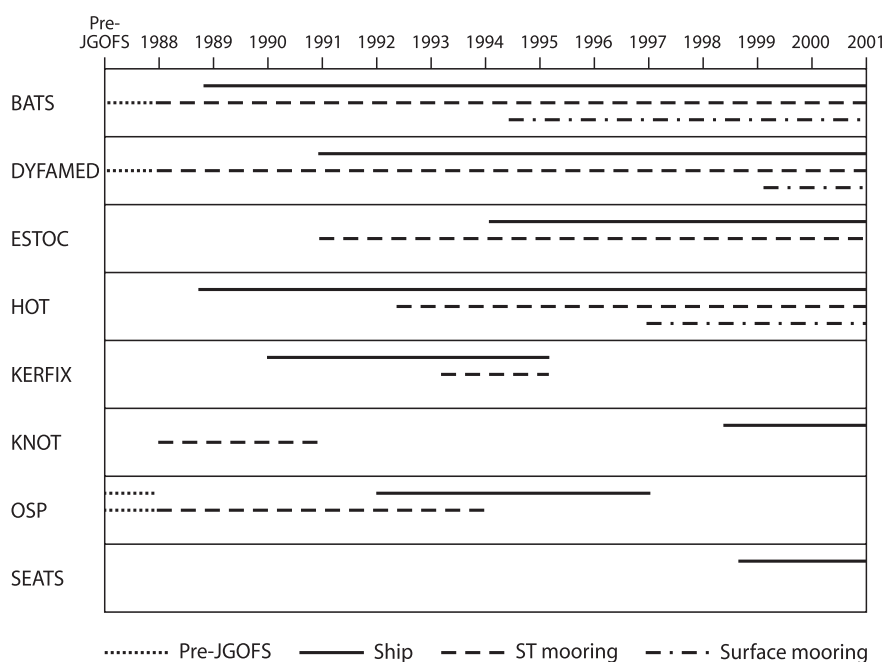


Fig. 10.5. Timelines for the eight JGOFS ocean time-series stations discussed in this chapter. Shown as coded horizontal lines are the periods of ship-based biogeochemical sampling and the deployments of bottom-moored sediment traps (ST) and surface meteorological-biogeochemical moorings



variables at the start of the JGOFS program. This is clearly 'work in progress.'

10.3.1 Bermuda Atlantic Time-Series Study (BATS)

Location: The primary station is located at 31° 50' N, 64° 10' W approximately 82 km SE of St. David's Light, Bermuda in 4500 m of water. The BATS sampling site is near, but not co-located with, Hydrostation 'S' (32° 10' N, 64° 30' W), one of the longest running hydrographic-chemical ocean time-series stations in existence. The BATS time-series station is intended to be representative of the western North Atlantic subtropical gyre (Sargasso Sea).

Inauguration and present status: BATS field sampling began in October 1988 and has continued to the present (Fig. 10.5). The current JGOFS sampling program builds on the Hydrostation 'S' program that was initiated in June 1954, but current BATS sampling is conducted at a new station approximately three times the distance from shore to eliminate any biogeochemical influences of the coastal zone. A bottom-moored sediment trap program located near the current BATS site began in 1976 (Deuser 1986; Conte et al. 2001), and independent physical-biogeochemical mooring and atmospheric sampling programs presently complement the BATS sampling program (Dickey et al. 2001).

Objectives: (1) to observe and interpret hydrographic, chemical and biological variations that occur on time scales ranging from subseasonal to decadal, (2) to esti-

mate the dynamics of gaseous, dissolved inorganic, dissolved organic and particulate organic carbon pools, (3) to determine the impact of mode water intrusion on biogeochemical processes, and (4) to understand the linkages between the atmospheric delivery of nutrients and organic matter export processes.

Sampling frequency and methods: Approximately bi-weekly to monthly field observations are conducted using the UNOLS vessel R/V *Weatherbird II* which is based in Bermuda and operated by the Bermuda Biological Station for Research, Inc. (BBSR). The interdisciplinary station work includes physical, chemical and biological observations and rate measurements.

Logistical management and funding sources: BATS is maintained by scientists and staff from the BBSR as well as several key guest investigators. Funding is provided primarily from the US National Science Foundation.

Data availability and key contact persons: All BATS core measurement data are publicly available approximately 1 year after collection (<http://www.bbsr.edu>), or by request from the US National Oceanic Data Center. Annual Data Reports are published and distributed through the US JGOFS-Planning Office in Woods Hole, MA. The principal contact persons are A. Knap (knap@sargasso.bbsr.edu) and N. Bates (nick@sargasso.bbsr.edu).

Key references: Michaels and Knap (1996), Steinberg et al. (2001).

Table 10.1. Selected core measurements made at the JGOFS ocean time-series sites¹

Parameter	Technique, instrument
Continuous CTD-based measurements	
Temperature	Thermistor(s) on CTD
Salinity	Conductivity sensor(s) on CTD
Depth	Digiquartz pressure sensor on CTD
Dissolved oxygen	Oxygen electrode on CTD
Fluorescence	Fluorometer on CTD
PAR	Scalar irradiance sensor on CTD
Discrete measurements	
Salinity	Conductivity, using a salinometer
Oxygen	Winkler titration with automated photometric or potentiometric endpoint detection
Total CO ₂	Manual or automated coulometric analysis
Alkalinity	High precision acid titration with potentiometric endpoint detection
Nitrate, phosphate, silicate	Autoanalyzer
Dissolved organic C	High-temperature combustion-oxidation
Total dissolved N and P	UV or chemical oxidation, autoanalyzer
Particulate C	High-temperature combustion, CHN analyzer
Particulate N	High-temperature combustion, CHN analyzer
Particulate biogenic silica	Chemical digestion, autoanalyzer
Fluorometric chlorophyll a	Acetone extraction, fluorescence detection
Phytoplankton pigments	HPLC, fluorescence detection
Bacteria	Fluorescence microscopy or flow cytometry
Zooplankton	Net tows, wet and dry weights, CHN analyzer
Rate measurements	
Primary production	Trace-metal clean, in situ incubation, ¹⁴ C uptake
Particle fluxes	Free-drifting cylindrical sediment traps (PITs)
Mass	Gravimetric analysis
Total carbon	CHN analysis
Total nitrogen	CHN analysis

10.3.2 Dynamique des Flux Atmosphérique en Méditerranée (DYFAMED)

Location: The primary station is located at 43° 25' N, 7° 52' E in the northwestern sector of the Mediterranean Sea (Ligurian Sea) approximately 45 km south of Cape Ferrat, France, in 2 350 m of water. This region is believed to be free from coastal zone fluxes, but it does receive a significant atmospheric input from the deserts of North Africa and from the industrialized countries bordering the Mediterranean Sea. These atmospheric fluxes are measured at nearby Cape Ferrat.

Inauguration and present status: Field sampling began in 1986, pre-JGOFS, with a sediment trap mooring and atmospheric deposition survey (Miguel et al. 1994; Migon et al. 2002) that were enhanced with a ship-based biogeochemistry measurement program and benthic survey in 1991 (Guidi-Guilvard 2002); all three components have continued to the present.

Objectives: (1) to study variations of hydrography and biogeochemistry at the seasonal and interannual scale, (2) to investigate the ecosystem response to atmospheric deposition events and to long-term environmental/climate forcing, (3) to investigate and understand the ecological effects of meteorological forcing, especially the transition in community structure from spring mesotrophy to summer oligotrophy and (4) to estimate the air-to-sea exchange of carbon dioxide.

¹ JGOFS has established a suite of biogeochemical measurements that has been recommended as the core parameters necessary for a comprehensive investigation of the ocean's carbon cycle. Nevertheless, the exact list of core measurements and specific analytical methods used varies considerably from site to site, and has even changed within a given site over time. Furthermore, some sites routinely measure parameters that are not part of the 'JGOFS core' (e.g., inherent and apparent optical properties, natural CN isotopes, radionuclides, atmospheric deposition, etc.). The program objectives and the science questions should always be the motivation behind the sampling and measurement programs.

Sampling frequency and methods: Approximately monthly field observations are conducted using the French R/V *Tethys II* which is operated by the Centre National de la Recherche Scientifique (CNRS) Institut National des Sciences de l'Univers (INSU) and based in Marseille, France. The interdisciplinary station work includes physical, chemical and biological observations and rate measurements. In March 1999, a meteorological buoy was deployed with plans to add in-water optical and biogeochemical sensors in the near future.

Logistical management and funding sources: DYFAMED is maintained by scientists from the Laboratoire d'Océanographie de Villefranche and of IAEA Marine Environment Laboratory in Monaco. Funding is provided by INSU/CNRS.

Data availability and key contact persons: Most DYFAMED data sets can be obtained at: <http://www.obs-vlfr.fr/jgofs2/sodyf/home/htm>. The principal contact person is J.-C. Marty (marty@obs-vlfr.fr).

Key reference: Marty et al. (2002).

10.3.3 European Station for Time-Series in the Ocean Canary Islands (ESTOC)

Location: The primary station is located at 29° 10' N, 15° 30' W approximately 100 km north of the islands of Gran Canaria and Tenerife in 3600 m of water. This time-series station is intended to be representative of the eastern boundary regime of the Northeast Atlantic Ocean.

Inauguration and present status: ESTOC field sampling began in February 1994 and has continued to the present.

Objectives: (1) to investigate the long-term changes of stratification and circulation on seasonal and interannual time scales, and (2) to investigate biogeochemical cycles in this region to understand controls on flux of carbon and associated bioelements on seasonal and interannual time scales.

Sampling frequency and methods: Approximately monthly field observations are conducted using the Spanish R/V *Taliarte* which is operated by the Instituto Canario de Ciencias Marinas and based in Telde, Gran Canaria. German research vessels have complemented these baseline observations. These latter cruises also maintain two long-term moorings; one deep-sea mooring supports current meters and thermistors and the other supports sediment traps. The interdisciplinary station work includes physical, chemical and biological observations and rate measurements.

Logistical management and funding sources: ESTOC is maintained by a consortium of four institutions: (1) Instituto Canario de Ciencias Marinas, Telde Gran Canaria, Spain (ICCM), (2) Instituto Español de Oceanografía, Madrid, Spain (IEO), (3) Institut für Meereskunde, Kiel, Germany (IFMK) and (4) Fachbereich Geowissenschaften, Universität Bremen, Germany (UBG). ESTOC has received funding in part from the German Ministry for Education and Research (BMBF).

Data availability and key contact persons: Most ESTOC data sets can be obtained at: (1) <http://www.iccm.rcanaria.es/estocing.htm>, (2) <http://www.ifm.uni-kiel.de/general/estoc.htm> and (3) <http://www.pangea.de/Projects/ESTOC/>. Key contact persons include O. Llinás (ollinas@iccm.rcanaria.es), G. Siedler (gsiedler@ifm.uni-kiel.de) and G. Wefer (gwefer@marum.de).

Key references: Neuer et al. (1997), Davenport et al. (1999) and Freudenthal et al. (2001).

10.3.4 Hawaii Ocean Time-Series (HOT)

Location: The primary deep ocean station, Sta. ALOHA (A Long-term Oligotrophic Habitat Assessment), is located at 22° 45' N, 158° W approximately 100 km north of Kahuku Point, Oahu, in 4740 m of water. A coastal station is also maintained at a location approximately 10 km offshore from Kahe Point, Oahu in 1500 m of water. Sta. ALOHA is believed to be representative of the North Pacific Subtropical Gyre biome.

Inauguration and present status: HOT field sampling began in October 1988 and has continued to the present. A bottom-moored sediment trap program was added in June 1992, and between January 1997 and June 2000 a meteorological-physical-biogeochemical mooring was deployed for high frequency atmospheric and in-ocean observations.

Objectives: (1) to document seasonal and interannual variability in water mass structure, (2) to relate water mass variations to gyre fluctuations, (3) to develop a climatology of biogeochemical rates and processes including microbial community structure, primary and export production and nutrient inventories and (4) to estimate the annual air-to-sea flux of carbon dioxide.

Sampling frequency and methods: Approximately monthly field observations are conducted primarily using the UNOLS vessel R/V *Moana Wave*, based in Honolulu and operated by the University of Hawaii (1988–2000) and the State of Hawaii owned vessel R/V *Kaimikai-O-Kanaloa* (2000 to present). Over the 13-year lifetime of HOT at least 10 different public and private research vessels have been employed in the field effort. The sediment trap mooring is

serviced annually from these same vessels. The interdisciplinary station work includes physical, chemical and biological observations and rate measurements.

Logistical management and funding sources: HOT is maintained by scientists from the University of Hawaii. Funding derives primarily from the US National Science Foundation and the State of Hawaii.

Data availability and key contact persons: All HOT core measurement data are publicly available approximately 1 year after collection (<http://hahana.soest.hawaii.edu>), or by request from the US National Oceanic Data Center. Annual data reports are published and distributed through the US JGOFS Planning Office in Woods Hole, MA, or as downloadable PDF files at the above referenced website. The principal contact persons are D. Karl (dkarl@soest.hawaii.edu) and R. Lukas (rlukas@soest.hawaii.edu).

Key references: Karl and Winn (1991), Karl and Lukas (1996) and Karl (1999).

10.3.5 Kerguelen Point Fixe (KERFIX)

Location: The primary station is located at 50° 40' S, 68° 25' E, approximately 100 km southwest of Kerguelen Islands in 1700 m of water. This site, south of the polar front, is characteristic of the Permanently Open Ocean Zone (POOZ) of the Southern Ocean. A second site (Bio-Station) located 24 km off Kerguelen was also used for selected biological rate measurements.

Inauguration and present status: KERFIX field sampling began in January 1990 and was terminated as a JGOFS effort in March 1995. Since the end of KERFIX, a new hydrographic (temperature and salinity) sampling program called CLIOKER (CLImat Océanique a KERguelen; Y Park, Principal Investigator) has emerged at the KERFIX site as a component of the international CLIVAR program. The biogeochemical studies, with a special focus on air-to-sea CO₂ gas exchange have continued under the OISO (Océan Indien Service d'Observation; N. Metzl, Principal Investigator), but with only two cruises per year.

Objectives: (1) to parameterize the air-sea flux of CO₂ and O₂, (2) to understand the physical and biological processes that control these exchanges and (3) to observe and interpret the seasonal and interannual variability in production, flux and decomposition of carbon and associated elements.

Sampling frequency and methods: Approximately monthly field observations were conducted using the French R/V *La Curieuse* which is operated by the French Polar Institute (IFRTP) and based in Port-aux-Français (Kerguelen).

From April 1993 to March 1995 a mooring was also in place for continuous measurements of the downward flux of particulate matter and current velocity and direction. The mooring deployments and maintenance were supported by the R/V *Marion Dufresne* which is operated by IFRTP and based in Port-aux-Français.

Logistical management and funding sources: KERFIX is supported locally by staff from the Biologie Marine (BIOMAR) on Kerguelen, with financial support from the Scientific Mission of the Terres Australes and Antarctiques Française (1990–1992), and subsequently by the Center National de la Recherche Scientifique (INSU/France-JGOFS; 1991–1995) and the IFRTP (1992–1995).

Data availability and key contact persons: Additional information on KERFIX can be obtained at <http://www.obs-vlfr.fr/jgofs/html/bdjgofs.htm>. KERFIX was initiated by A. Poisson (LPCM, Paris) and since 1993 has been led by C. Jeandel (Catherine.Jeandel@cnes.fr).

Key references: Jeandel et al. (1999) and Louanchi et al. (1999).

10.3.6 Kyodo Northwest Pacific Ocean Time-Series (KNOT)

Location: The primary station is located at 44° N, 155° E, approximately 400 km northeast of Hokkaido Island, Japan in 4900 m of water. This time-series station is intended to be representative of the southwestern subarctic gyre.

Inauguration and present status: KNOT field sampling began in June 1998 and was terminated in October 2000. Research at this site evolved from a previous (1988–1991) sediment trap experiment at the same location (Noriki 1999). The establishment of KNOT was a joint JGOFS-Japan and JGOFS-NPTT (North Pacific Task Team) effort. Kyodo is the Japanese word for collaboration.

Objectives: (1) to investigate the inorganic carbon system dynamics in response to variations in hydrography and biological processes, (2) to investigate the response of the biological pump to climate forcing and (3) to provide a data set from the western subarctic Pacific gyre for comparison to OSP in the eastern subarctic Pacific gyre.

Sampling frequency and methods: Approximately monthly field observations were conducted using the Japanese vessels T/S *Hokusei Maru* of Hokkaido University, R/V *Bosei Maru* of Tokai University, R/V *Mirai* of JAMSTEC, R/V *Hakuho Maru* of Tokyo University, and the *Hakurei Maru II* of the Metal Mining Agency of Japan.

Key contact person: Y. Nojiri (nojiri@ees.hokudai.ac.jp).

Key reference: Tsurushima et al. (1999).

10.3.7 Ocean Station Papa (OSP or Sta. P)

Location: The primary station is located at 50° N, 145° W, approximately 1500 km due west from the approaches to the Juan de Fuca Strait at 125° W in 4200 m of water. JGOFS relevant sampling is also periodically conducted along the transect from Vancouver to OSP at several locations along 'line P.' Conditions at OSP are believed to be representative of the northeast subarctic Pacific Ocean (southern edge of the Alaska gyre).

Inauguration and present status: JGOFS relevant research at OSP evolved from the co-located Canadian weather-ship sampling program (1956–1981), the Subarctic Pacific Ecosystem Research (SUPER) program (1984–1988) and the Canadian JGOFS program commencing in 1992 and terminating in 1997. From 1998 to the present, the Department of Fisheries and Oceans, Canada (DFO) has continued to support two or three cruises to OSP per year to continue the previous decades of seasonal sampling. A bottom-moored sediment trap program at OSP began in 1983 and ran through 1994. A deep-sea mooring was deployed from 1995 to 1997 which recorded T, S, light and solar-induced fluorescence at ~30 m.

Objectives: (1) to document seasonal, interannual and decadal variations in hydrographic and key biogeochemical parameters and determine their relationship to carbon export, (2) to investigate the role of atmospherically-deposited iron on ecosystem dynamics, including carbon dioxide drawdown and (3) to determine the impact of El Niño events on biogeochemical cycling.

Sampling frequency and methods: Ship-based field observations at OSP were obtained approximately three times per annum using the Canadian Coast Guard vessel *John P. Tully* based in Victoria, British Columbia, Canada. These cruises were usually in the periods February, May–June, and August–September to coincide with winter, late spring and late summer periods, respectively. Line 'P', 12 stations from Victoria to OSP, occupied from 1959–1981, was also re-occupied during the JGOFS campaign.

Logistical management and funding resources: The scientific programs at OSP are maintained by scientists and technical support in the Ocean Science and Productivity Division of the DFO. Salary and shiptime are provided by DFO. Research and time-series activities are funded by the Panel for Energy Research and Development (PERD) of Natural Resources Canada under programs of Time-series and Oceanic CO₂ Uptake. Monitoring of water properties is funded by the Ocean Climate Program of DFO.

Data availability and contact persons:

C.S. Wong (WongCS@pac.dfo-mpo.gc.ca) and P.J. Harrison (pharrison@unixg.ubc.ca).

Key references: Whitney et al. (1998), Wong et al. (1995), Wong et al. (1999) and Harrison et al. (1999).

10.3.8 South East Asia Time-Series Station (SEATS)

Location: The primary station is located at 18° N, 116° E about 700 km southwest of Taiwan (Shiah et al. 1999). The SEATS time-series station is in the South China Sea (SCS), the largest ice-free marginal sea in the world (the ice-covered Arctic Sea is the largest). It has a wide continental shelf to the south, significant runoff from several large rivers, including the Mekong River and the Pearl River, and a deep (>3000 m) basin. The SCS is subject to physical forcing of the alternating southeastern Asian monsoons (Shaw and Chao 1994), typhoons, strong internal waves (Liu et al. 1998) and ENSO (Chao et al. 1996). SEATS is potentially sensitive to climate change because of its locality between the third pole of the world, namely the Tibet Plateau, and the western Pacific warm pool, which are two of the most important heat engines of the earth's climate.

Inauguration and present status: The pilot study of the SEATS project began in August 1998 (Shiah et al. 1999). A suite of stations just west of the Luzon Strait was occupied on bimonthly cruises between August 1998 and June 1999. Because the hydrography of these stations are strongly influenced by the Kuroshio intrusion through the strait as well as the monsoon driven upwelling off northwest Luzon (Shaw et al. 1996), the location of SEATS was changed to the site mentioned above in August 1999. The observational program, including shipboard measurements and moored instruments for physical and biogeochemical measurements, is yet to be fully developed.

Objectives: (1) to understand how monsoonal forcing controls biogeochemical cycles in the SCS and how ENSO modulation of the monsoon strength influences it, (2) to monitor how the episodic events, such as typhoons or mesoscale eddies, affect biogeochemical processes in the upper water column, and (3) to link the present day biogeochemical processes with paleorecords preserved in sediment cores taken by IMAGES and the Ocean Drilling Project for better understanding of the effect of climate change on the ocean biogeochemistry in the marginal sea.

Sampling frequency and methods: Ship-based hydrographic and biogeochemical surveys are conducted every 2–3 months. Moored ADCP and thermister chains have been deployed since 1997. Moored light sensors and fluorometers have been deployed since October 2001.

Logistical management and funding sources: SEATS is maintained by scientists and staff from the National Center for Ocean Research (NCOR), Taipei. Funding is provided by the National Science Council, Republic of China (ROC).

Data availability and key contact persons: The data archive of SEATS is being compiled and will be available from NCOR (<http://www.ncor.ntu.edu.tw>). The principal contact person is K. K. Liu (kkliu@ccms.ntu.edu.tw).

10.4 Some Practical Lessons Learned from the JGOFS Time-Series Programs

There is a very broad range of natural ecosystem variability in the sea. Each part of this variance spectrum is derived from specific physical, biogeochemical and biological forcing, and each has unique consequences for the ocean's carbon cycle. For example, diel variations are tied to the daily and seasonal solar cycles and are very predictable for a given latitude. However, for phototrophic microorganisms in the sea, there can be large day-to-day variations in total irradiance at a given reference depth as a result of inertial period oscillations, internal waves and clouds. On subseasonal time scales there are discrete nutrient-enhancing upwelling and mixing events that can occur on mesoscale (100–1 000 km) spatial scales (McGillicuddy et al. 1998, 1999). In the North Pacific Ocean, there are also decade-scale transitions or regime shifts such as the Pacific Decadal Oscillation (PDO; Mantua et al. 1997) that can fundamentally alter community structure and nutrient dynamics (Karl et al. 2001a). In the North Atlantic Ocean, the North Atlantic Oscillation (NAO) similarly influences upper ocean hydrography and biogeochemistry at BATS (Bates 2001). Finally, there are gradual, continuous, unidirectional changes such as the increasing atmospheric and oceanic burdens of CO₂ (Winn et al. 1994; Bates et al. 1996b; Bates 2001).

Ecosystem variance will respond simultaneously, in a non-linear fashion, to the combination of all these independent forces. The JGOFS ocean time-series programs were designed to observe and interpret these complex interactions on time scales from months to years. At the very least, these repeat biogeochemical measurements provide – largely for the first time – the data necessary to define a mean state or climatology from which a quantitative anomaly field can be prepared. These anomalies are then used to assess change in the biogeochemical state variables and carbon fluxes. The longer the time-series record, the more valid the climatology and the more relevant and diagnostic the anomalies. The mission and method of the JGOFS time-series programs are straightforward, but in practice these are easier said than done. The large-scale, low-frequency changes, in particular, will likely be the most

difficult to observe and interpret. Another complication is the assimilation of Eulerian, fixed-point time-series data into a four-dimensional context with various mesoscale and submesoscale natural variability (see McGillicuddy et al. 1998, 1999; Siegel et al. 1999). Nevertheless, we submit that ocean time-series measurement programs remain the most effective means for studying seasonal, interannual and decadal scale physical-biogeochemical processes. They also remain the most cost effective and efficient programs for understanding local and regional scale ecosystem dynamics and serve as floating platforms of opportunity for the support of complementary ocean and atmosphere research.

Sampling should, ideally, be continuous in order to resolve all relevant high- and low-frequency scales of habitat variability. Unfortunately, many biogeochemical parameters and most carbon fluxes cannot be measured remotely and a continuous human-operated station would be prohibitively expensive. Consequently, in JGOFS we have compromised with approximately monthly-to-quarterly cruises, supplemented with continuous moored observations to the extent possible. Despite their recognized importance, comprehensive ocean time-series field sampling programs are very difficult to sustain. Sampling during the past 40 years at OSP is a case in point. During the period 1965–1981, seawater was collected twice per week; the temporal resolution was excellent, but the core measurement list was relatively limited. This initial period of sampling was well situated for investigating intraseasonal and interannual variability, but the ecological consequences of the event-scale habitat perturbations that were observed could not be constrained. As complementary programs emerged to enhance the core measurement suite, the weathership program was discontinued. During the JGOFS era, the two-to-three cruises per year measurement frequency at OSP was insufficient to capture episodic events despite the comprehensive core measurement program that was assembled for this purpose.

Another frustrating example of the tradeoffs between time-series sampling design and logistics is the California Cooperative Oceanic Fisheries Investigation (CalCOFI). This sampling program began as a physical-biological observation program in 1949 to study the factors controlling the abundance of major pelagic fish stocks in the Southern California Current System. From 1950 to 1960, monthly cruises were conducted with few interruptions. But in 1961, the sampling frequency was reduced to approximately quarterly and this frequency was maintained through 1968. It was soon realized that this reduced frequency was insufficient for the intended program objectives, but fiscal resources precluded a return to the higher-frequency sampling mode. So in 1969, the CalCOFI sampling reverted back to monthly cruises, but only every third year (1969, 1972, 1975, 1978, 1981). This sampling strategy inadvertently imposed serious

limitations on an otherwise robust data set (Chelton et al. 1982). For example, the 1976–1977 phase shift in the PDO occurred during a period of infrequent sampling, and the major 1982–83 El Niño event was ‘conveniently scheduled’ between sampling years. From 1984, the spatial grid was reduced significantly as a compromise to accommodate quarterly cruises every year. This has been retained as the CalCOFI sampling frequency to the present. These sampling changes were forced primarily by financial and logistical considerations, not by science. Likewise, the North Pacific Ocean Climax time-series sampling program (Hayward et al. 1983), which lasted from 1968 to 1985, also had serious logistical constraints. Of the 22 cruises during the 17-year observation period, four were in 1973, three in 1985, two each in 1971, 1972, 1974, 1976 and 1983, one each in 1968, 1969, 1977, 1982 and none in 1970, 1975, 1978, 1979, 1981 and 1984. In this data set, the impact of the major 1982–1983 El Niño event may have, therefore, been over-represented relative to the longer term climatology.

There are two points regarding sampling frequency that are relevant to the JGOFS era time-series programs. First, of the eight programs discussed in this chapter, only three (BATS, DYFAMED and HOT) have a continuous, approximately monthly frequency, decade-long record of core biogeochemical parameters (Fig. 10.5). One program (SEATS) has just begun, and routine sampling at three of the sites (KERFIX, KNOT and OSP) has already been terminated as high-frequency biogeochemical sampling programs (Fig. 10.5). Even Hydrostation ‘S,’ which started in 1954, lost funding for a brief period (1977–1979), as it was considered not important science, ‘just monitoring.’ In light of the past lessons learned, this is unfortunate because it is impossible to re-sample the past. Adding another year to these emergent records is probably more valuable than starting a time-series measurement program at a new location, if funding is the limiting factor. Second, the JGOFS era (1987–present) has coincided with a period of unprecedented El Niño favorable conditions (Karl et al. 2001a), and warm-phase Pacific Decadal Oscillation and North Pacific Mode indices (Barlow et al. 2001). The JGOFS era has also been a period of predominantly positive NAO, which may have significant implications for the North Atlantic time-series programs (BATS and ESTOC). To the extent that these large-scale climate variations impact upper ocean ecosystem dynamics, and there is strong evidence that they do, then the biogeochemical data sets collected during JGOFS era may not be wholly representative of the long-term (century scale) ocean climatology at these respective sites. The recent shift to a cold phase of the PDO may create limitations on how easily these time-series data can be used to understand future ocean dynamics.

One advantage of the JGOFS time-series data sets may be their use for evaluating and predicting higher fre-

quency biogeochemical variability, e.g., seasonality. The systematic repeat core measurements provide unique data for diagnostic, prognostic and predictive syntheses, and for developing and testing models of biological/biogeochemical processes. These model results provide an interpretational context for extrapolating our knowledge of key mechanisms to the biomes and regions of interest.

An important research consideration is the statistical treatment of time-series data sets once in hand. For many ecological studies, central tendency analyses (e.g., regression, ANOVA) are employed to estimate the relationships between dependent or independent variables, or both. If time-series data sets are available, more sophisticated statistical analyses are also possible. For ecological and biogeochemical processes that are characteristically ‘noisy,’ that means that trend analysis is more robust and, generally, more meaningful. The successful separation of signal from noise depends on the choice and application of any of a number of statistical data filtering or smoothing techniques that are key elements in the analysis of time-series observations (Diggle 1990). An important question still remains. How do we treat data that are unusual (e.g., fluctuations of more than ± 2 or 3 standard deviations from the mean); flag them? remove them? focus future studies on them? Single point anomalies, particularly when they could be significant parts of an annual signal, may be important. Some of the most significant advances in the existing time-series studies came as the scientists were confronted with repeats of previous (one-off) patterns from isolated expeditions and forced to explain these patterns.

Finally, it is essential to emphasize that the combination of sufficient funding and credible research goals is a necessary but insufficient condition for the successful operation of an ocean time-series program. These programs also require a staff of dedicated, well-trained support personnel who are not prone to seasickness. These skilled technicians maintain the high level of data quality in spite of unexpected and demanding circumstances and the inevitable doldrums that come from repeated sampling of the same system. The ocean sciences community owes a debt of gratitude to these dedicated staff members. As time-series programs mature, it has become apparent to the principal investigators that the human infrastructure is one of the most challenging components of running and sustaining a time-series program.

10.5 Cross Ecosystem Habitat Comparisons: Nutrient, Chlorophyll and Production-Export Relationships

Cross-habitat comparisons of selected state variables and carbon fluxes have proven invaluable in ecological research. Key parameters relevant to the functioning of the ocean’s biological pump include near-surface and

Fig. 10.6. Nitrate concentration vs. water column depth profiles for BATS, DYFAMED, HOT, KNOT, OSP and SEATS time-series study sites. The data shown are climatological mean values and 95% confidence intervals which are generally less than the size of the symbols used. Inserts show the depth variation in the dissolved molar nitrate-to-phosphate (N:P) ratios as mean values and 95% confidence intervals. Note the high variability in the BATS N:P data set in the 0–200 m portion of the water column and the generally opposing trends in the N:P ratio profiles (i.e., decreasing for BATS vs. increasing for HOT with increasing water depth)

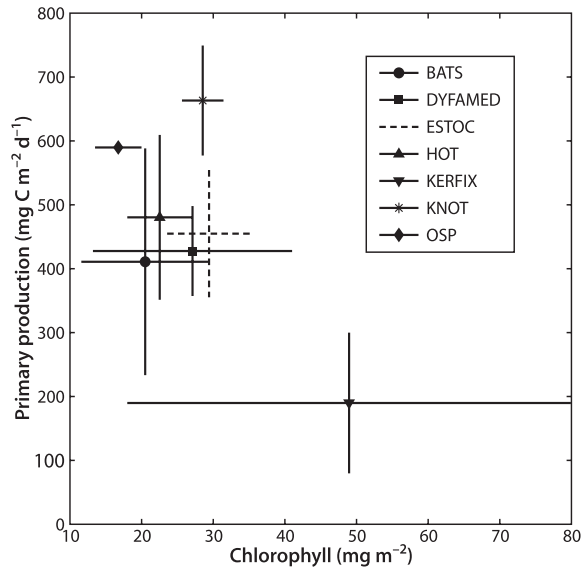
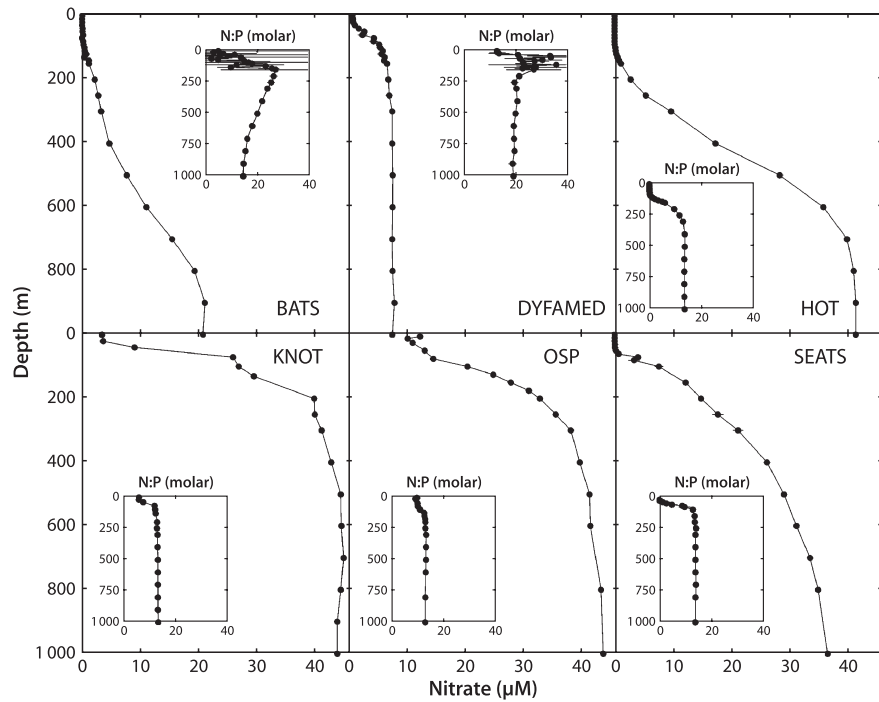


Fig. 10.7. Cross-site ecosystem comparisons during the JGOFS era. Data shown are the euphotic zone depth integrated chlorophyll *a* concentrations vs. contemporaneous rates of primary production presented as mean ± 1 standard deviation for most data sets (see Table 10.2 for values)

euphotic zone depth-integrated nitrate and Chl *a* inventories, and rates of primary, new and export production (Fig. 10.6–10.9, Tables 10.2 and 10.3).

Due to space limitations and, in part, to the proprietary nature of selected data sets we have not attempted a comprehensive integration or cross-site ecological interpretation of these biogeochemical data sets; however, a few general comments are warranted. First, de-

spite the broad geographic range and cross-site variations in physical forcing and biological community structure, there is a fairly narrow range in standing stocks of photoautotrophs (as measured by euphotic zone Chl *a*) and in rates of primary production (Table 10.2 and Fig. 10.7). Integrated Chl *a* concentrations varied by approximately a factor of two and rates of primary production by, at most, a factor of three. The rate measurements are harder to compare because of the different methodologies that were employed; for those programs utilizing the standard ¹⁴C JGOFS measurement protocol (BATS, DYFAMED, HOT and OSP) the rates of primary production were nearly identical with values ranging from $416 \pm 178 \text{ mg C m}^{-2} \text{ d}^{-1}$ at BATS to $589 \text{ mg C m}^{-2} \text{ d}^{-1}$ at OSP. These values are much higher than previous (pre-JGOFS) estimates would have implied, which may be a reflection of improved techniques or, possibly, habitat change.

The measured values for particulate carbon export from the euphotic zone were more variable, as would be expected, given the uncertainties and potential bias of free-drifting sediment traps (Table 10.2 and Fig. 10.8). Nevertheless, methodology aside, there appears to be a large variation in the *e*-ratio both between sites, and over time at a given site (Fig. 10.8 and 10.9). For example, for the two most extensive data sets (BATS and HOT; Fig. 10.9) there are substantial aseasonal, multi-year changes in the *e*-ratio of nearly an order of magnitude, suggesting variations in biogeochemical processes including, but not limited to, possible changes in community structure. The means and standard deviations for the *e*-ratios at BATS and HOT are 0.072 ± 0.038

Fig. 10.8.

Cross-site ecosystem comparisons during the JGOFS era. Data shown are the individual values of primary production and contemporaneous carbon flux for field experiments conducted at BATS, DYFAMED, ESTOC and HOT sites. Each graph also shows lines that are equivalent to e -ratios of 0.20 and 0.01 for comparison. The particle fluxes, measured using drifting sediment traps, are from either 150 m (BATS and HOT) or 200 m (DYFAMED and ESTOC). Values are presented in Table 10.2

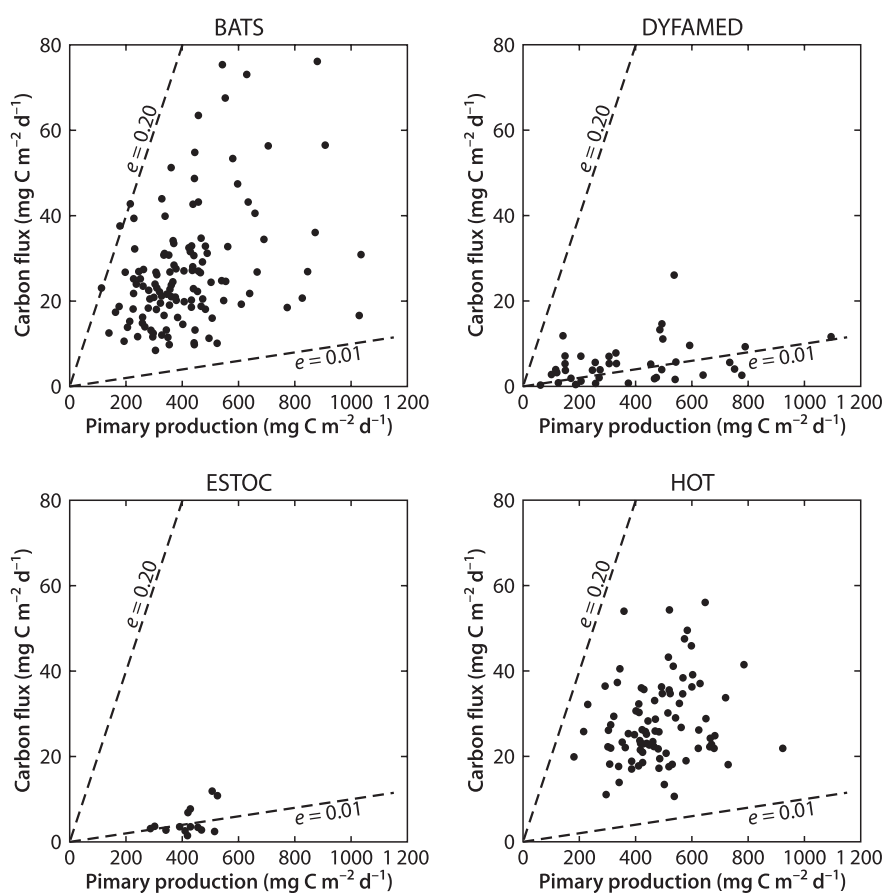


Table 10.2. A cross-ecosystem comparison of selected JGOFS core parameters. Data presented as minimum and maximum values for each site. This generally reflects a regular seasonal variation in the parameter noted, e.g., summer-to-winter extremes. However, it is important to emphasize that the values of the individual parameters do not always align with summer vs. winter. For example, mixed-layer depth is maximum in winter but temperature and, generally, chlorophyll values are highest in summer. The data presented are simply the climatological extremes or, in certain data entries, the mean ± 1 standard deviation

Location	Mixed layer properties				Euphotic zone properties		
	Depth (m)	T (°C)	[NO ₃ ⁻ + NO ₂ ⁻] (μM)	Chl <i>a</i> (μg l ⁻¹)	Chl <i>a</i> (mg m ⁻²)	Primary production ^a (mg C m ⁻² d ⁻¹)	C export (mg C m ⁻² d ⁻¹)
BATS	10 – 300	19 – 29	<0.05 – 0.5	0.05 – 0.3	20.5 ± 8.8	416 ± 178	27.2 ± 13.9
DYFAMED	10 – 500	12 – 25	0.1 – 2	0.02 – 1.5	27.1 ± 13.9	427 ± 70	11.5 ± 4.5
ESTOC	35 – 150	17 – 24	<0.05	0.05 – 0.4	29.4 ± 5.7	456 ± 98	4.5 ± 2.9
HOT	20 – 100	22 – 30	0.01 – 0.03	0.05 – 0.1	22.5 ± 4.5	480 ± 129	28.3 ± 9.9
KERFIX	<50 – 250	1.5 – 4.5	23 – 28	0.3 – 1.5	18 – 80	189 ± 110	1.9 – 2.9
KNOT	15 – 60	3 – 7.5	10 – 23	–	28.6 ± 2.9	663 ± 86	–
OSP	40 – 120	5.5 – 13	8.5 – 16	0.2 – 0.4	13.5 – 20	589	18.2 ± 7.2

^a Primary production is estimated by: (a) ¹⁴C or ¹³C incubation techniques (BATS, DYFAMED, HOT, OSP), (b) spring-to-summer nutrient drawdown (KERFIX, KNOT), and (c) bio-optical model that considered both chlorophyll and temperature (ESTOC; S. Neuer, pers. comm.).

(range = 0.016–0.215; $n = 125$) and 0.062 ± 0.026 (range = 0.020–0.149; $n = 89$), respectively. The e -ratio variability at both sites also has a lower frequency signal with higher than average e -ratios in 1989–1990 and 1997–1999, and lower than average e -ratios in the mid-decade especially 1991–1992 and 1995–1996 (Fig. 10.7 and

10.8). These changes in e -ratio are driven mostly by changes in particulate C flux rather than by changes in primary production; the latter displays distinct seasonality at both sites, but no secular trend. An accurate estimate of the annual organic matter export from the zone of net oxygen production of the ocean requires time-series meas-

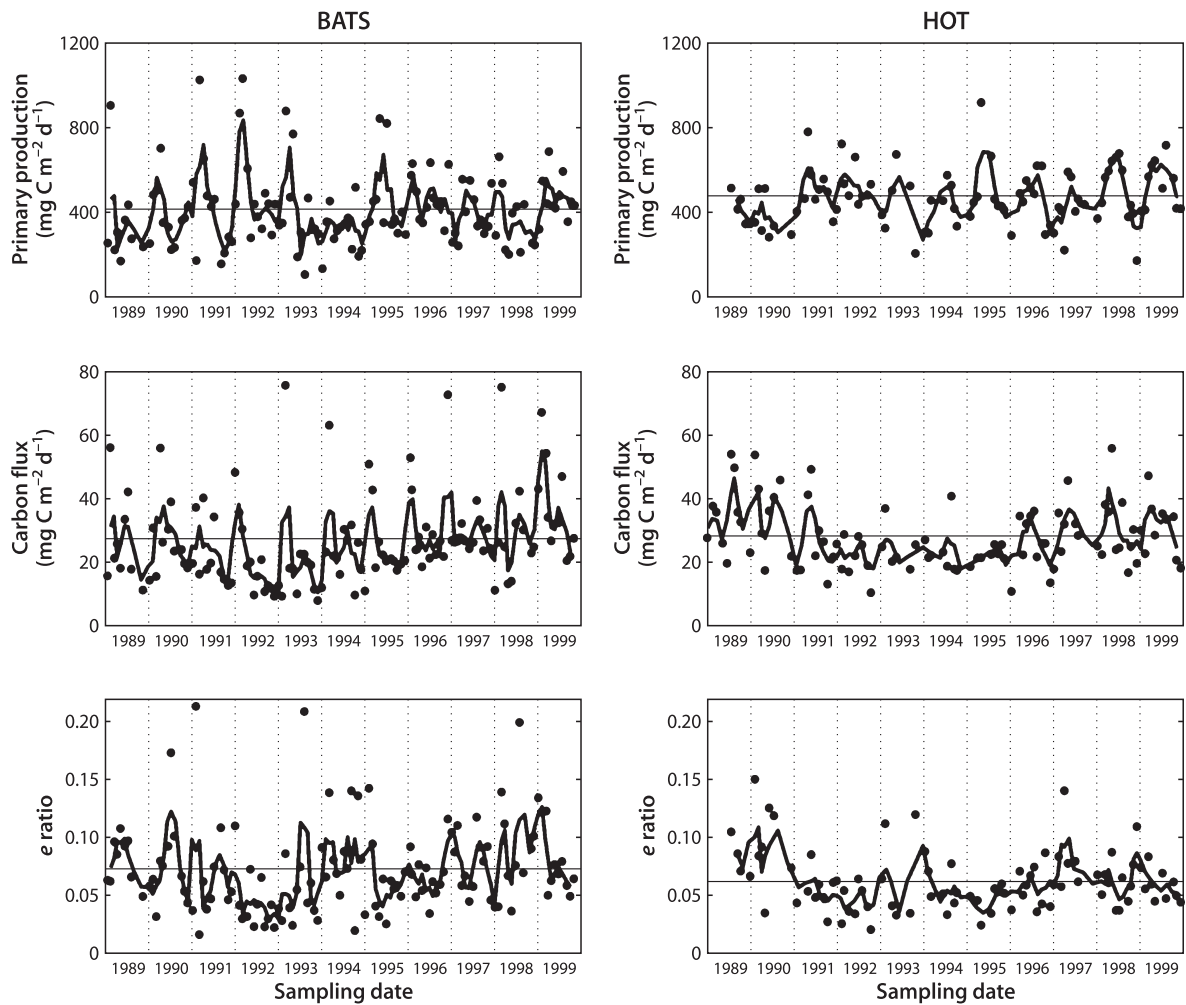


Fig. 10.9. Temporal variations of primary production (measured by the ^{14}C technique) and carbon flux (measured using free-drifting sediment traps positioned at the base of the euphotic zone) for an 11-year period at BATS and HOT time-series sites. Also shown at the bottom is the corresponding e -ratio (flux \div production). The solid symbols represent the individual cruise data for each parameter and the heavy solid line is the 3-point running mean. *Left:* BATS data sets showing the climatological mean values (horizontal lines): primary production = $416 \text{ mg C m}^{-2} \text{ d}^{-1}$, carbon flux = $27.2 \text{ mg C m}^{-2} \text{ d}^{-1}$, and e -ratio = 0.072 . *Right:* HOT data sets showing the climatological mean values (horizontal lines): primary production = $480 \text{ mg C m}^{-2} \text{ d}^{-1}$, carbon flux = $28.3 \text{ mg C m}^{-2} \text{ d}^{-1}$, and e -ratio = 0.062

Table 10.3. Inorganic carbon pool dynamics at selected JGOFS time-series sites (data are presented as the measured range (minima and maxima) or as mean and, in parentheses, 95% confidence intervals, as shown. n = number of observations)

Location	Measurement period	Annual N-DIC range ^a ($\mu\text{mol kg}^{-1}$)	Secular N-DIC change ($\mu\text{mol kg}^{-1} \text{ yr}^{-1}$)	Annual $f\text{CO}_2$ range (μatm)	Secular $f\text{CO}_2$ change ($\mu\text{atm yr}^{-1}$)	Reference
BATS	10/88 to 12/99 (11 yr)	35 – 45	+1.6	60 – 120	+1.4	Bates (2001)
DYFAMED	2/98 to 2/00 (2 yr)	100	–	120	–	Copin-Montégut and Begovic (2002)
ESTOC	10/95 to 12/00 (5 yr)	20 – 25	1.2 ± 0.2	60 – 80	$+1.1 (\pm 0.2)$	Gonzalez-Davila (unpubl.)
HOT	10/88 to 12/99 (11 yr)	15 – 20	$+1.18 (0.79 - 1.58), n = 94$	25 – 60	$+2.51 (1.59 - 3.44), n = 86$	Dore et al. (2002)
KNOT	6/88 to 2/00 (1.5 yr)	107	–	–	–	Nojiri et al. (unpubl.)

^a N-DIC is dissolved inorganic carbon concentration normalized to a constant salinity of 35.0.

urements, and in this regard, the ocean is still dramatically under-sampled.

Just prior to the start of JGOFS there was a somewhat heated debate regarding the validity of the ^{14}C method, as generally applied, for the determination of primary production. The controversy derived, in part, from estimates of rates of oxygen utilization in the intermediate depths of the ocean (Jenkins 1982; Jenkins and Goldman 1985) and assumptions that were applied to derive estimates of new and export production under steady-state conditions. Platt and Harrison (1985) later reconciled the data sets by concluding that the f -ratio (new / total production) was an ecosystem variable that positively scaled on ambient nitrate concentration. Application of their model to the 4-year nitrate data set (1959–1963) from Hydrostation S near Bermuda, predicted that the f -ratio could vary from 0.03 to 0.53, with an annual mean of 0.31 (Platt and Harrison 1985). This variable and higher than previously assumed mean value, when considered along with measured rates of primary production, fully accommodated the export production (assuming new production \approx export production) that was needed to balance the subeuphotic zone oxygen consumption rates. From this analysis, Platt and Harrison (1985) made a very important conclusion regarding the biological carbon pump, namely that it is “untenable to speak about a particular ocean province, and certainly not the Sargasso Sea, as being oligotrophic (also see Lipschultz et al. 2002). Rather, a given oceanic province can be expected, locally in (x, y, z and t), to manifest a range of characteristics from apparent extreme oligotrophy to eutrophy as evidenced by the nearly 20-fold range in f -ratios.” The data sets from the JGOFS time-series programs (Fig. 10.8), especially BATS and HOT (Fig. 10.9) confirm the Platt and Harrison (1985) prediction of variable e -ratios, and the implied f -ratios.

Below we present four JGOFS case studies that provide selected vignettes of key oceanic processes that have been explored at the time-series stations during JGOFS.

10.5.1 Case Study 1: Estimates of the Biological Carbon Pump at Ocean Times Series Sites

The mass balance of carbon in the upper ocean includes the fluxes of DIC, DOC and PC, which are influenced by numerous physical and biological processes including gas exchange, upwelling, horizontal advection, eddy diffusion, and the nature of the biological carbon pump. The strength of the carbon pump can be determined by a variety of methods at the ocean time-series sites for comparison to contemporaneous photosynthetic carbon production (Table 10.4). Net oxygen flux estimates are derived from periodic (typically monthly) measurements of dissolved O_2 , argon (Ar) and nitrogen (N_2) and a model of processes that affect dissolved gas concentrations (gas exchange, seasonal temperature change, mixing, bubble collapse). A comparison of O_2 and Ar saturation state can be used to estimate the impact of biological processes on O_2 gas concentration (Fig. 10.10). This is because O_2 is produced by net photosynthesis whereas Ar is biologically inert. For the HOT site, about half of the shallow O_2 maximum is the result of biological processes (Emerson et al. 1995). Particle fluxes were determined from monthly floating sediment trap deployments at 100–200 meters. Other methods include carbon isotope mass balance, ^{15}N incubations and mass balances of both particulate and dissolved organic matter.

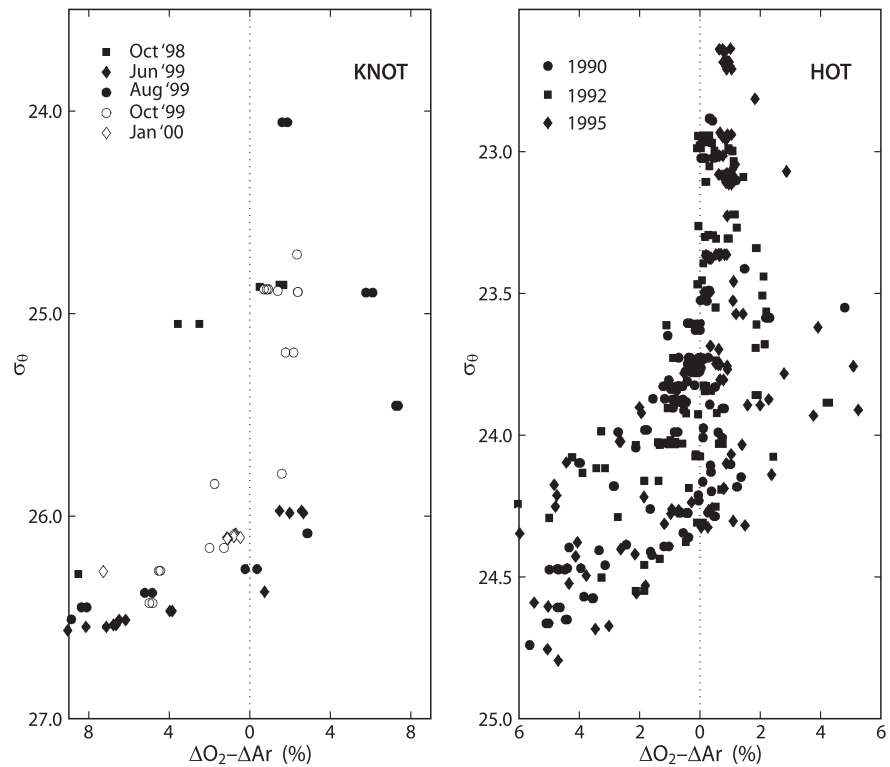
At Sta. ALOHA the values determined by O_2 mass balance are within the uncertainties ($\pm 50\%$) of those measured by organic carbon fluxes, and carbon isotope mass balances (Emerson et al. 1997). At the OSP site the mean annual organic carbon export rate from O_2 mass balance is about 40% lower than that determined from recent annual measurements of ^{14}C productivity and ^{15}N uptake (Boyd and Harrison 1999b; Varela and Harrison 1999b), which is also likely within the uncertainties of these

Table 10.4. Upper water column carbon fluxes as measured by a variety of techniques: A cross-ecosystem comparison. Total primary production and particulate fluxes are from compilations of the time-series data. Net O_2 production estimates are from BATS (Spitzer and Jenkins 1989); HOT (Emerson et al. 1997); and OSP (Emerson et al. 1991). Other methods are: BATS, particulate + DOC fluxes (Carlson et al. 1994); HOT, $\delta^{13}\text{C}$ mass balance and particulate and organic carbon fluxes (Emerson et al. 1997); KNOT, seasonal NO_3 change (Wong et al. 2002); and OSP, calculated from ^{14}C primary production and a ^{15}N f -ratio measurements (Boyd and Harrison 1999b; Varela and Harrison 1999a)

Location	Total primary production ($\text{mol C m}^{-2} \text{ yr}^{-1}$)	Particulate C flux ($\text{mol C m}^{-2} \text{ yr}^{-1}$)	Net O_2 production method ($\text{mol C m}^{-2} \text{ yr}^{-1}$)	Other methods
BATS	12.7	0.83	3.3 ± 1.1	1.8 ± 1.0
DYFAMED	13.0	0.35	–	–
ESTOC	13.9	0.14	–	–
HOT	14.6	0.86	2.7 ± 1.7	1.6 ± 0.9 , 2.0 ± 1.0
KERFIX	5.7	0.07	–	–
KNOT	20.2	–	–	6–7
OSP	17.9	0.55	2.0 ± 1.1	2.8

Fig. 10.10.

Dissolved oxygen and argon data for the upper water columns at the KNOT (*left*) and HOT (*right*) study sites. Data presented are the difference in the degree of saturation, Δ (in %), between oxygen (O_2) and argon (Ar) as a function of potential density, σ_θ , indicating a maximum in net biological O_2 production beneath the mixed-layer (*note*: for KNOT a σ_θ of 25.0 is approximately 39 m and for HOT, a σ_θ of 24.0 is approximately 100 m) (data from Emerson et al. (1997) and Wong et al. (1999))



determinations (Table 10.4). This type of closure has not been achieved for BATS where the O_2 mass-balance estimates continue to be about a factor of two greater than that determined from organic matter mass balances (Carlson et al. 1994). This discrepancy may have to do with the depths over which each of these techniques integrate the net carbon export, but this problem remains an open question.

The preliminary results from KNOT are based on the summertime decrease in nitrate concentration determined by surface water measurements across the subarctic Pacific on a ship of opportunity 8–9 times per year since 1995 (Goes et al. 1999; Wong et al. 1999, 2002). This estimate agrees with independent determinations of new production in this area based on satellite-determined Chl *a* and sea surface temperature and also an east-west comparison of sediment trap observations (Goes et al. 1999). Other estimates of the net carbon export rate are presently being determined by a time-series of measurements of ^{13}C primary production and new production and O_2 , Ar and N_2 measurements (see Fig. 10.10).

Values for the biological pump determined at these time series sites indicate some very interesting contrasts. The fact that the export production in the subtropical and subarctic Pacific are the same to within the error of our measurements was unexpected based on satellite color measurements (Falkowski et al. 1998), but may be partially explained by recent studies of the effect of temperature on carbon export (Laws et al. 2000). The ap-

parent difference in the biological carbon pump between the western and eastern subarctic Pacific begs the question about the processes controlling export at these high latitudes. Are the very high estimates from the west caused by greater mixed-layer depths and thus more efficient nutrient transport from below, or are they due to the enhanced role of large diatoms caused by the supply of Fe from the Asian continent?

An estimate of the global net biological carbon export of 10–15 Gt yr^{-1} has been made, based on a summary of these estimates (Table 10.4), including independent estimates for values in the Equatorial and near shore regions, and the assumption that these measured values are representative of their different ocean provinces. This value is much larger than originally determined by Eppley and Peterson (1979), but is consistent with the model-based estimates of Laws et al. (2000) which fall within this range. A remaining discrepancy in these approaches, however, is the role of subtropical oceans. If the measurements at HOT are typical of subtropical values, up to 40% of the biological pump may be located in these regions (Emerson et al. 1997). As we shall see below (Case Study 3), biogeochemical conditions at the HOT site are time-variable and climate-sensitive (also see Karl et al. 2001a,b). It appears that we are reaching consensus for the value for the global carbon export flux, but there are still great uncertainties in the global distribution of the biological pump that will require estimates from a greater number of time-series stations.

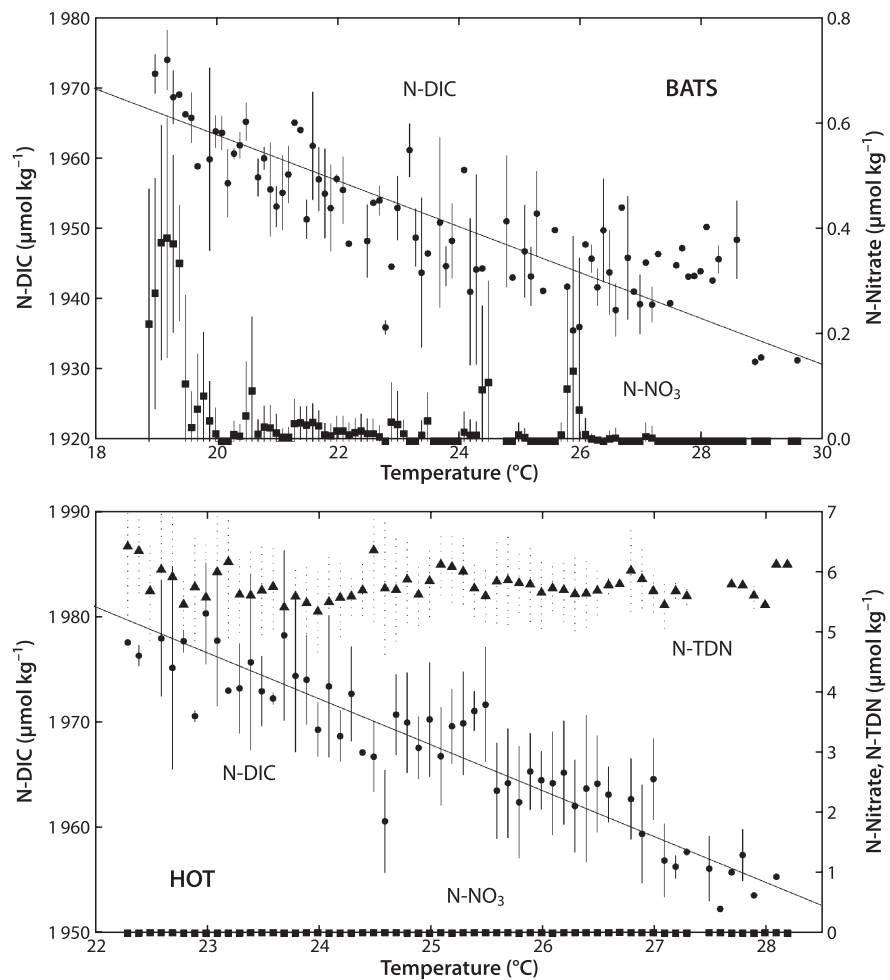
10.5.2 Case Study 2: A 'Bermuda Triangle' Carbon Mystery with Global Implications

When photoautotrophic microorganisms produce new organic matter during the process of photosynthesis, current models predict that they remove dissolved inorganic C, N, P and other essential bioelements in proportions equivalent to the new organic matter that is formed. When careful mass balance studies are conducted, the removal of dissolved nutrients has been shown to equal the sum of newly formed euphotic zone dissolved and particulate organic matter, plus that which has been exported from the local source. During the initiation of the spring bloom in the BATS study area there is a systematic, simultaneous drawdown of all required nutrients, which is fully anticipated. The mystery begins to develop after the nitrate, upwelled to the surface during deep winter mixing events, disappears from the water column as the annual summer oligotrophy returns to Sargasso Sea (Fig. 10.11, top). As the pre-

sumptive rate-limiting nutrient for organic matter production, the exhaustion of nitrate should cause an immediate cessation of new primary production and coupled organic matter export.

The continued disappearance of salinity normalized dissolved inorganic carbon (N-DIC) in the absence of nitrate was first reported by Michaels et al. (1994). They reasoned that if nitrate was added by episodic wind mixing or mesoscale eddy motions, the nitrate would be delivered along with DIC, so simple enhancements of nitrate-supported new and export production could not be responsible for the repeatable summertime N-DIC disappearance at BATS. They also evaluated, then rejected, the potential role of CO₂ outgassing during local warming of the near surface ocean, and the accumulation of nascent carbon-enriched dissolved organic matter as mechanisms for a net removal of N-DIC (Michaels et al. 1994; Bates et al. 1996b). More recently the role of short-term wind variability on air-to-sea CO₂ gas exchange (Bates et al. 1998) and the vertical migration of zooplankton (Steinberg et al. 2000) have been suggested as potentially important processes, but neither flux

Fig. 10.11. Relationships between carbon removal and fixed nitrogen in the surface waters of the subtropical North Atlantic (*top*: BATS) and subtropical North Pacific (*bottom*: HOT) during the period of summertime warming of the sea surface. At the BATS site, DIC normalized to a salinity of 35 (N-DIC) shows a systematic decrease with increasing temperature even in the absence of nitrate. At the HOT site, a similar summertime N-DIC drawdown in the absence of nitrate (the surface water nitrate concentration at Sta. ALOHA during the summer period is always less than $0.01 \mu\text{mol kg}^{-1}$). Analyses of salinity-normalized total dissolved N (N-TDN) also failed to document a simultaneous loss of fixed N from the much larger pool of dissolved organic N



seems large enough to account for the observed upper ocean carbon imbalance. Regional horizontal gradients were weak (Bates et al. 1996c) and, therefore, insufficient for local N-DIC removal (Ono et al. 2001); where is this substantial pool of carbon ($\sim 35\text{--}40 \mu\text{mol kg}^{-1}$) going, and what process(es) are responsible for the recurrent summertime loss of N-DIC in the absence of nitrate?

A summertime drawdown of N-DIC of nearly equivalent magnitude is also observed at the HOT site (Fig. 10.11, bottom). At this oligotrophic Pacific Ocean Station, the nitrate is even lower than it is near Bermuda, with surface concentrations always $\leq 10 \text{ nM}$ (Karl et al. 2001b). Because there is a fairly large ($5\text{--}6 \mu\text{M}$) but poorly characterized pool of dissolved organic nitrogen that dominates ($>99\%$) the total dissolved N (TDN) pool at Sta. ALOHA, it is conceivable that its utilization could support the summertime drawdown of N-DIC. For a measured C:N export ratio of 8 at Sta. ALOHA (Karl et al. 1996), the DON pool if fully utilized could support the removal of approximately $45 \mu\text{mol DIC kg}^{-1}$, and could fully reconcile the 'mystery.' However, an analysis of the N-TDN data set for Sta. ALOHA indicates that the summertime concentration changes very little, if at all, during the period of N-DIC disappearance (Fig. 10.11, bottom).

The variability in total N-DIC in seawater is controlled by at least three processes: photosynthesis/respiration, air-to-sea CO_2 gas exchange and vertical and horizontal advection/diffusion. Of these processes, only the net biological production of organic matter can explain the Bermuda (and now Hawaii) mystery. There are three potential sources of new N: (1) N_2 -fixation, (2) atmospheric deposition, and (3) active transport via vertically migrating phytoplankton. A careful assessment of these potential sources at both sites has revealed a significant role for N_2 fixation as a new export and production pathway (Michaels et al. 2000). This does not necessarily solve the BATS and HOT disappearing N-DIC mysteries, but it does provide a hypothesis for future field evaluation.

The consumption of N-DIC in the absence of nitrate was also observed in the upper portion (0–20 m) of the water column at the DYFAMED site (Copin-Montégut 2000). The C:N utilization ratio was two to three times higher than the Redfield ratio, when nitrate concentration was less than $0.5 \mu\text{M}$. As nitrate appeared with increasing water depth (to approximately $6 \mu\text{M}$ at 40 m), the C:N utilization ratio approached the Redfield ratio. Because phosphate was also depleted in surface water, the hypothesis of N_2 fixation seems to be insufficient to explain DIC consumption at the DYFAMED site unless the N_2 -fixing microorganisms are capturing P via active vertical migrations (Karl et al. 1992), or by other means. An alternative explanation for the N-DIC drawdown in the absence of inorganic nutrients at the DYFAMED site is the formation of N- and P-depleted dissolved organic matter, but this mechanism has not been confirmed.

A recent global ocean analysis of the "disappearing DIC in the absence of measurable nitrate" has shown it to be a recurrent feature of all tropical and subtropical marine habitats (Lee 2001). Application of several fairly well-constrained assumptions, enable the author to estimate a global rate of new carbon production that is supported by N_2 fixation of $0.8 \pm 0.2 \text{ Gt C yr}^{-1}$ for subtropical and tropical marine habitats. Apparently the summertime drawdown of N-DIC in the absence of nitrate, first reported near Bermuda from the BATS data sets, is a ubiquitous global phenomenon. This process takes on an added significance because it can decouple C, N and P cycles, and provides a mechanism for the net sequestration of atmospheric carbon as defined by the N_2 -primed Prokaryote Carbon Pump (Fig. 10.3b).

10.5.3 Case Study 3: Decade-Scale, Climate-Driven Changes in the N_2 -Primed Prokaryote Carbon Pump

Nutrient dynamics and their role in the stoichiometric variability of dissolved and particulate organic matter pools is a central aspect of biogeochemical studies. All known organisms contain a nearly identical suite of biomolecules with common structural and metabolic functions. This biochemical uniformitarianism serves to constrain the bulk elemental composition of life. In a seminal paper, Redfield and his colleagues (Redfield et al. 1963) summarized much of the earlier research on C, N and P stoichiometry of dissolved and particulate matter pools in the sea and combined these data sets into an important unifying concept which has served as the basis for many subsequent field and modeling studies in oceanic biogeochemistry. The so-called 'Redfield, Ketchum and Richards ratio' (or simply, the Redfield ratio) of 106C:16N:1P has, over the intervening decades, achieved nearly canonical status in aquatic sciences.

Despite this perceived uniformity, it is well known that the chemical composition of living organisms can vary considerably as a function of growth rate, energy (including light) availability, ambient nutrient (including both major and trace elements) concentrations and nutrient concentration ratios (Sakshaug and Holm-Hansen 1977; Rhee 1978; Laws and Bannister 1980; Tett et al. 1985). For example, under conditions of saturating light and limiting N, certain photoautotrophic organisms can store C as lipid or as carbohydrate, thereby increasing their C:N and C:P ratios relative to the expected Redfield ratios of 6.6:1 and 106:1, respectively. Likewise, if P is present in excess of cellular demands, it may be taken up and stored as polyphosphate causing a decrease in the bulk C:P and N:P ratios. Conversely, when the bioavailable N:P ratio is greater than that which is present in 'average' organic matter (i.e., $>16\text{N}:1\text{P}$ by atoms) selected groups of microorganisms

can reduce their cell quotas of P, relative to C and N, and effect net biomass production with C:P and N:P ratios significantly greater than the canonical Redfield ratios of 106:1 and 16:1, respectively.

Open ocean ecosystems are characterized by low concentrations of fixed, bioavailable N which would appear to make them a suitable niche for the proliferation of N_2 -fixing prokaryotes. In their now classic treatise on nutrient dynamics in the sea, Dugdale and Goering (1967) introduced the unifying concept of 'new' (i.e., nutrients imported to the local environment from surrounding regions) vs. 'regenerated' (i.e., nutrients that are locally remineralized) forms of nitrogen. They were careful to emphasize that there were several potential sources of new N for the euphotic zone, each of equal value but with potentially different ecological consequences. Since there were few data on N_2 fixation rates when their paper was published, importation of nitrate from below the euphotic zone was considered to provide the majority of new N in the sea.

Now, thirty years after the new production concept was introduced, there is increasing evidence that rates of oceanic N_2 fixation may have been systematically underestimated (see Case Study 2, above), or, perhaps, have increased in relative importance over time. This new evidence comes from several independent lines of investigation. One of the most interesting and provocative modern data sets is that derived from the application of novel molecular methods to detect the presence and abundance of N_2 -fixing microbes either by hybridization or amplification of nitrogenase (*nif*; the enzyme system used to reduce N_2 to ammonia) genes (Zehr et al. 1998, 2000). Application of these methods to open ocean biomes in the North Atlantic and North Pacific Oceans has revealed a spectrum of previously uncharacterized *nif* gene phylotypes. Furthermore, significant *nif* phylo-type diversity is apparent both within and between open ocean ecosystems. These novel data sets, when considered in concert with other recent reports of high rates of oceanic N_2 fixation, support the hypothesis that N_2 fixation is a major source of new N over vast regions of the world ocean (Michaels et al. 1996; Gruber and Sarmiento 1997; Karl et al. 1997, 2002).

Several lines of evidence from Sta. ALOHA suggest that N_2 fixation is an important contemporary source of new nitrogen for the pelagic ecosystem of the North Pacific Ocean. These independent measurements and data syntheses include: (a) N-DIC drawdown in absence of nitrate or other forms of fixed N (Case Study 2, above); (b) *Trichodesmium* (the putative, dominant open ocean N_2 fixer) population abundances and estimates of their potential rates of biological N_2 fixation; (c) assessment of the molar N:P stoichiometries of surface-ocean dissolved and particulate matter pools and development of a one-dimensional model to calculate N and P mass balances; (d) seasonal variations in the natural ^{15}N iso-

topic abundances of particulate matter exported to the deep sea and collected in bottom-moored sediment traps; and (e) observations on secular changes in soluble reactive P (SRP), soluble nonreactive P (SNP) and dissolved organic N (DON) pools during the period of increased rates of N_2 fixation (Karl et al. 1997).

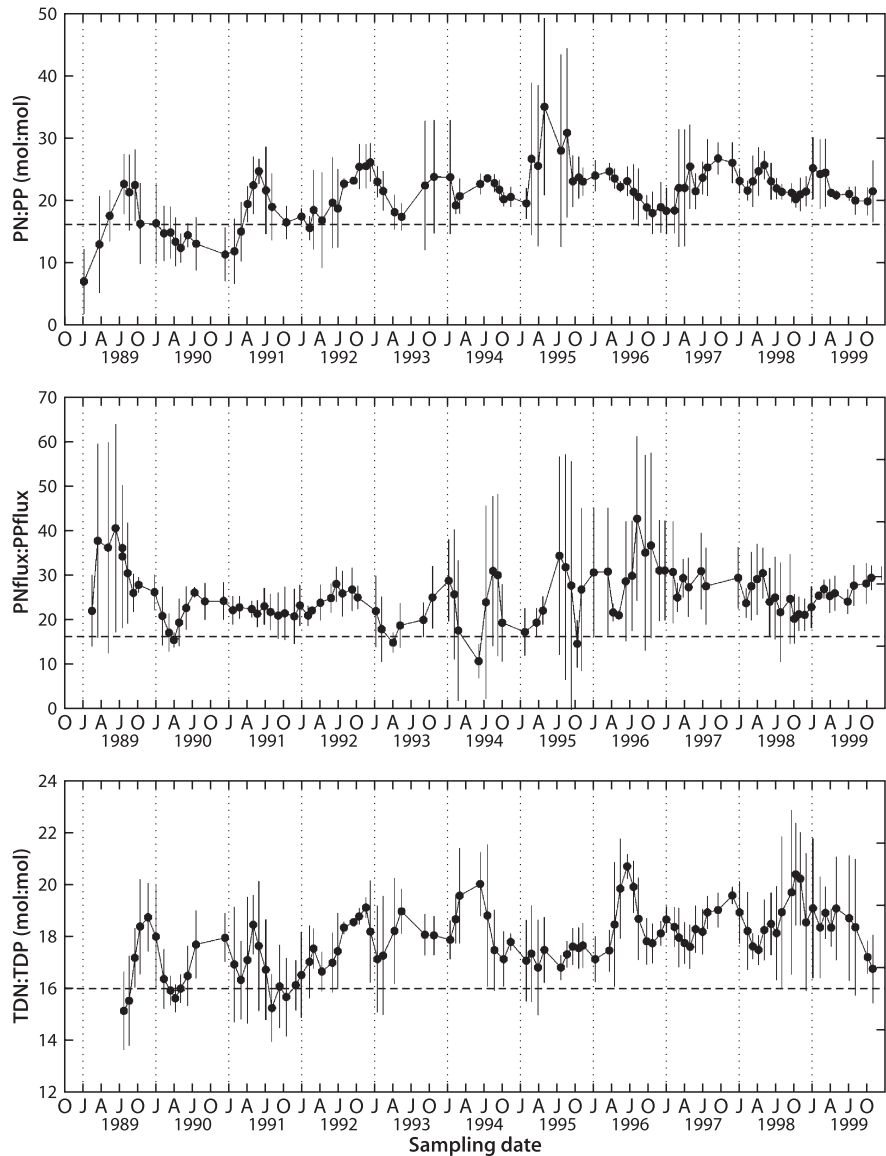
The production, export and remineralization of N-enriched (relative to P) dissolved and particulate organic matter (Fig. 10.12) is a diagnostic characteristic of a N_2 -supported ecosystem. Following the selection for N_2 -fixing microorganisms in response to N starvation, the ecosystem will eventually replenish the fixed N deficit via the remineralization of high N:P from exported organic matter. In theory, the N:P ratio in dissolved nutrients beneath the euphotic zone will increase above the Redfield ratio of 16N:1P, and the subsequent replenishment of surface waters with this high N:P ratio water will serve to repress further N_2 fixation and thereby select against these populations. Because the residence time of nutrients in the top of the thermocline of the North Pacific subtropical gyre is on the order of a few decades, one might predict an episodic selection for, followed by selection against N_2 -fixing microbial assemblages. This feedback will be bounded by the, yet unknown, constraints on the elemental stoichiometry of the full oceanic ecosystem.

Apparently, the HOT program began at or near the beginning of one of these 1–2 decade long episodes of enhanced N_2 fixation and may be moving towards the opposite phase. The best evidence for this comes from a time-series of the N:P ratio for suspended/sinking particulate matter and dissolved matter near the top of the thermocline (200–250 m). The continued production and export of particulate matter with a N:P ratio higher than the Redfield ratio is strong evidence for N_2 fixation (Fig. 10.12). However, at the beginning of the HOT program in 1988, the N:P ratio in the thermocline was approximately 16, which suggests that the biogeochemical trends observed during the HOT program cannot be representative of the longer term (100 yr) climatology. During the 1990s, however, the N:P ratio has increased significantly at a sustained increase equivalent to nearly 3–4 Redfield 'units' per decade (i.e., from a N:P of 16 in 1989 to nearly 20 in 2000). Although N budget estimates suggest that N_2 fixation may presently supply up to half of the N required to sustain particulate matter export from the euphotic zone, these processes are clearly not in steady-state. The relatively high percentage of N_2 -supported production may represent a transient ecosystem state reflecting either oceanic variability or, perhaps, an unusual state established in response to the well-documented, decade-long shift in North Pacific climate (Karl 1999).

There is now ample evidence to suggest that major changes in the structure of the NPSG can occur over decadal time scales (Emerson et al. 2001); both the po-

Fig. 10.12.

The average N:P stoichiometry of suspended particulate matter in the upper (0–100 m) portion of the water column (*top*), the average N:P ratio for exported matter (*center*) collected at 150 m reference depth, and the average N:P ratio for total dissolved matter at the top of the nutricline (200–250 m depth interval) for Sta. ALOHA at the HOT site. Data are presented as three point running mean values ± 1 standard deviation of the mean. The Redfield ratio (N:P = 16) is shown as a horizontal dashed line in all three panels



sitions and intensities of major ocean currents (e.g., Kuroshio Current and extension) and atmospheric circulation features (e.g., Aleutian Low) can have profound effects on ocean biogeochemical processes. However, the precise linkages between climate and the biological carbon pump are not well documented, in part, due to lack of relevant time-series data sets on community structure and carbon fluxes. This altered view of biogeochemical dynamics in the gyre may have a profound influence on how one models ecosystem processes, including the potential impacts of natural or human-induced environmental change and its relationship to carbon sequestration.

Trichodesmium, a non-heterocystous filamentous N_2 -fixing cyanobacterium with buoyancy regulation capabilities, is a major contributor to global N_2 fixation (Capone et al. 1997), especially in subtropical and tropi-

cal marine habitats. It is well known that rates of N_2 fixation by *Trichodesmium*, and perhaps other N_2 fixing microorganisms as well, are enhanced under periods of low turbulence. Massive blooms of *Trichodesmium*, easily recognizable from aircraft and satellites, have been reported during extended periods of low wind and calm seas (Carpenter and Price 1976; Karl et al. 1992). For the NPSG, we have used meteorological data from the NOAA-NDBC buoy #51001 ($23^\circ 24' N, 162^\circ 18' W$) near Sta. ALOHA to hindcast periods that would be conducive for the growth of *Trichodesmium*. We used diel variations in sea surface temperature (ΔT), defined as the daily maximum SST (SST-max) minus the minimum (SST-min), as an indirect measure of the combined influence of wind, wave height and degree of ocean stratification (Karl et al. 1992). During rough periods, ΔT would be small ($<0.2^\circ C$) because of an efficient dis-

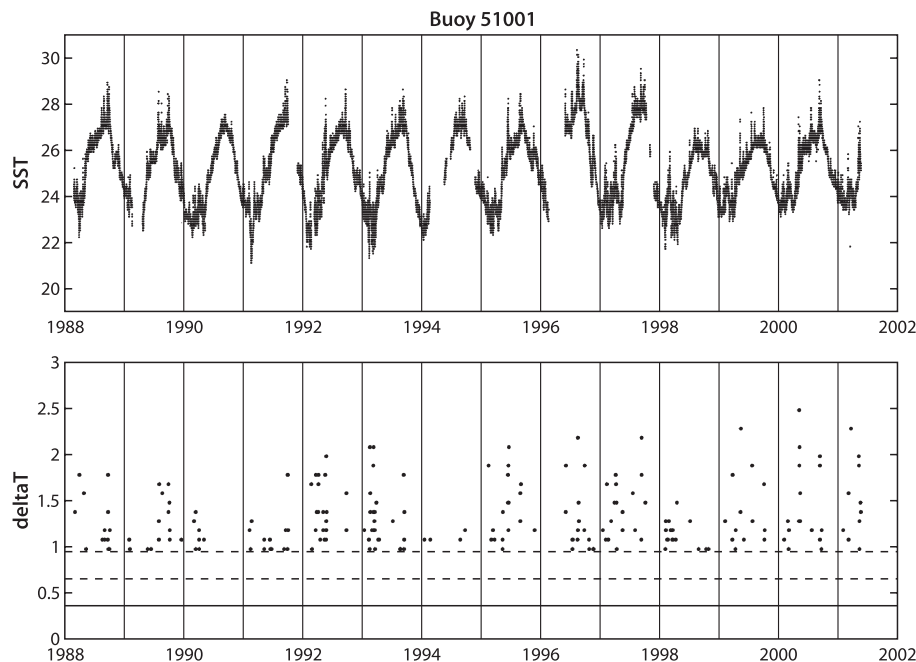


Fig. 10.13. Time-series measurement of sea surface temperature (SST) at the 1 m reference depth in the North Pacific Subtropical Gyre as observed at the NOAA-NDBC 6-m Nomad buoy at 23° 24' N, 162° 16' W. The *panel at the top* shows the full data set during the JGOFS (HOT program) period. In addition to the expected seasonal variability, there are significant interannual differences including the warmer than normal summers in 1996 and 1997 and the colder than normal summers in 1998–2000. The *bottom panel* shows the daily temperature excursions, expressed as ΔT (°C) as determined by daily maximum minus daily minimum SST. The *solid horizontal line* is the mean ΔT for the complete data set (0.36 °C) and the *dashed lines* are the +1 and +2 standard deviations (1 standard deviation = 0.29 °C), respectively for the 13.5 yr climatology. Also shown are those individual data points that are > +2 standard deviations above the mean ΔT . These large temperature excursions reflect well-stratified ocean conditions that are known to be conducive for the growth of N_2 -fixing microorganisms at the HOT site

sipation of the daily solar heating. During calm periods, ΔT can reach values of 2 °C, or greater (Fig. 10.13). This nearly continuous record reveals the following trends: (1) SST has a regular seasonal, as well as irregular interannual and subdecadal trends that are related to climate variations in the North Pacific and, more important for the discussion here; (2) the frequency of large positive ΔT excursions (the frequency of calm seas) has increased during the period of the HOT program investigations (Fig. 10.13). These meteorological data support the biogeochemical data sets and indicate an enhancement of N_2 fixation favorable conditions. While this discussion has focused on *Trichodesmium*, the same mechanism of local habitat stratification, dust deposition and N_2 -fixing cyanobacterial bloom formation would also hold for large diatoms with N_2 -fixing endosymbionts as well as for other free-living N_2 -fixing picocyanobacteria.

With this new general understanding of the meteorological controls on potential rates of N_2 fixation in the NPSG, it may soon be possible to provide forecasts of N_2 -based new production and carbon sequestration by the combined N_2 -primed prokaryote and Fe-stimulated diatom aggregation carbon pumps. A 'hypothetical' forecast might be: "light trade winds with a diurnal SST excursion of 3 °C and a 50% probability of signifi-

cant N_2 fixation, increasing to 90% during periods of aperiodic dust (Fe) deposition!"

Dugdale and Goering (1967) were careful to warn that if N_2 fixation was (later) found to be a quantitatively important pathway for nutrient supply, then a revision of the new vs. recycled N conceptual framework would be necessary; it may now be time for a reconsideration of this paradigm (Karl 2000; Lipschultz et al. 2002). First, the net rate of CO_2 sequestration into the interior portion of the ocean is directly controlled by the source(s) of new N (Fig. 10.3). If the nitrate flux dominates and nitrate is completely removed from the surface ocean, then the bidirectional mass fluxes of C and N would be nearly in balance as predicted by the new production – export production model (i.e., the 'Redfield ratio – dissolved/particulate carbon pump'). On the other hand, if N_2 fixation sustains a significant amount of new and export production in open ocean ecosystems, then net CO_2 will be sequestered (Michaels et al. 2000). Furthermore, N_2 fixation in the world's oceans may be controlled by the atmospheric deposition of Fe and the degree of surface ocean stratification, both of which are variable, climate sensitive parameters (see also Case Study 4). Total atmospheric dust transport is also affected by humankind, including population demographics, global economies and land use patterns. These

complex natural and anthropogenic interactions, with multiple potential feedback loops, provide a mechanism for biogeochemical variability in otherwise 'stable and homogeneous' biomes. In this regard, the seascape even in remote regions may be strongly influenced by the landscape, and there is no question that the latter has changed significantly over the past 250 years.

10.5.4 Case Study 4:

OSP Ecosystem Dynamics and the Role of Iron

During the 25 year weathershipe era, temperature, salinity, dissolved inorganic nutrients, chlorophyll *a* (Chl *a*) and zooplankton were sampled at OSP. This excellent temporal coverage firmly established the annual biogeochemical cycle. This cycle is presented in detail by Whitney and Freeland (1999), so only the highlights are summarized here. In the winter, winds average 12 m s⁻¹ and the surface waters are mixed to about 120 m. Surface temperature reaches a minimum of 5–6 °C and maximum winter nitrate and silicate are 15.8 ± 2.3 and 24.0 ± 3.4 μM, respectively; winter Chl *a* is approximately 0.2 μg l⁻¹. As radiant energy increases in spring, and the mixed-layer shoals, Chl *a* increases from 0.2 to 0.4 μg l⁻¹, but, in contrast to the North Atlantic Ocean, no significant 'spring bloom' occurs.

OSP is a good example of an HNLC region, poised to fuel the biological carbon pump, but not currently functioning at maximum capacity. Initially it was thought that mesozooplankton grazing was responsible for the lack of a spring bloom, but this hypothesis was tested and rejected during the SUPER research program (Frost 1987). More recently, it has been suggested that dissolved Fe, present at a concentration of approximately 0.1 nM (Martin and Fitzwater 1988), limits the growth of large bloom forming diatoms and, thereby controls the efficiency of the biological carbon pump. Despite daily summertime production rates of 500–600 mg C m⁻² d⁻¹, the phytoplankton community consists mainly of nanoflagellates that utilize primarily ammonium, not nitrate (Harrison et al. 1999).

At the beginning of the Canadian JGOFS OSP project in 1992, the issue of Fe limitation was not broadly accepted (Banse 1990; Miller et al. 1991; Miller 1993). During the early 1990s, further shipboard Fe enrichment experiments by Boyd and colleagues confirmed that Fe limitation did limit the drawdown of nitrate in May and September experiments (Boyd et al. 1996). When Fe was added in their experiments, mainly large (>18 μm) pennate diatoms (primarily *Pseudonitzschia* sp.) grew up, confirming the Martin and Fitzwater (1988) observations. Iron limitation was also confirmed by an increase in the molecular biomarker for Fe limitation, flavodoxin (LaRoche et al. 1996). In February, when Boyd added Fe, little or no increase in Chl *a* was obtained after a 5 day

incubation and it was suggested that light may be a co-limiting factor along with Fe (Boyd et al. 1996). This suggestion was later confirmed by Maldonado et al. (1999) who demonstrated co-limitation of phytoplankton growth by Fe and light during winter.

In contrast to the classical phytoplankton-mesozooplankton food chain paradigm of the 1970s, it is now necessary to have two nitrogen sources and two size fractions of phytoplankton and zooplankton to explain the ecosystem dynamics at OSP (Harrison et al. 1999). The large phytoplankton (mainly pennate diatoms) exhibit bottom-up control by Fe, while the small phytoplankton exhibit top down control by microzooplankton grazing. The large phytoplankton increase quickly when Fe is deposited and they grow rapidly until nitrate and silicate are used up. They are not rapidly assimilated into the food web (Boyd et al. 1999), and therefore they aggregate and sink out of the euphotic zone after the limiting nutrient has been exhausted, thereby enhancing carbon export and sequestration (Fig. 10.2 and 10.3). Apparently there is an ammonium inhibition of nitrate uptake by small (<2 μm) phytoplankton cells (Varela and Harrison 1999a), and an iron limitation of nitrate uptake by larger (>2 μm) phytoplankton cells, including diatoms (Harrison et al. 1999). Fe is not required for ammonium or urea assimilation, but it is needed for growth on nitrate. Large diatoms cannot compete with the smaller cells for the uptake of ammonium and possibly urea also, so Fe availability controls the metabolic activity and growth of large diatoms.

Interannual variation in nitrate and silicate has been well documented in the 1970s due to the weekly sampling by weathershipe personnel (Whitney et al. 1998). During the summers of 1972, 1976 and 1979, silicate was depleted to <1 μM compared to the longer term climatology of about 10 μM (Wong and Matear 1999). Both 1972 and 1976 were high silicate and nitrate utilization years, while 1976 had low nitrate utilization relative to silicate utilization. It has been suggested that these periods of complete removal of silicate and nitrate may be manifestations of a large, pulsed Fe deposition event, but no direct evidence is available. The dominant source of new Fe is atmospheric deposition (Duce and Tindale 1991); episodic storm events over China lead to dust transport and fallout into the NE Pacific less than one week later. Because the NE subarctic Pacific is a Fe-limited ecosystem, pulsed deposition of bioavailable Fe from atmospheric sources would be expected to result in pulses of primary production, selection for large diatoms and a subsequent export pulse of organic matter, including biogenic silica. This Fe supply – carbon export prediction was tested by Boyd et al. (1998) using field data from OSP. While an explicit cause-and-effect could not be firmly established due to the episodic timing and short duration of the dust deposition events, historical data showing an aperiodic, order of magnitude, increase

in mixed-layer chlorophyll and the flux patterns from bottom-moored sediment traps (which had a continuous record of pulsed export events) suggest a frequency of approximately three to five major dust events per decade. With this superannual frequency, the design of the field sampling program would need to be carefully evaluated and reliance on remote, continuous instrumentation imperative. While emphasis has been on atmospheric inputs of Fe from dust, transport of coastal waters offshore cannot be ruled out. Even though drifter studies show that surface water transport at OSP is eastward (i.e., shoreward; Bograd et al. 1999), recent TOPEX/POSEIDON satellite images show that very large eddies (~200 km in diameter) form near the southwest corner of the Queen Charlotte Islands and move offshore in the direction of OSP (Thomson and Gower 1998). These eddies could carry Fe-rich coastal water seaward and they could explain the increases in Chl *a* that are occasionally observed along Line P (Harrison et al. 1999).

A warming of 1.2 °C per century and freshening of 0.2 psu per century in the surface waters has been estimated for OSP (Freeland et al. 1997). From these data, they calculated that the mean mixed-layer depth has also decreased significantly from 130 m in the 1960s to 100 m in the late 1990s. Whitney and Freeland (1999) compared the nitrate and silicate concentrations of the 1970s to the 1990s and observed that the winter nitrate has decreased by 2.5 μM and silicate by 3.6 μM. Their removal rate between February and September has declined from 7.8 to 6.5 μM NO₃ and 8.5 to 6.0 μM Si (Si:NO₃ ratio decreased from 1.08 to 0.92). The larger decrease in silicate uptake (29%) relative to the decrease in nitrate uptake (17%) indicates that there was a marked decrease in diatom growth, suggesting that the supply of Fe to these latitudes may have also declined during these two decades, or a shift in diatom community composition to species having lower Si:N ratios. The decrease in the mixed-layer depth likely explains the decrease in the winter nutrient concentrations, but one would expect an increase in Fe because the atmospherically deposited Fe would be mixed into a smaller volume of surface water.

The critical role of large, eukaryotic phytoplankton (especially large diatoms) in the production of exportable particulate matter cannot be overstated (see Fig. 10.2 and 10.3), and in this context the importance of aperiodic, pulsed events is paramount. However, Legendre and Le Fèvre (1989) have already shown that there is no a priori direct equivalence between the new production and export production concepts. The former concerns particulate matter production by photoautotrophs and the latter is controlled by the creation of large, relatively dense sinking particles by numerous trophic levels and processes. Consequently, the formation of a near surface phytoplankton bloom via natural fertilization by micro- or macronutrient addition is probably a necessary but insufficient condition to result in pulsed car-

bon export. Documentation of the export phase of the implied production-export process is as important as the documentation of the growth phase. Furthermore, the fate of these export pulses is critical to the geochemical implications of blooms.

At Sta. ALOHA, there also appears to be an episodic, but recurrent, diatom aggregation-sinking event in late summer of every year (Scharek et al. 1999a, 1999b). This could be the manifestation of a N₂-primed 'echo' bloom following disappearance, by autolysis, of the seasonally accumulated, N₂-fixing microbial assemblage, or could be the de novo growth of eukaryotic phytoplankton (including diatoms) following the episodic deposition of bioavailable Fe (e.g., DiTullio and Laws 1991). Regardless of the mechanism, the diatom species selected under these oligotrophic conditions (summertime at Sta. ALOHA) are mostly those with endosymbiotic N₂-fixing cyanobacteria. The aggregates that are formed eventually, upon nutrient exhaustion (Fe, P or Si) sink rapidly (>200 m d⁻¹) and reach the 5 000-m seabed as 'bioavailable' organic matter (e.g., Fig. 10.3c). These large, exportable N₂-supported organic aggregates also remove bioavailable Fe and P that would otherwise be retained in the euphotic zone by efficient grazing and remineralization processes. Because of the rapid sinking rates and high percentage of living biomass, these aggregates also largely escape mesopelagic zone mineralization and carry their exported carbon and associated bioelements to the abyss (Fig. 10.3c). This dramatic diatomic diatom dump emphasizes the importance of episodic export in the NPSG, and the complexities of modeling an ecosystem where high-export cell aggregation and low-export microbial loop processes can occur simultaneously, and probably in direct competition.

Natural or artificial Fe fertilization of both HNLC and LNLc ocean regions could, theoretically, lead to an increase in the ocean's capacity to assimilate atmospheric CO₂ but by different ecological processes. In high latitude HNLC regions like OSP, the pulsed Fe additions would lead to the growth and eventual export of large pennate diatoms, as discussed above. In the LNLc subtropical gyres like HOT, the effect is less direct and is manifest through a stimulation of N₂-fixing microorganisms and a change in the total stock of nitrate in the ocean. This combined N₂-primed prokaryote and Fe-stimulated diatom aggregation carbon pump (see Fig. 10.3c) may be one of the most efficient export processes in the sea.

10.6 Beyond JGOFs: a Prospectus

All biogeochemical processes in the sea reside in a temporal domain and each process has characteristic time scales of variability. A major achievement of the Joint

Global Ocean Flux Study (JGOFS) is an improved understanding of the time-varying fluxes of carbon and associated biogenic elements, both within the ocean and the exchanges of carbon between the ocean and the atmosphere. This legacy derives, in part, from a network of ocean time-series stations located in representative biogeochemical provinces ranging from low-latitude, subtropical ocean gyres to high latitude coastal and oceanic regions. The JGOFS time-series programs were designed to capture low frequency (>1 year) changes, stochastic events and complex processes that may have multiple causes and unconstrained biogeochemical consequences. A basic underpinning of these time-series programs is the ecosystem concept; by investigating selected habitats and their inhabitants, and by conducting relevant cross-ecosystem inter-comparisons, a general ecological understanding will emerge.

Significant biogeochemical features include variations in the mechanisms of nutrient supply, especially the ecological consequences of 'pulsed' nutrient delivery including atmospheric dust (Fe), mesoscale eddy-induced upwelling of nutrients, and the nitrification of low latitude regions in the absence of turbulence (e.g., enhanced N₂ fixation). In this regard, microbial community structure is one of the most important ecosystem variables for predicting carbon export. Additionally, the bioelemental stoichiometry of exported organic matter (i.e., the C:N:P:Si:Ca:Fe ratio), and the selective remineralization of particles beneath the euphotic zone (i.e., C vs. P regeneration length scales) together constrain the efficiency the biological pump as a mechanism for the net sequestration of atmospheric carbon dioxide. The decoupling of primary organic matter production, particulate matter export and remineralization processes in time and space, and the detection of decade-scale, climate-driven ecosystem perturbations and feedbacks combine to reveal a time-varying, biogeochemical complexity that is just now becoming evident in our independent ocean time-series data sets.

A crucial issue as existing time-series programs mature, is data management as well as timely, user-friendly data accessibility. A related issue – that of data ownership – is less straightforward but equally important. Beyond careful archiving and peer review publication, the long-term data sets should be used to generate new ideas that serve as the basis for controlled experimentation or other forms of hypothesis testing (Coull 1985). Generation of hypotheses by systematic analyses of the collected data is as important as the subsequent hypothesis-testing. Science must be the driving force if any time-series program is to succeed beyond a few years. As G. Likens (1983) concluded, "A real danger of long-term research with reliable funding is that it could become static, pedantic, generally uninteresting and unproductive." These JGOFS era ocean observation programs have

already yielded invaluable ecological insights even without deliberate manipulation or other forms of direct hypothesis-testing. Nevertheless it is apparent that whole ecosystem experiments would add further to the value of the field programs, and in this regard their introduction to these ongoing time-series research portfolios would be desirable. Furthermore, these sites provide invaluable research opportunities for other scientists, and the ongoing encouragement of extensive ancillary programs helps to keep the science of these time-series stations timely and interdisciplinary.

JGOFS did not begin as a field program focused on Fe control of carbon export, non-Redfield organic matter production stoichiometry, N₂ fixation or the physiological ecology of the recently discovered planktonic *Archaea*, but these are important biogeochemical issues in the twilight of JGOFS era. Quite frankly, without many of the JGOFS time-series data sets that presently exist, we would have never questioned the extant ecological paradigms, or realized that new ecological understanding was even needed. As the JGOFS era of ocean exploration comes to a close, new observational and hypothesis-driven research programs must emerge to assimilate and extend these retired and ongoing field studies. Planning is now underway for the development of a complementary set of integrated measurements including satellite altimetry (Jason), a global array of profiling floats (Argo) and a network of fixed point time-series stations. The eventual establishment of a comprehensive global ocean observation network of key biogeochemical parameters would provide unlimited opportunities for basic and applied research, ocean climate prediction and for marine science education. Human-operated time-series stations will be the intellectual heart and soul of this new age of ocean exploration.

Acknowledgements

Sufficient space does not exist to express the collective debt of gratitude that we owe to the numerous scientists, technical staff, computer specialists/data managers, students and ship officers and crew who have assisted in the collection, analysis and interpretation of our respective time-series data sets. We likewise thank our various public and private sector sponsors for their generous financial support of the time-series programs. The lead author thanks L. Lum and L. Fujieki for their assistance with the preparation of text, tables and graphics, and C. Benitez-Nelson and K. Björkman for their helpful comments on an earlier draft of the chapter. Finally, we thank Professor Michael Fasham for his efforts compiling this volume, and for his kind patience during our long gestation period. This is US JGOFS contribution #768.

References

- Anderson LA, Sarmiento JL (1994) Redfield ratios of remineralization determined by nutrient data analysis. *Global Biogeochem Cy* 8:65–80
- Baines SB, Pace ML, Karl DM (1994) Why does the relationship between sinking flux and planktonic primary production differ between lakes and oceans? *Limnol Oceanogr* 39:213–226
- Banse K (1990) Does iron really limit phytoplankton production in the offshore subarctic Pacific? *Limnol Oceanogr* 35:772–775
- Barlow M, Nigam S, Berbery EH (2001) ENSO, Pacific decadal variability, and U.S. summertime precipitation, drought, and stream flow. *J Climate* 14:2105–2128
- Bates NR (2001) Interannual variability of oceanic CO₂ and biogeochemical properties in the Western North Atlantic subtropical gyre. *Deep-Sea Res Pt II* 48:1507–1528
- Bates NR, Michaels AF, Knap AH (1996a) Alkalinity changes in the Sargasso Sea: geochemical evidence of calcification? *Mar Chem* 51:347–358
- Bates NR, Michaels AF, Knap AH (1996b) Seasonal and interannual variability of oceanic carbon dioxide species at the U.S. JGOFS Bermuda Atlantic Time-series Study (BATS) site. *Deep-Sea Res Pt II* 43:347–383
- Bates NR, Michaels AF, Knap AH (1996c) Spatial variability of CO₂ species in the Sargasso Sea. *Caribb J Sci* 32:303–304
- Bates NR, Takahashi T, Chipman DW, Knap AH (1998) Variability of pCO₂ on diel to seasonal timescales in the Sargasso Sea. *J Geophys Res* 103:15567–15585
- Benitez-Nelson C, Buesseler KO, Karl DM, Andrews J (2001) A time-series study of particulate matter export in the North Pacific Subtropical Gyre based on ²³⁴Th:²³⁸U disequilibrium. *Deep-Sea Res Pt I* 48:2595–2611
- Bograd SJ, Thomson RE, Rabinovich AB, Leblond PH (1999) Near-surface circulation of the northeast Pacific Ocean derived from WOCE-SVP satellite-tracked drifters. *Deep-Sea Res Pt II* 46:2371–2403
- Boyd P, Harrison PJ (eds) (1999a) Canadian JGOFS in the NE Subarctic Pacific. *Deep-Sea Res Pt II* special issue, vol. 46, issue 11–12, pp 2345–3017, Elsevier Science, Oxford, UK
- Boyd P, Harrison PJ (1999b) Phytoplankton dynamics in the NE subarctic Pacific. *Deep-Sea Res Pt II* 46:2405–2432
- Boyd PW, Muggli DL, Varela DE, Goldblatt RH, Chretien R, Orians KJ, Harrison PJ (1996) In vitro iron enrichment experiments in the NE subarctic Pacific. *Mar Ecol Prog Ser* 136:179–193
- Boyd PW, Wong CS, Merrill J, Whitney F, Snow J, Harrison PJ, Gower J (1998) Atmospheric iron supply and enhanced vertical carbon flux in the NE subarctic Pacific: Is there a connection? *Global Biogeochem Cy* 12:429–441
- Boyd PW, Goldblatt RH, Harrison PJ (1999) Mesozooplankton grazing manipulations during in vitro iron enrichment studies in the NE subarctic Pacific. *Deep-Sea Res Pt II* 46:2645–2668
- Buesseler KO (1998) The decoupling of production and particle export in the surface ocean. *Global Biogeochem Cy* 12:297–310
- Capone DG, Zehr JP, Paerl HW, Bergman B, Carpenter EJ (1997) *Trichodesmium* a globally significant marine cyanobacterium. *Science* 276:1221–1229
- Carlson CA, Ducklow HW, Michaels AF (1994) Annual flux of dissolved organic carbon from the euphotic zone in the northwestern Sargasso Sea. *Nature* 371:405–408
- Carpenter EJ, Price CC IV (1976) Marine *Oscillatoria* (*Trichodesmium*): explanation for aerobic nitrogen fixation without heterocysts. *Science* 191:1278–1280
- Chao SY, Shaw PT, Wu SY (1996) El Niño modulation of the South China Sea circulation. *Prog Oceanogr* 38:51–93
- Chelton DB, Bernal PA, McGowan JA (1982) Large-scale interannual physical and biological interaction in the California Current. *J Mar Res* 40:1095–1125
- Christian JR, Lewis MR, Karl DM (1997) Vertical fluxes of carbon, nitrogen and phosphorus in the North Pacific Subtropical gyre near Hawaii. *J Geophys Res* 102:15667–15677
- Coale KH, Bruland KW (1987) Oceanic stratified euphotic zone as elucidated by ²³⁴Th:²³⁸U disequilibria. *Limnol Oceanogr* 32:189–200
- Conte MH, Ralph N, Ross EH (2001) Seasonal and interannual variability in deep ocean particle fluxes at the Oceanic Flux Program (OFF)/Bermuda Atlantic Time Series (BATS) site in the western Sargasso Sea near Bermuda. *Deep-Sea Res Pt II* 48:1471–1505
- Copin-Montégut C (2000) Consumption and production on scales of a few days of inorganic carbon, nitrate and oxygen by the planktonic community: results at the Dyfamed Station in the northwestern Mediterranean Sea (May 1995). *Deep-Sea Res Pt I* 47:447–477
- Copin-Montégut C, Begovic M (2002) Distributions of carbonate properties and oxygen along the water column (0–2000 m) in the central part of the Northwestern Mediterranean Sea (Dyfamed site). Influence of the winter vertical mixing on air-sea CO₂ and O₂ exchanges. *Deep-Sea Res Pt II* 49:2049–2066
- Coull BC (1985) The use of long-term biological data to generate testable hypotheses. *Estuaries* 8:84–92
- Cullen JJ, Franks PJS, Karl DM, Longhurst A (2002) Physical influences on marine ecosystem dynamics. In: Robinson AR, McCarthy JJ, Rothschild BJ (eds) *The sea*, vol. 12. John Wiley & Sons, New York, pp 297–336
- Davenport R, Neuer S, Hernández-Guerra A, Rueda MJ, Llinás O, Fischer G, Wefer G (1999) Seasonal and interannual pigment concentration in the Canary Islands region from CZCS data and comparison with observations from ESTOC. *Int J Remote Sens* 20:1419–1433
- Deuser WG (1986) Seasonal and interannual variations in deep-water particle fluxes in the Sargasso Sea and their relation to the surface hydrography. *Deep-Sea Res Pt I* 33:225–246
- Dickey T, Zedler S, Yu X, Doney SC, Frye D, Jannasch H, Manov D, Sigurdson D, McNeil JD, Dobeck L, Gilboy T, Bravo C, Siegel DA, Nelson N (2001) Physical and biogeochemical variability from hours to years at the Bermuda Testbed Mooring site: June 1994–March 1998. *Deep-Sea Res Pt II* 48:2105–2140
- Diggle PJ (1990) *Time series: a biostatistical introduction*. Oxford University Press, New York, 257 pp
- DiTullio GR, Laws EA (1991) Impact of an atmospheric-oceanic disturbance on phytoplankton community dynamics in the North Pacific Central gyre. *Deep-Sea Res Pt I* 38:1305–1329
- Dore JE, Carrillo CJ, Hebel DV, Karl DM (2002) Carbon cycle observations at the Hawaii Ocean Time-series Station ALOHA. In: Nojiri Y, Feely R (eds) *Proceedings of the PICES North Pacific CO₂ Data Synthesis Symposium*, Tsukuba, Japan, October 2000 (in press)
- Duce RA, Tindale NW (1991) Atmospheric transport of iron and its deposition in the ocean. *Limnol Oceanogr* 36:1715–1726
- Dugdale RC, Goering JJ (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol Oceanogr* 12:196–206
- Emerson S, Quay PD, Stump C, Wilbur D, Knox M (1991) O₂, Ar, N₂ and ²²²Rn in surface waters of the subarctic ocean: net biological O₂ production. *Global Biogeochem Cy* 5:49–69
- Emerson S, Quay PD, Stump C, Wilbur D, Schudlich R (1995) Chemical tracers of productivity and respiration in the subtropical Pacific Ocean. *J Geophys Res* 100:15,873–15,887
- Emerson S, Quay P, Karl D, Winn C, Tupas L, Landry M (1997) Experimental determination of the organic carbon flux from open-ocean surface waters. *Nature* 389:951–954
- Emerson S, Mecking S, Abell J (2001) The biological pump in the subtropical North Pacific Ocean: nutrient sources, Redfield ratios, and recent changes. *Global Biogeochem Cy* 15:535–554
- Eppley RW, Peterson BJ (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282:677–680
- Falkowski PG, Barber RT, Smetacek U (1998) Biogeochemical controls and feedbacks on ocean primary production. *Science* 281:200–206
- Freeland HJ, Denman K, Whitney F, Jacques R (1997) Evidence of change in the mixed layer in the northeast Pacific Ocean. *Deep-Sea Res Pt I* 44:2117–2129

- Freudenthal T, Neuer S, Meggers H, Davenport R, Wefer G (2001) Influence of lateral particle advection and organic matter degradation on sediment accumulation and stable nitrogen isotope ratios along a productivity gradient in the Canary Islands region. *Mar Geol* 177:93–109
- Frost BW (1987) Grazing control of phytoplankton stock in the open subarctic Pacific Ocean: a model assessing the role of mesozooplankton, particularly the large calanoid copepods *Neocalanus* spp. *Mar Ecol Prog Ser* 39:49–68
- Goes JI, Saino T, Gomes HR, Ishizaka J, Nojiri Y, Wong CS (1999) A comparison of new production in the north Pacific ocean for 1997 and 1998 estimated from remotely sensed data. In: Nojiri Y (ed) Proceedings of the 2nd International symposium on CO₂ in the Oceans. NIES, Tsukuba, Japan, pp 141–146
- Gruber N, Sarmiento JL (1997) Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochem Cy* 11:235–266
- Guidi-Guilvard LD (2002) DYFAMED-BENTHOS, a long time-series benthic survey at 2347 m depth in the NW Mediterranean: general introduction. *Deep-Sea Res Pt II* 49:2183–2193
- Hansell DA, Carlson CA, Bates NR, Poisson A (1997) Horizontal and vertical removal of organic carbon in the equatorial Pacific Ocean: a mass balance assessment. *Deep-Sea Res Pt II* 44:2115–2130
- Harrison PJ, Boyd PW, Varela DE, Takeda S, Shiimoto A, Odate T (1999) Comparison of factors controlling phytoplankton productivity in the NE and NW subarctic Pacific gyres. *Prog Oceanogr* 43:205–234
- Hayward TL, Venrick EL, McGowan JA (1983) Environmental heterogeneity and plankton community structure in the central North Pacific. *J Mar Res* 41:711–729
- Jeandel C, Ruiz-Pino D, Gjata E, Poisson A, Brunet C, Charriaud E, Dehairs F, Delille D, Fiala M, Fravallo C, Miquel JC, Park Y-H, Pondaven P, Quéguiner B, Razouls S, Shauer B, Tréguer P (1999) KERFIX, a time-series station in the Southern Ocean: a presentation. *J Marine Syst* 17:555–569
- Jenkins WJ (1982) Oxygen utilization rates in North Atlantic subtropical gyre and primary production in oligotrophic systems. *Nature* 300:246–248
- Jenkins WJ, Goldman J (1985) Seasonal oxygen cycling and primary production in the Sargasso Sea. *J Mar Res* 43:465–491
- Karl DM (1999) A sea of change: Biogeochemical variability in the North Pacific subtropical gyre. *Ecosystems* 2:181–214
- Karl DM (2000) A new source of 'new' nitrogen in the sea. *Trends Microbiol* 8:301
- Karl DM, Lukas R (1996) The Hawaii Ocean Time-series (HOT) program: background, rationale and field implementation. *Deep-Sea Res Pt II* 43:129–156
- Karl DM, Winn CD (1991) A sea of change: monitoring the ocean's carbon cycle. *Environ Sci Technol* 25:1976–1981
- Karl DM, Letelier R, Hebel DV, Bird DF, Winn CD (1992) *Trichodesmium* blooms and new nitrogen in the North Pacific gyre. In: Carpenter EJ, et al. (eds) Marine pelagic cyanobacteria: *Trichodesmium* and other Diazotrophs. Kluwer Academic, Dordrecht, pp 219–237
- Karl DM, Christian JR, Dore JE, Hebel DV, Letelier RM, Tupas LM, Winn CD (1996) Seasonal and interannual variability in primary production and particle flux at Station ALOHA. *Deep-Sea Res Pt II* 43:539–568
- Karl D, Letelier R, Tupas L, Dore J, Christian J, Hebel D (1997) The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* 388:533–538
- Karl DM, Bidigare RR, Letelier RM (2001a) Long-term changes in plankton community structure and productivity in the North Pacific Subtropical Gyre: the domain shift hypothesis. *Deep-Sea Res Pt II* 48:1449–1470
- Karl DM, Björkman KM, Dore JE, Fujieki L, Hebel DV, Houlihan T, Letelier RM, Tupas LM (2001b) Ecological nitrogen-to-phosphorus stoichiometry at station ALOHA. *Deep-Sea Res Pt II* 48:1529–1566
- Karl DM, Michaels A, Bergman B, Capone D, Carpenter E, Letelier R, Lipschultz F, Paerl H, Sigman D, Stal L (2002) Dinitrogen fixation in the world's oceans. *Biogeochemistry* 57/58:47–98
- Knauer GA, Martin JH, Bruland KW (1979) Fluxes of particulate carbon, nitrogen and phosphorus in the upper water column of the northeast Pacific. *Deep-Sea Res Pt I* 26:97–108
- Knauer GA, Redalje DG, Harrison WG, Karl DM (1990) New production at the VERTEX time-series site. *Deep-Sea Res Pt I* 37:1121–1134
- Lampitt RS (1985) Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Res Pt I* 32:885–897
- LaRoche J, Boyd PW, McKay RML, Gelder RJ (1996) Flavodoxin as in situ marker for iron stress in phytoplankton. *Nature* 382:802–805
- Laws E, Falkowski P, Smith WO, Ducklow H, McCarthy JJ (2000) Temperature effects on export production in the open ocean. *Global Biogeochem Cy* 14:1231–1246
- Laws EA, Bannister TT (1980) Nutrient- and light-limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the ocean. *Limnol Oceanogr* 25:457–473
- Lee K (2001) Global net community production estimated from the annual cycle of surface water total dissolved inorganic carbon. *Limnol Oceanogr* 46:1287–1297
- Legendre L, Le Fèvre J (1989) Hydrodynamical singularities as controls of recycled versus export production in oceans. In: Berger WH, Smetacek VS, Wefer G (eds) Productivity of the ocean: present and past. John Wiley & Sons, New York, pp 49–63
- Likens GE (1983) A priority for ecological research. *Bull Ecol Soc Am* 64(4):234–243
- Lipschultz FJ, Bates NR, Carlson CA, Hansell DA (2002) New production in the Sargasso Sea: history and current status. *Global Biogeochem Cy* (in press)
- Liu AK, Chang YS, Hsu MK, Liang NK (1998) Evolution of nonlinear internal waves in the East and South China Seas. *J Geophys Res* 103:7995–8008
- Longhurst AR, Harrison WG (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. *Prog Oceanogr* 22:47–123
- Louanchi F, Ruiz-Pino DP, Poisson A (1999) Temporal variations of mixed-layer oceanic CO₂ at JGOFS-KERFIX time-series station: physical versus biogeochemical processes. *J Mar Res* 57: 165–187
- Maldonado MT, Boyd PW, Harrison PJ, Price NM (1999) Co-limitation of phytoplankton growth by light and Fe during winter in the subarctic Pacific Ocean. *Deep-Sea Res Pt II* 46:2475–2485
- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *B Am Meteorol Soc* 78:1069–1079
- Margalef R (1978) Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol Acta* 1:493–509
- Martin JH, Fitzwater SE (1988) Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature* 331:341–343
- Martin JH, Knauer GA, Karl DM, Broenkow WW (1987) VERTEX: carbon cycling in the northeast Pacific. *Deep-Sea Res Pt I* 34:267–285
- Martinez L, Silver MW, King JM, Alldredge AL (1983) Nitrogen fixation by floating diatom mats: a source of new nitrogen to oligotrophic ocean waters. *Science* 221:152–154
- Marty JC, Chiavérini J, Pizay MD, Avril B (2002) Seasonal and inter-annual dynamics of nutrients and phytoplankton pigments in the Western Mediterranean Sea at the DYFAMED time-series station (1991–1999). *Deep-Sea Res Pt II* 49:1965–1985
- McCave IN (1975) Vertical flux of particles in the ocean. *Deep-Sea Res Pt I* 22:491–502
- McGillicuddy DJ, Robinson AR, Siegel DA, Jannasch HW, Johnson R, Dickey TD, McNeil JD, Michaels AF, Knap AH (1998) New evidence for the impact of mesoscale eddies on biogeochemical cycling in the Sargasso Sea. *Nature* 394:263–265
- McGillicuddy DJ Jr., Johnson RJ, Siegel DA, Michaels AF, Bates N, Knap AH (1999) Mesoscale variability of ocean biogeochemistry in the Sargasso Sea. *J Geophys Res* 104:13381–13394
- Michaels A, Knap A (1996) Overview of the U.S.-JGOFS Bermuda Atlantic Time-series Study and Hydrostation S program. *Deep-Sea Res Pt II* 43:157–198
- Michaels AF, Bates NR, Bueseler KO, Carlson CA, Knap AH (1994) Carbon-cycle imbalances in the Sargasso Sea. *Nature* 372:537–540
- Michaels AF, Olson D, Sarmiento JL, Ammerman JW, Fanning K, Jahnke R, Knap AH, Lipschultz F, Prospero JM (1996) Inputs, losses and transformations of nitrogen and phosphorus in the pelagic North Atlantic Ocean. *Biogeochemistry* 35:181–226

- Michaels AF, Karl DM, Knap AH (2000) Temporal studies of biogeochemical dynamics in oligotrophic oceans. In: Hanson RB, Ducklow HW, Field JG (eds) *The changing ocean carbon cycle: a midterm synthesis of the Joint Global Ocean Flux Study*. Cambridge University Press, Cambridge, UK, pp 392–413
- Migon C, Sandroni V, Marty JC, Gasser B, Miquel JC (2002) Transfer of atmospheric matter through the euphotic layer in the northwestern Mediterranean: seasonal pattern and driving forces. *Deep-Sea Res Pt II* 49:2125–2141
- Miquel JC, Fowler SW, LaRosa J, Buat-Menard P (1994) Dynamics of the downward flux of particles and carbon in the open northwestern Mediterranean sea. *Deep-Sea Res I* 41:243–261
- Miller CB (1993) Pelagic production processes in the subarctic Pacific. *Prog Oceanogr* 32:1–15
- Miller CB, Frost BW, Wheeler PA, Landry ML, Welschmeyer N, Powell TM (1991) Ecological dynamics in the subarctic Pacific, a possibly iron-limited system. *Limnol Oceanogr* 33:1600–1615
- Neuer S, Ratmeyer V, Davenport R, Fischer G, Wefer G (1997) Deep water particle flux in the Canary Island region: seasonal trends in relation to long-term satellite derived pigment data and lateral sources. *Deep-Sea Res Pt I* 44:1451–1466
- Noriki S (1999) Particulate fluxes at Stn. KNOT in the western North Pacific during 1988–1991. In: Nojiri Y (ed) *Proceedings of the 2nd International Symposium on CO₂ in the Oceans*. National Institute for Environmental Studies, Tsukuba, Japan, pp 331–337
- Ono S, Najjar R, Ennyu A, Bates NR (2001) Shallow remineralization in the Sargasso Sea estimated from seasonal variations in oxygen and dissolved inorganic carbon. *Deep-Sea Res Pt II* 48:1567–1582
- Pace ML, Knauer GA, Karl DM, Martin JH (1987) Primary production, new production and vertical flux in the eastern Pacific Ocean. *Nature* 325:803–804
- Platt T, Harrison WG (1985) Biogenic fluxes of carbon and oxygen in the ocean. *Nature* 318:55–58
- Redfield AC, Ketchum BH, Richards FA (1963) The influence of organisms on the composition of seawater. In: Hill MN (ed) *The sea, ideas and observations on progress in the study of the seas*, vol. 2. Interscience, New York, pp 26–77
- Rhee G-Y (1978) Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnol Oceanogr* 23:10–25
- Risser PG (ed) (1991) *Long-term ecological research: an international perspective*. John Wiley & Sons, New York, 294 pp
- Sakshaug E, Holm-Hansen O (1977) Chemical composition of *Skeletonema costatum* (Grev.) Cleve and *Pavlova (Monochrysis) lutheri* (Droop) Green as a function of nitrate-, phosphate-, and iron-limited growth. *J Exp Mar Biol Ecol* 29:1–34
- Scharek R, Tupas LM, Karl DM (1999a) Diatom fluxes to the deep sea in the oligotrophic North Pacific gyre at Station ALOHA. *Mar Ecol Prog Ser* 182:55–67
- Scharek R, Latasa M, Karl DM, Bidigare RR (1999b) Temporal variations in diatom abundance and downward vertical flux in the oligotrophic North Pacific gyre. *Deep-Sea Res Pt I* 46:1051–1075
- SCOR (1990) *Oceans, carbon and climate change: an introduction to the Joint Global Ocean Flux Study*. Scientific Committee on Oceanic Research, Halifax, Canada, 61 pp
- Shaw P-T, Chao S-Y (1994) Surface circulation in the South China Sea. *Deep-Sea Res Pt I* 41:1663–1683
- Shaw P-T, Chao S-Y, Liu K-K, Pai S-C, Liu C-T (1996) Winter upwelling off Luzon in the north-eastern South China Sea. *J Geophys Res* 101:16435–16448
- Shiah F-K, Liu K-K, Tang TY (1999) South East Asia Time-series Station established in South China Sea. *U.S. JGOFS Newsletter* 10(1):8–9
- Siegel DA, Fields E, McGillicuddy DJ Jr. (1999) Mesoscale motions, satellite altimetry and new production in the Sargasso Sea. *J Geophys Res* 104:13,359–13,379
- Siegel DA, Karl DM, Michaels AF (2001) Interpretations of biogeochemical processes from the US JGOFS Bermuda and Hawaii time-series sites. *Deep-Sea Res Pt II* 48:1403–1404
- Smith CR, Hoover DJ, Doan SE, Pope RH, DeMaster DJ, Dobbs FC, Altabet MA (1996) Phytodetritus at the abyssal seafloor across 10° of latitude in the central equatorial Pacific. *Deep-Sea Res Pt II* 43:1309–1338
- Spitzer WS, Jenkins WJ (1989) Rates of vertical mixing, gas exchange and new production: estimates from seasonal gas cycles in the upper ocean near Bermuda. *J Mar Res* 47:169–196
- Steinberg DK, Carlson CA, Bates NR, Goldthwait SA, Madin LP, Michaels AF (2000) Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. *Deep-Sea Res Pt I* 47:137–158
- Steinberg DK, Carlson CA, Bates NR, Johnson RJ, Michaels AF, Knap AH (2001) Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): a decade-scale look at ocean biology and biogeochemistry. *Deep-Sea Res Pt II* 48:1405–1447
- Suess E (1980) Particulate organic carbon flux in the oceans – surface productivity and oxygen utilization. *Nature* 288:260–263
- Tett P, Heaney SI, Droop MR (1985) The Redfield ratio and phytoplankton growth rate. *J Mar Biol Assoc UK* 65:487–504
- Thomson RE, Gower JFR (1998) A basin-scale instability event in the Gulf of Alaska. *J Geophys Res* 103:3033–3040
- Timmermans KR, Gerringa LJA, de Baar HJW, van der Wagt B, Veldhuis MJW, de Jong JTM, Croot PL (2001) Growth rates of large and small Southern Ocean diatoms in relation to availability of iron in natural seawater. *Limnol Oceanogr* 46:260–266
- Tsurushima N, Nojiri Y, Watanabe S (1999) New ocean time series KNOT in the western sub arctic Pacific from June 1998. In: Nojiri Y (ed) *Proceedings of the 2nd International Symposium on CO₂ in the Oceans*. National Institute for Environmental Studies, Tsukuba, Japan, pp 605–609
- Varela DE, Harrison PJ (1999a) Effect of ammonium on nitrate utilization by *Emiliania huxleyi* a coccolithophore from the northeastern Pacific. *Mar Ecol Prog Ser* 186:67–74
- Varela DE, Harrison PJ (1999b) Seasonal variability in nitrogenous nutrition of phytoplankton assemblages in the northeastern subarctic Pacific Ocean. *Deep-Sea Res Pt II* 46:2505–2538
- Villareal TA, Altabet MA, Culver-Rymsza K (1993) Nitrogen transport by migrating diatom mats in the North Pacific Ocean. *Nature* 363:709–712
- Wassman P (1990) Relationship between primary and export production in the boreal coastal zone of the North Atlantic. *Limnol Oceanogr* 35:464–471
- Whitney FA, Freeland HJ (1999) Variability in upper-ocean water properties in the NE Pacific Ocean. *Deep-Sea Res Pt II* 46:2351–2370
- Whitney FA, Wong CS, Boyd PW (1998) Interannual variability in nitrate supply to surface waters of the Northeast Pacific Ocean. *Mar Ecol Prog Ser* 170:15–23
- Winn CD, Mackenzie FT, Carrillo CJ, Sabine CL, Karl DM (1994) Air-sea carbon dioxide exchange in the North Pacific subtropical gyre: implications for the global carbon budget. *Global Biogeochem Cy* 8:157–163
- Wong CS, Matear RJ (1999) Silicate limitation of phytoplankton productivity in the northeast subarctic Pacific. *Deep-Sea Res Pt II* 46:2539–2555
- Wong CS, Whitney FA, Iseki K, Page JS, Zeng J (1995) Analysis of trends in primary production and chlorophyll-*a* over two decades at Ocean Station P (50° N, 145° W) in the subarctic north-east Pacific Ocean. In: Beamish RJ (ed) *Climate change and northern fish populations*. Canadian special publication of *Journal of Fisheries and Aquatic Sciences* 12:107–117
- Wong CS, Whitney FA, Crawford DW, Iseki K, Matear RJ, Johnson WK, Page JS, Timothy D (1999) Seasonal and interannual variability in particle fluxes of carbon, nitrogen and silicon from time series of sediment traps at Ocean Station P, 1982–1993: relationship to changes in subarctic primary productivity. *Deep-Sea Res Pt II* 46:2735–2760
- Wong CS, Waser NAD, Nojiri Y, Whitney FA, Page JS, Zeng J (2002) Seasonal cycles of nutrients and dissolved inorganic carbon at high and mid latitudes in the North Pacific Ocean: determination of new production and nutrient uptake ratios. *Deep-Sea Res Pt II* 49:5317–5338
- Zehr JP, Mellon MT, Zani S (1998) New nitrogen-fixing microorganisms detected in oligotrophic oceans by amplification of nitrogenase (nifH) genes. *Appl Environ Microb* 64:3444–3450
- Zehr JP, Carpenter EJ, Villareal TA (2000) New perspectives on nitrogen-fixing microorganisms in tropical and subtropical oceans. *Trends Microbiol* 8:68–73
- Zhang J, Quay PD (1997) The total organic carbon export rate based on DIC and DIC₁₃ budgets in the equatorial Pacific Ocean. *Deep-Sea Res Pt II* 44:2163–2190

