THIRD EDITION

DYNAMICS OF MARINE ECOSYSTEMS

BIOLOGICAL–PHYSICAL INTERACTIONS IN THE OCEANS

K. H. MANN AND J. R. N. LAZIER

Blackwell Publishing

Copyrighted Material

Contents

Part B Processes on a scale of 1–1000 kilometers

Part D Discussion and conclusions

Dedicated to the memory of
GORDON A. RILEY
a good friend and colleague
who was thinking and writing about
these same topics 60 years ago

DYNAMICS OF MARINE ECOSYSTEMS

Biological–Physical Interactions in the Oceans

Third Edition

K.H. Mann & J.R.N. Lazier

Department of Fisheries and Oceans
Bedford Institute of Oceanography
Dartmouth, Nova Scotia
Canada

Blackwell Publishing

BLACKWELL PUBLISHING

350 Main Street, Malden, MA 02148-5020, USA

9600 Garsington Road, Oxford OX4 2DQ, UK

550 Swanston Street, Carlton, Victoria 3053, Australia

First edition published 1991 by Blackwell Publishing Ltd

Second edition published 1996

Third edition published 2006

1 2006

Library of Congress Cataloging-in-Publication Data

Mann, K.H. (Kenneth Henry), 1923–

Dynamics of marine ecosystems : biological-physical interactions in the oceans / K.H. Mann & J.R.N. Lazier.—3rd ed.

p. cm.

Includes bibliographical references and index.

ISBN-13: 978-1-4051-1118-8 (pbk. : alk. paper)

ISBN-10: 1-4051-1118-6 (pbk. : alk. paper) 1. Marine ecology. 2. Biotic communities.

I. Lazier, J.R.N. II. Title.

QH541.5.S3M25 2005

577.7—dc22

2005004139

A catalogue record for this title is available from the British Library.

For further information on

Blackwell Publishing, visit our website:

www.blackwellpublishing.com

Preface to third edition

Since the appearance of the second edition of this book, in 1996, there have been major changes in our understanding of the relationships between physics and the biology of the oceans on the large scale. We now see clearly that decadal-scale changes in physical properties of ocean basins are linked to changes in the biological components of the ecosystems. At times these changes in both physical properties and biology are so striking that they are described as regime shifts. Major changes occur in patterns of atmospheric circulation and, with the inevitable lags, in the major fish stocks. It seems probable that such shifts have occurred many times in the past, but over the last one hundred years or so the patterns have been somewhat modified by human exploitation and possibly the 0.6 °C warming of the globe.

It has been noticed that that changes in one ocean basin occur concurrently with changes in the others, and in 1998 Klyashtorin put forward a hypothesis to explain the connections. He observed that for 20–30 consecutive years the atmospheric circulation over the North Atlantic Ocean and Asia was dominated by east–west zonal movement, then a change occurred and north–south meridional movement became more prominent, while east–west movements diminished in strength and frequency. This condition persisted for another 20–30 years, before shifting back to the zonal regime. The cycle has a periodicity of about 55 years. During the twentieth century there was one complete cycle, and we are apparently now in the later stages of a second cycle. It is probable that the dominant circulation pattern over the North Atlantic and Asia also occurs simultaneously in other regions of the northern and southern hemispheres, allowing the ocean basins to react similarly. Of the 10 or 11 major commercial fish stocks of the global ocean, some thrive and expand during zonal regimes, while others do so during meridional regimes. At this scale, there is a predictability to the changes that holds exciting possibilities of being able to anticipate trends in exploited populations and adjust harvesting regimes accordingly.

The physical–biological interactions reviewed in various chapters of this book provide plausible mechanisms by which the atmospheric changes might be linked to the food webs and the fish-stock changes. We might say, following Steele (1998), that the area of study now ranges from carbon flux to regime shift.

Steele (1998) also stated that the basic assumption in biological oceanography is that physical forcing at a wide range of space and time scales determines most of the dynamics of marine populations. Evidence for this assumption has been the theme of the two previous editions of this book. However, recent developments have drawn attention to the part played by the properties of the organisms themselves, and of the biological communities, in modifying the outcomes of physical–biological interactions.

For example, it now appears that in large areas of the ocean the larger cells of the phytoplankton are limited in their reproduction by a shortage of iron. The phytoplankton biomass is dominated by very small cells capable of growth in low concentrations of iron but incapable of using nitrate. Their numbers are controlled by predators in the microplankton. The arrival of a pulse of iron in the form of iron-rich dust permits the larger iron-limited phytoplankton to bloom. The predators of this size group cannot multiply fast enough to prevent this happening. The physiological properties of the various organisms and the predator–prey relationships within the community play a major role in the dynamics of this situation. Development of models that adequately reflect biological community responses to physical forcing at time scales ranging from days to decades are badly needed as contributions to the prediction of global climate change.

The writing of this volume was carried out while the authors were holding positions of Research Scientists Emeritus in the Department of Fisheries and Oceans, Canada. We thank Neil A. Bellefontaine, Director of the Maritimes Region, Michael Sinclair, Director of Science, and Paul Keizer and John Loder, our respective Division Managers, for support in the appointments and generous allocation of the resources of the Bedford Institute of Oceanography. Many colleagues, including Allyn Clarke, Glen Harrison, Peter Jones, Bill Li, and Trevor Platt, offered valuable advice and assistance.

To Hannah Berry, Sarah Shannon, and Rosie Hayden in the Oxford office of Blackwell we extend our thanks for expert advice and encouragement throughout the process. We are grateful to Anna Fiander and the staff of the library in the Bedford Institute of Oceanography for friendly assistance with the literature, and for providing one of us with working space over an extended period. We also wish to thank Ms Linda Paysant, and Drs J.P. Ryan, J. Pineda, and R.G. Lough for providing digital versions of color plates. We thank our wives Isabel Mann and Catherine Lazier for their continuing support and encouragement.

K.H.M., J.R.N.L.

Preface to second edition

We have been surfing a wave of interest in biological-physical interactions in the ocean. In the course of updating this text we have found that there has been an explosion of publications in integrated oceanography, particularly at the two ends of the space–time scale.

At the scale of millimeters to meters there have been important advances in our understanding of the influence of turbulence on processes in plankton. There have been numerous experimental studies on the effects of turbulence on nutrient uptake by phytoplankton, and on the encounter rate between predator and prey. A new understanding has been reached of the physical processes that cause dissolved organic matter to aggregate on surfaces and form colloids, which in turn aggregate until there are organic particles of the size range suitable for food for plankton and benthos.

At the scale of hundreds of meters, there have been numerous field experiments on the relationship between the mixed layer and the deep ocean, designed to elucidate the mechanisms governing the seasonal rise and fall of phytoplankton and zooplankton biomass. When combined with the results of remote sensing on a much larger scale, it has been possible to describe and quantify the seasonal patterns of primary production for all parts of the world ocean. This development holds enormous potential for advancing our understanding of the role of the ocean biota in global climate change.

In the past five years we have come to a much deeper understanding of the importance of the major interannual patterns of atmospheric change, such as the Southern Oscillation and the Aleutian and Icelandic low pressure systems. Local shifts in biological production and the concomitant changes in fish stocks are now seen as part of global scale processes.

A view of the global ocean and the atmosphere as a coupled system is just coming into focus for the first time and the implications for biology are exciting. They are likely to lead to a new appreciation of the role of global processes, over which we have little or no control, in determining the magnitude and distribution of the fish and shellfish stocks that are an important part of the food resources of the human population. This, in turn, should lead to a more conservative approach to the management of marine living resources.

We thank Neil Bellefontaine, Steve McPhee, Jim Elliott, Allyn Clarke, Mike Sinclair, Don Gordon, and Paul Keizer for their continued interest and support during the revision of this volume. We are especially grateful to Jane Humphreys, our editor in the Cambridge office of Blackwell Science, for her friendly advice and assistance throughout the process, and to our wives Isabel Mann and Catherine Lazier for their continuing support and encouragement.

K.H.M., J.R.N.L.

Preface to first edition

In an earlier book by the senior author entitled *Ecology of Coastal Waters: A Systems Approach*, marine ecosystems were described in terms of their characteristic primary production, whether by phytoplankton, seaweed, mangrove, marsh grass or seagrass. Estimates were presented of the annual mean values for primary production, and pathways of energy flow were traced through the food webs. One chapter was devoted to water movement and productivity. A reviewer commented that the book was too much about mean flows and not enough about variance.

Reflecting on this, it was clear that much of the variance in marine productivity is a function of water movement. Decomposition and liberation of nutrients tend to take place in deep water or on the sea floor and water movement is needed to bring those nutrients back up into the euphotic zone for use by the primary producers. Tides give water movement a diurnal and fortnightly periodicity, while seasonal changes in solar heating impose changes in the mixed layer on scales of months to a year. Long-term climatic cycles impose their own variations on water movement and hence on biological productivity. The theme for this book began to crystallize as an expansion of the earlier chapter on water movement and productivity considered at a range of temporal and spatial scales.

While the ideas were developing, remarkable changes were occurring in oceanography. More and more, biological oceanographers were teaming up with physical and chemical oceanographers to study marine ecosystems in their totality. Physical oceanographers were increasingly able to explain to their colleagues what was going on in gyres, at fronts, on banks or in estuaries, and the biologists were developing the instrumentation needed to obtain continuous records of biological variables to supplement the spot samples that had been characteristic of biological oceanography for decades. Satellite observations of ocean color were giving large-scale perspectives on ocean productivity undreamed of by earlier generations. The feeling emerged that marine ecology was coming of age. It was developing a new maturity based on the integration of disciplines, and in the process yielding important new understanding about ecosystem function. We therefore decided to use the theme of physical processes and productivity as a starting point for an account of recent developments in marine ecology, in which physics, chemistry and biology are inter-related aspects of the dynamics of marine ecosystems.

Formal courses in oceanography tend to separate marine biology and marine physics. Our aim is to emphasize the links between the two subjects by presenting in each chapter the relevant physical processes along with the biology. Because the reader is expected to have a more complete background in biology than in physics the two subjects are written from slightly different viewpoints. The presentation of the physics is fairly elementary and emphasizes the important physical processes, while the presentation of the biology emphasizes the recent development of the field. To assist the physical presentation we have used some mathematical symbols and equations simply because they are part of the language of the subject and provide a useful shorthand for presenting ideas. It is for example much easier and more precise to write the symbol for the derivative of a variable than to write it out every time it is used. In a further attempt to present the physics in manageable portions some of the details required for a more advanced understanding have been separated into boxes which may be skipped on first reading. The references for both the physics and biology, though numerous, are by no means exhaustive and where good reviews exist we have drawn attention to them and left the reader to find the original sources.

In view of the current concern about the role of the oceans in climate change, we believe that there will be an increasing need to understand the integrated biological-physical functioning of marine ecosystems. We therefore hope that professional researchers in the various disciplines of oceanography will find this book of value in broadening their understanding of marine ecology, as an aid to defining those research programs that will be needed if we are to anticipate the consequences of global change.

In covering such a broad field we have relied heavily on the advice and assistance of many colleagues. For biological material Glen Harrison, Steve Kerr, Alan Longhurst, Eric Mills, Trevor Platt, and Mike Sinclair have been particularly helpful, while on the physics and chemistry side we have enjoyed the advice of Allyn Clarke, Fred Dobson, David Greenberg, Ross Hendry, Edward Horne, Peter Jones, Hal Sandstrom, John Loder, Neil Oakey, and Stuart Smith. We thank Mark Denny, Mike Keen, and Jim McCarthy for helpful comments on various parts of the manuscript, and we particularly thank our editor, Simon Rallison, for his most helpful advice and guidance at all stages of this project. We wish to thank Betty Sutherland and her library staff in the Bedford Institute of Oceanography for expert assistance with the literature and for suffering more or less continuous occupation of part of the library over an extended period. We also wish to thank Steve McPhee, Jim Elliott and Mike Sinclair of the Science Branch of the Department of Fisheries and Oceans for supporting us in our endeavors and our wives Isabel Mann and Catherine Lazier for their encouragement, enthusiasm and patience.

K.H.M., J.R.N.L.

1

Marine ecology comes of age

Marine ecology of the open ocean, as traditionally understood, is the study of marine organisms and their relationships with other organisms and with the surrounding environment. The subject parallels similar studies of organisms on land but, while terrestrial organisms are relatively easy to observe and manipulate, marine organisms are much more inaccessible. This inaccessibility has led to a slower growth of knowledge. The physical factors leading to fertile and infertile areas are very different on land than in the ocean. The nutrients required by land plants are generated nearby from the decaying remains of previous generations, but decaying matter in the ocean tends to sink and leave the sunlit euphotic layer where phytoplankton grow. The nutrients supplied by the decay are thus unavailable for phytoplankton growth unless some physical mechanisms bring the nutrients back up to the surface. This book is largely concerned with those mechanisms and the resulting biological phenomena. Compared with the extensive body of knowledge about physical–biological interactions in open water, much less is known about physical–biological interactions in intertidal communities. Hence the greater part of this book is about the ecology of open-ocean communities.

It is now possible to add an extra dimension to marine ecology. Instead of putting the organisms at the center of the picture and considering them in relationship to other organisms and the environment, it is possible to work with marine ecosystems in which physical, chemical, and biological components are equally important in defining total system properties. Those properties include production of living organisms such as fish, but flux of carbon dioxide as determined by both physical and biological processes may be more important in the context of climate change.

Interest in and research activity in marine ecology are intensifying. There are many reasons for this trend, of which four may be mentioned:

1 The physical processes underlying some of the large-scale biological phenomena are now better understood. For example, the North Pacific Ocean and the North Atlantic Ocean are seen to undergo oscillations in their near-surface physical properties on a time scale of about five decades, and these oscillations have a profound effect on biological processes, including the production of fish. The changes in physical oceanography appear to be driven by changes in the atmospheric circulation. In tropical regions, an atmospheric cycle known as the Southern Oscillation is seen to drive major changes in the coastal upwelling system in the Humboldt Current, and to have links to changes in climate and biological production in many parts of the world.

2 There have been important advances in our ability to make continuous, fine-scale biological measurements by means of automated sensors feeding into computers. It is now possible to collect biological data with a coverage and resolution comparable with the best physical data and to make integrated biological–physical studies at a wide range of time scales. For example, on a global scale the satellite image in Plate 1 shows the distribution of chlorophyll in surface waters, and reveals a great deal about the incidence of upwelling and the exchange of gases with the atmosphere. On a scale of tens of meters, Plate 5 shows how timely deployment of an intensive array of instruments made it possible to investigate the functioning of a breaking internal wave and its relationship to plankton.

3 The need to understand marine ecological processes influencing the greenhouse effect and other aspects of world climate is becoming more urgent. The flux of carbon dioxide from the atmosphere into surface waters and on down into the deep ocean, as a result of biological processes, is believed to be an important part of the mechanism of climate change. In this connection, there is important new information on the limitation of phytoplankton production in some areas by low concentrations of iron in the water, and on the stimulation of primary production in otherwise unproductive areas by a variety of intermittent mechanisms.

4 Our enormous increase in understanding fundamental processes over second to decadal time scales and centimeter to megameter space scales is beginning to influence the management of the ocean's living resources. We are seeing that year-to-year and decade-to-decade changes in the atmosphere are reflected in property changes in the near-surface ocean. The way in which these changes affect the growth and survival of fish larvae and the distribution of fish are two topics that will receive a great deal of attention in the coming decades.

For all of these reasons, marine ecology has changed rapidly and may be said to have come of age. The dominant theme of this book is that physical processes create the conditions for many important biological processes; the biology cannot be understood in isolation. One good example is the jump in understanding why shelf-break fronts are so productive. This came about through a combination of a high-resolution numerical model and some clever field experiments. The model revealed details of the physical processes that would be impossible to observe with fixed instruments such as moored current meters. The field experiment tracked dye to reveal flow details that bring nutrient-rich water from deeper to shallower water within the front. In this volume, the connections between the physical and biological processes are emphasized and brought into focus more sharply than before.

The nature of the relationships between physical and biological processes is subtle and complex. Not only do the physical processes create a structure, such as a shallow mixed layer, or a front, within which biological processes may proceed, but they also influence the rates of biological processes in many indirect ways. Discussion of this relationship has most often been in terms of energy flow. Biologists often model food-web relationships in terms of the flow of solar energy, captured in photosynthesis by the phytoplankton and passed from organism to organism by means of feeding transfers. The physical phenomena such as currents, turbulence, and stratification also rely on solar energy, transmitted to the water directly as heat or indirectly as momentum from the wind. These two fluxes of solar energy are in one sense quite distinct: organisms do not use the energy of water motion for their metabolic needs. In another sense, they are interrelated. Water movement alters the boundary layers around organisms, transports nutrients and waste products, assists migrations, and influences the rate of encounter between planktonic predators and their prey. Stratification causes the retention of planktonic organisms in the upper layer of the ocean, making light more available but limiting access to inorganic nutrients. Water temperature has a profound influence on the rates at which biological processes proceed, and differences in water motion, from place to place, largely determine the kinds of organisms colonizing those places. From a biological point of view, the physical energy is termed auxiliary energy, which literally means “helping energy.”

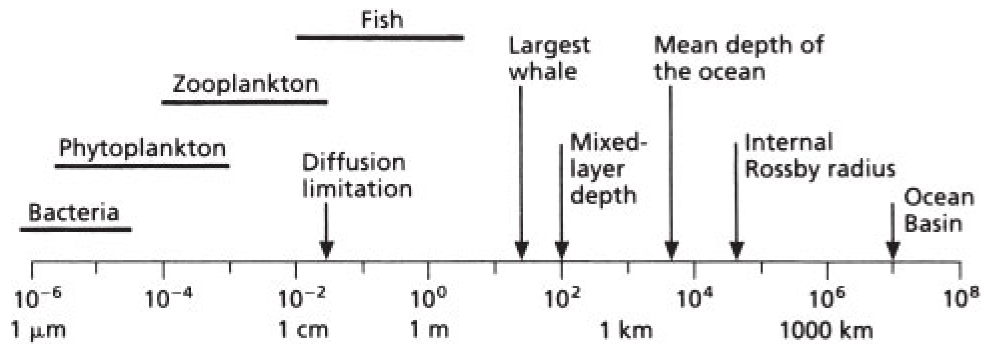
However, it is important not to fall into the trap of assuming that there are strict and unvarying relationships between physical oceanography and the dynamics of biological communities. It is now becoming clear that interactions between organisms modify the responses of communities to physical conditions. For example, the size composition of a phytoplankton community may be determined by the types of zooplankton feeding upon it, and when nitrate-rich water is brought up into the mixed layer the response of a community of large phytoplankton cells will be very different from the response of a community of very small cells.

LENGTH SCALES

In approaching the subject it is useful to have a feeling for the dimensions of the organisms and phenomena to be discussed (Fig. 1.01). Ocean basins are typically 10,000 km wide and confine the largest biological communities. The average depth of the ocean is 3800 m but the depths of the euphotic layer (~100 m) and the mixed layer (~100 m) are more often critical to open-ocean biological processes.

The Coriolis and gravitational forces give rise to the Rossby internal deformation scale or radius, a frequently encountered length scale in physical/biological oceanography (see Section 5.2.3). It arises in flows of stratified water when a balance between the two forces is established. This scale, which varies strongly with latitude, is the typical width of ocean currents such as the Gulf Stream, the width of the coastal upwelling regions, or the radius of the eddies in the ocean.

Fig. 1.01 The size scale from 1 μm to 100,000 km, showing some characteristic size ranges of organisms and physical length scales.



The viscous or Kolmogoroff length is the scale where viscous drag begins to become important, that is, where viscosity starts to smooth out turbulent fluctuations in the water (see Section 2.2.6). The scale represents the size of the turbulent eddies where the viscous forces are roughly equal to the inertial forces of the turbulent eddies. The scale also indicates an important change in the methods of locomotion and feeding. Organisms larger than ~10 mm are not seriously affected by viscous drag, while for the smallest organisms swimming is akin to a human swimming in honey. Because of the change in the turbulent motions the smallest organisms must depend on molecular diffusion for the transfer of nutrients and waste products. For the larger animals nutrients and wastes are moved rapidly by turbulent diffusion, which is not affected by viscosity. These topics are developed in Chapter 2.

TIME SCALES

As a first approximation, time scales change in direct proportion to length scales. On the global scale, the thermohaline circulation may take 1000 years to complete a circuit. On the ocean-basin scale, the major gyres may require several years to complete a circuit. Eddies and gyres spun off from the major currents have lifetimes of weeks to months, and as energy cascades through smaller and smaller scales of turbulence, the characteristic time for rotation decreases to seconds at the smallest scale.

While physical features determine the spatial scales of ecological processes, the organisms determine the time scales. While the life span of a large marine mammal may be close to 100 years, those of fish are more like 1–10 years, and zooplankton may complete a generation in a few days or weeks. Phytoplankton have doubling times on the order of days, and bacteria of hours. It follows that small organisms are likely to undergo more rapid fluctuations in numbers than large ones. Since, in general, each type of organism tends to feed on organisms smaller than itself, the process of trophic transfer has the effect of smoothing out the rapid fluctuations. Conversely, predators may impose on their prey longer-term fluctuations that correspond with fluctuations in predator numbers.

PLAN OF THE BOOK

Part A begins by introducing turbulent motion and viscous boundary layers, which determine the unusual feeding and locomotion techniques of the very small organisms. These phytoplankton and zooplankton are the base of the food chain and account for about half of the total biomass of the ocean. Their survival depends on a variety of physical processes outlined in Chapters 3 and 4. In the open ocean survival depends on the annual creation and destruction of the seasonal pycnocline. In shallow coastal waters the effects of freshwater run-off and tidal mixing can be the dominant processes.

In Part B, Chapter 5 describes the consequences of winds near coasts and of the Coriolis force that lead to the Ekman drift in the surface layers and coastal up-welling. This process is responsible for some of the most productive regions in the ocean. The enhanced biological activity near various types of fronts is covered in Chapter 6 and is followed by a discussion of tides including explanations of tidally generated internal waves that transport nutrients onto the continental shelves.

Large-scale phenomena are treated in Part C, beginning with an explanation of the wind-driven circulation, the intense western boundary currents such as the Gulf Stream (Plate 2), and the warm- and cold-core rings that are generated by instabilities in the boundary currents. The unique biological properties of the rings and other circular circulation patterns such as gyres are then reviewed. The El Niño – Southern Oscillation story in Chapter 9 introduces the effect on biological productivity of changing circulation in the ocean. It is now clear that regular multi-decadal cycles in the atmosphere–ocean interactions of the major ocean basins cause predictable large-scale cycles in the abundance of fish. Chapter 10 reviews the greenhouse effect and the role of the oceans in this cycle, emphasizing the biological pump that is an important mechanism transferring carbon dioxide from the upper layers to the bottom of the ocean.

In the final chapter we discuss questions for the future. There is a sense in which the whole book is an exploration of these questions, so we give them here:

1 Is there a common mechanism to account for the occurrence of high biological productivity in a variety of physical environments?

2 To what extent are events in marine ecosystems determined by physical processes, and to what extent are the outcomes modified by interactions within the biological community?

3 How can we develop concepts and models that span the enormous range of scales in marine ecology, from the microscopic to the global and from seconds to geological ages?

4 How do we explain an apparent synchrony in the variations in the biomasses of fish stocks worldwide?

We shall see that a tentative answer to the first question was provided by Legendre (1981). He said, in effect, that vertical mixing followed by stratification of the water column leads to a phytoplankton bloom, and that this effect can be seen to happen in a variety of habitats and at a range of temporal and spatial scales. Our review supports this answer, but are there other mechanisms?

One is tempted to respond to the second question by saying that physical factors obviously determine the course of biological events, and the converse rarely happens. In fact, if we take a long-term view, we see that the greater part of the carbon dioxide released into the atmosphere during the life of the earth has been fixed by phytoplankton and deposited in marine sediments as carbonates or organic matter. Without these processes the carbon dioxide content of the atmosphere would be much higher, the earth would be much hotter, and the circulation of the oceans would be totally different. Even on the short time scale there are examples of phytoplankton altering the penetration of light and heat into the water column and hence the functioning of the ecosystem. Interactions between physics and biology are not entirely, or even mainly, in one direction. Moreover, while physical processes have predictable effects on individual organisms, their effects on whole biological communities are much less predictable. Community responses may be modified by the substitution of one species by another, or by predator–prey interactions.

The third question has been much discussed without any real resolution. It is a problem for ecologists generally, for we do not understand how to include bacterial processes on scales of millimeters and seconds in the same models that deal with animals that live for decades and may range over thousands of kilometers. Marine ecologists have the added difficulty that the biological events take place in a medium that exhibits physical processes on the same range of scales, thus compounding the difficulties.

The fourth question came into sharp focus at the end of the twentieth century. Multi-decadal changes in global patterns of atmospheric circulation correlate well with biomass changes in many of the major fish stocks. An enormous amount of work will be required to investigate, at a range of scales, the mechanisms responsible for the links between atmospheric changes and changes in marine ecosystems.

We have found it useful to keep these questions in mind as we review the developments of marine ecology as an integrated physical, chemical, and biological discipline.

Part A

Processes on a scale of less than 1 kilometer