

Marine Ecosystems

Diversity and Functions

Edited by André Monaco and Patrick Prouzet



WILEY

From the **Seas and Oceans** Set coordinated by André Mariotti and Jean-Charles Pomerol

Marine Ecosystems

Diversity and Functions

Edited by

André Monaco Patrick Prouzet





First published 2015 in Great Britain and the United States by ISTE Ltd and John Wiley & Sons, Inc.

Apart from any fair dealing for the purposes of research or private study, or criticism or review, as permitted under the Copyright, Designs and Patents Act 1988, this publication may only be reproduced, stored or transmitted, in any form or by any means, with the prior permission in writing of the publishers, or in the case of reprographic reproduction in accordance with the terms and licenses issued by the CLA. Enquiries concerning reproduction outside these terms should be sent to the publishers at the undermentioned address:

ISTE Ltd 27-37 St George's Road London SW19 4EU UK

www.iste.co.uk

John Wiley & Sons, Inc. 111 River Street Hoboken, NJ 07030 USA

www.wiley.com

© ISTE Ltd 2015

The rights of André Monaco and Patrick Prouzet to be identified as the authors of this work have been asserted by them in accordance with the Copyright, Designs and Patents Act 1988.

Library of Congress Control Number: 2015948076

British Library Cataloguing-in-Publication Data A CIP record for this book is available from the British Library ISBN 978-1-84821-782-9



Foreword

We have been asked by ISTE to stimulate work in the area of the environment. Therefore, we are proud to present the "Seas and Oceans" set of books, edited by André Monaco and Patrick Prouzet.

Both the content and the organization of this collection have largely been inspired by the reflection, initiatives and prospective works of a wide variety of national, European and international organizations in the field of the environment.

The "oceanographic" community, in France and internationally – which is recognized for the academic quality of the work it produces, and is determined that its research should be founded on a solid effort in the area of training and knowledge dissemination – was quick to respond to our call, and now offers this set of books, compiled under the skilled supervision of the two editing authors.

Within this community, there is a consensus about the need to promote an interdisciplinary "science of systems" – specifically in reference to the Earth's own "system" – in an all-encompassing approach, with the aim of providing answers about the planet's state, the way it works and the threats it faces, before going on to construct scenarios and lay down the elementary foundations needed for long-term, sustainable environment management, and for societies to adapt as required. This approach facilitates the shift of attention from this fundamental science of systems (based on the analysis of the processes at play, and the way in which they interact at all levels and between all the constituent parts making up the global system) to a "public"

type of science, which is finalizable and participative, open to decision-makers, managers and all those who are interested in the future of our planet.

In this community, terms such as "vulnerability", "adaptation" and "sustainability" are commonly employed. We speak of various concepts, approaches or technologies, such as the value of ecosystems, heritage, "green" technologies, "blue" chemistry and renewable energies. Another foray into the field of civilian science lies in the adaptation of research to scales which are compatible with the societal, economic and legal issues, from global to regional to local.

All these aspects contribute to an in-depth understanding of the concept of an ecosystemic approach, the aim of which is the sustainable usage of natural resources, without affecting the quality, the structure or the function of the ecosystems involved. This concept is akin to the "socio-ecosystem approach" as defined by the Millennium Assessment (http://millenniumassessment.org).

In this context, where the complexity of natural systems is compounded with the complexity of societies, it has been difficult (if only because of how specialized the experts are in fairly reduced fields) to take into account the whole of the terrestrial system. Hence, in this editorial domain, the works in the "Seas and Oceans" set are limited to fluid envelopes and their interfaces. In that context, "sea" must be understood in the generic sense, as a general definition of bodies of salt water, as an environment. This includes epicontinental seas, semi-enclosed seas, enclosed seas, or coastal lakes, all of which are home to significant biodiversity and are highly susceptible to environmental impacts. "Ocean", on the other hand, denotes the environmental system, which has a crucial impact on the physical and biological operation of the terrestrial system – particularly in terms of climate regulation, but also in terms of the enormous reservoir of resources they constitute, covering 71% of the planet's surface, with a volume of 1,370 million km³ of water.

This set of books covers all of these areas, examined from various aspects by specialists in the field: biological, physical or chemical function, biodiversity, vulnerability to climatic impacts, various uses, etc. The systemic approach and the emphasis placed on the available resources will guide readers to aspects of value-creation, governance and public policy. The long-term observation techniques used, new techniques and modeling

are also taken into account; they are indispensable tools for the understanding of the dynamics and the integral functioning of the systems.

Finally, treatises will be included which are devoted to methodological or technical aspects.

The project thus conceived has been well received by numerous scientists renowned for their expertise. They belong to a wide variety of French national and international organizations, focusing on the environment.

These experts deserve our heartfelt thanks for committing to this effort in terms of putting their knowledge across and making it accessible, thus providing current students with the fundaments of knowledge which will help open the door to the broad range of careers that the area of the environment holds. These books are also addressed to a wider audience. including local or national governors, players in the decision-making authorities, or indeed "ordinary" citizens looking to be informed by the most authoritative sources.

Our warmest thanks go to André Monaco and Patrick Prouzet for their devotion and perseverance in service of the success of this enterprise.

Finally, we must thank the CNRS and Ifremer for the interest they have shown in this collection and for their financial aid, and we are very grateful to the numerous universities and other organizations which, through their researchers and engineers, have made the results of their reflections and activities available to this instructional corpus.

> André MARIOTTI Professor Emeritus at University Pierre and Marie Curie Honorary Member of the Institut Universitaire de France France

> Jean-Charles POMEROL Professor Emeritus at University Pierre and Marie Curie France

Contents

Foreword	ix
Chapter 1. Marine Biosphere, Carbonate Systems and the Carbon Cycle	1
1.1. Introduction	1
1.2. Marine organisms and carbon	3
1.3. Variability in the production of organic matter	4
1.4. From the biosphere to the atmosphere to climate	7
1.5. Carbonate production	9
in the evolution of the planet	10
1.5.2. Carbonate compensation depth	12
1.5.3. Carbonates and climate	15
1.6. The coupling of carbonaceous and organic productions.1.7. Modification of equilibria and consequences	16
on marine life	17
1.8. Conclusion	20
1.9. Bibliography	21
Chapter 2. Biodiversity of Phytoplankton: Responses to Environmental Changes in Coastal Zones	25
2.1. Introduction	25
2.2. Phytoplankton ecology	26
2.2.1. General characteristics	26
2.2.2. Lifecycle	28

2.2.3. Spatial distribution	32
	33
	35
	40
	42
	44
	45
2.3.2. Responses with regard to biomass, abundance	
	48
	54
	56
	59
2.4. Observation systems for the identification	
	60
	60
	63
	65
	66
Chapter 3. Marine Seagrasses (Magnoliophyta) in the Intertropical Zone	81
2.1. From plant to habitat	0.1
	81
3.1.1. Taxonomy and morphology of marine magnoliophyta	85
3.1.3. The seagrass habitat	86 87
	89
	89
3.3.1. Production and metabolism	90
3.4. Challenges in the conservation of seagrass beds	92
3.4.1. Rare and endangered species	92
3.4.2. Specific role of seagrasses: ichthyofauna of	0.2
coastal environments.	93
3.4.3. Services provided by seagrass beds to humans	95
3.5. Pressures on and threats to seagrasses	95
3.5.1. Cyclones	96
3.5.2. Emersion	96
3.5.3. Global climate change	96
3.5.4. Fishing	97
3.5.5. Boating and water sports	98
3.5.6. The extraction of sandy or coral materials	98

192

194

5.4. What are the combined effects of local and

	194 197 208 208 209 210
Chapter 6. Hydrothermal Vents: Oases at Depth	225
6.1. Introduction to deep-sea ecosystems 6.2. Discovery of hydrothermal sources 6.3. Geology and geochemistry of hydrothermal systems 6.3.1. Formation of hydrothermal vents 6.3.2. Chemical composition of hydrothermal fluids 6.4. Microbial chemosynthesis 6.5. Symbioses and trophic chains 6.5.1. Symbioses 6.5.2. Trophic network 6.6. Distribution of fauna at different spatial scales 6.6.1. Ridges of the East Pacific 6.6.2. Ridges of the Northeast Pacific 6.6.3. Mid-Atlantic Ridge 6.6.4. Sites in the West Pacific 6.6.5. Ridges in the Indian Ocean 6.6.6. Ridges in the Southern Ocean 6.6.7. Cayman Ridge 6.8. Biogeography of deep hydrothermal vents 6.7. Faunal microdistribution and interactions 6.7.1. Environmental conditions 6.7.2. Biotic interactions 6.8. Temporal dynamics of hydrothermal ecosystems 6.8.1. Temporal studies associated with an eruption 6.8.2. Temporal studies of active sites 6.8.3. Deep-sea observatories 6.8.4. Dispersion of larvae and recruitment 6.9. Mineral resources and exploitation	225 228 229 232 233 236 241 244 245 246 250 252 253 254 255 266 263 272 273 275
6.10. Bibliography	279
List of Authors	293
IIIUCA	74

Marine Biosphere, Carbonate Systems and the Carbon Cycle

1.1. Introduction

It is now accepted that the recent increase in the concentration of carbon dioxide (CO_2) in the atmosphere is a consequence of human activities, in particular the combustion of fossil fuels and the production of cement. Approximately 30% of CO_2 emissions are absorbed by the ocean, which clearly indicates the importance of the sea in the regulation of the level of atmospheric CO_2 . Once absorbed by the ocean, this carbon becomes an important parameter in biogeochemical cycles.

For several million years, the concentration of CO₂ in the atmosphere has shown cyclic variations directly linked to global changes in volume. These changes occur at regular intervals of 100,000, 40,000 and 23,000 years (Figure 1.1) which represent the Earth's orbit about the Sun; these phases control the insolation on the surface of the Earth (solar forcing) and are responsible for the natural variability of the climate.

COMMENTS ON FIGURE 1.1.— These parameters, each with their own frequency, combine together and cause climatic variations, particularly glacial/interglacial variations. The two curves to the bottom of the figure show: the variations in isotopes of oxygen in the plankton shells (SPECMAP) [MAR 87] which are determined by water temperature and the global volume of ice over the past 400,000 years. Ice cores entrap bubbles

Chapter written by Luc BEAUFORT.

containing past atmospheres. The concentration of CO₂ in these bubbles (EPICA) [LUE 08] is very similar to that in the ocean, by identifying glacial (gray areas) and interglacial areas.

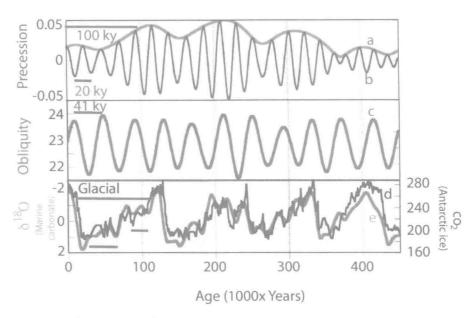


Figure 1.1. Parameters of the Earth's orbit [LAS 04] molding the global climate (CO₂ concentration in ice core d), oxygen stable isotopes in marine sediments e), precession b) and obliquity c) influence the seasonal contrasts, eccentricity a) modulates (amplifies or not) precession effects (Beaufort, compilation of [LAS 04, LUE 08, MAR 87])

The reasons why the atmospheric concentration of CO₂ follows climatic variations are still not fully understood, but the ocean could be responsible for their long term natural variations. In fact, the ocean surface layer contains an enormous reservoir of carbon than can react with the atmosphere over these orbital time scales. Marine organisms are of particular importance in these mechanisms as they help incorporate (pump) and transfer a large amount of carbon from the surface of the ocean to the deep sea and into sediments (sinks). Their role becomes crucial in the global carbon cycle.

If we know that human activities, by emitting large quantities of CO₂ into the atmosphere, disturb the biological fluxes of carbon in the ocean, it is

extremely difficult to predict the response of marine ecosystems and what the future holds for natural carbon in the biological cycle. Studying marine sediments, which can be considered as historical archives of ocean ecology, allows us to better understand how the ocean participates in the carbon cycle and how marine biodiversity adapts to global changes. In the past, these changes in biodiversity have sometimes had very significant retroactive effects on the environment and climate.

This contribution does not intend to describe the chemistry of oceans or biogeochemical cycles, widely developed in the first volume of this set of books [BER 14, LEG 14]. As stated by Legendre [LEG 14], despite their low biomass, pelagic ecosystems are the driver of biogeochemical cycles in the oceans. In this context, we will focus in particular on calcareous phytoplankton in the dynamics of carbon and its role in the evolution of past and future climates. The complexity of these processes is why this system is often disregarded in experimental research, models and projections.

1.2. Marine organisms and carbon

Marine organisms are clearly adapted to the ocean properties, in which they live, but they also actively contribute to its composition; since organismal biology is based on the chemistry of carbon, this is particularly true for the concentration of carbon dissolved in the sea. In fact, marine organisms use carbon to build their tissues (organic form of carbon), many of which also form solid skeletons, particularly in the form of calcium carbonate (inorganic form of carbon). The concentrations of dissolved and particulate carbon therefore change according to the mass and activity of these organisms. Two equations can express the dual effect of this activity on dissolved carbon: on the one hand, carbon sequestration by photosynthesis into their tissues [1.1] and, on the other hand, the release of CO₂ upon the construction of their carbonaceous skeleton from bicarbonate and dissolved calcium [1.2]:

$$CO_2 + H_2O + light \rightarrow CH_2O$$
 (organic matter) + O_2 [1.1]

$$Ca^{2+} + 2HCO_3 \rightarrow CaCO_3 \text{ (carbonate)} + CO_2 + H_2O$$
 [1.2]

These processes can be reversed depending on the environmental conditions. In addition, if the organic matter produced is used by another organism (grazing, predation), this will release carbon dioxide; however, if it is buried in the sediments; the carbon will be trapped, sometimes for very long periods of time (sequestration). With regard to the carbonates that form the skeletons (calcification), they will be either buried in sediment or dissolved in the ocean.

Calcification and biomineralization will depend on the biodiversity of the organisms; different species will not produce the same quantity of matter, skeletons do not have the same degree of calcification as they are produced at different paces. We will therefore see how marine biodiversity impacts the global carbon cycle and therefore climate.

1.3. Variability in the production of organic matter

During photosynthesis, marine algae absorb dissolved CO₂ to produce their biomass, thereby releasing oxygen (equation [1.1]). The algal production is not distributed uniformly throughout the ocean. Most multicellular algae live on the seabed and on a substrate; they are therefore known as benthic; and their distribution is limited to the shallowest depths of the ocean where sunlight can penetrate. On the contrary, algae that constitute the phytoplankton are almost all unicellular and floating; they are widely distributed along oceanic margins, and beyond, over a maximum of approximately 200 m wide in the water column.

Continental margins are generally much more productive in terms of organic matter than zones situated in the center of oceanic basins. In fact, rivers feed the coastal zones with nutritive salts (nitrogen, phosphorus, etc.), required for the growth of phytoplankton. Offshore, in the pelagic zone, this lateral input is increasingly less as one strays from the continents. The wind sometimes brings dust rich in nutritive salts, but these fluxes rarely compensate for this deficit.

Pelagic phytoplankton that lives exclusively in the photic zone (zone exposed to light) depletes the nutrient stores during photosynthesis; the only way to regenerate this stock at the surface is by the vertical pumping of nutritive salts in the deep sea (>200 m). These vertical nutrient transfers,

required for pelagic life, are only produced by updrafts caused by gusts of wind in favorable directions (upwelling) or by the deep mixing of surface layers during episodes of strong winds.

One example of this mechanism can be found in the Indian Ocean where monsoon winds are powerful enough to break down the vertical stratification and allow high phytoplanktonic production by fertilization at depth. This mixing acts over a certain depth and is called the mixed layer; when it reaches the thermocline that separates warm surface waters from cold deep waters, the nutritive salts then diffuse towards the surface. We can then easily understand that during periods favored by strong Indian monsoons, or strong trade winds, offshore of West Africa, oceanic primary production (produced by phytoplankton or PP) is reinforced.

Studying sediment cores taken from these zones has revealed that highly biologically productive periods alternate with depletions, and that these changes follow the rhythms of the Earth's orbit. Thus, primary production, expressed in grams of carbon per meter squared per year, has increased from 120 to 200 gC/m²/yr, since the previous precession cycle of the equinoxes in the center of the Indian Ocean [BEA 97] or in the Banda Sea (Figure 1.2). By causing seasonal variations and by heating different tropical zones, these cycles cause the increase or decrease in winds above the Indian Ocean, beginning with oceanic production.

COMMENTS ON FIGURE 1.2.— Top: variations in organic productivity, common (calculated by EOF) to the entire tropical band in the Indian and Pacific Ocean [BEA 01] (continuous line and circles). The organic production varies according to the concentration of CO₂ measured in the core of Antarctic ice [LUE 08] (dotted line and full squares). Bottom: recording of the organic production (dotted line, full circles and vertical error bars) in the Banda Sea. It is highly dependent on the intensity of the Australian monsoon [BEA 10]. The monsoon activity deduced follows the rhythms of insolation which are parameters of the Earth's orbit (continuous line) [LAS 04]. This highlights the difference that can exist between the local and global variations.

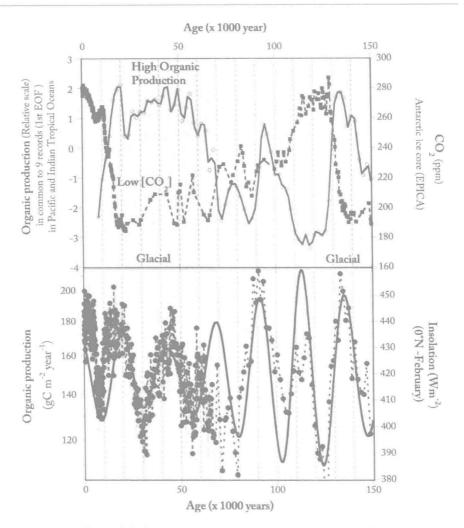


Figure 1.2. Example of the evolution of organic production in the tropical zone over 150,000 years

In this example, it is also clear that these changes in primary productivity are accompanied by significant variations in biodiversity. In the sediments deposited in the center of the Indian Ocean 20,000 years ago, 80% of fossil micro flora observed (Figure 1.3) is represented by species known to currently inhabit depths of 100 to 200 m beneath the ocean surface, at the lower limit of the photic zone, in conditions of very low levels of light. However, 10,000 years ago, this microflora represents only 10% of the assembly (assembly of a