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marine ecology

processes, systems, and impacts

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SECOND EDITION

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Marine Ecology: Processes, Systems, and Impacts

'It is likely that much present day published science depends on "fact" which has not been sufficiently checked. James Elroy Flecker, in his play Hassan, wrote: "Men who think themselves wise believe nothing until the proof. Men who are wise believe anything until the disproof." Perhaps in this complicated world, one should steer a careful path between Flecker's two extremes.'

G. E. (Tony) Fogg (1919–2005)

Preface

Marine ecology: an introduction

Approximately 2.2 billion people live within 100 km of a coastline. This figure is set to double by 2025. While the average population density along coastlines is currently 80 people km^{-2}, this increases to up to 1000 km^{-2} in countries such as Egypt and Bangladesh. Many of these coastal inhabitants depend directly upon marine resources for their subsistence or income. The world's oceans provide a wealth of goods and services, and are used as repositories for our waste products, yield renewable (wind and tidal energy) and non-renewable (oil and gas) forms of energy, provide important bulk transportation routes, provide a source of food, yield mined commodities (diamonds, heavy metals), and provide recreational benefits that support important tourism industries. Technological advances have enabled us to use areas of the oceans that previously were inaccessible to humans, and many marine resources are either fully or over-exploited. However, with technical advances, the increase in knowledge and material riches is often accompanied by increased consequences of technical failures, as seen in the Gulf of Mexico Deep Horizon blowout in 2010. Despite our growing use of the oceans and major efforts to catalogue the diversity and distribution, such as the Census of Marine Life, much of the marine realm has never been viewed by the human eye. Indeed, it is sobering to think that we probably know more about the surface of the moon than we do about the marine environment of our own planet. Understanding marine ecological processes and systems are urgent research priorities if we are to comprehend the ecological effects of human activities that impact upon them and more widely on global systems. This understanding is essential to help society find ways of achieving sustainable use of marine resources. Thus marine ecology remains an exciting and pivotal subject that has matured into an integrated science that encapsulates biological, chemical, and physical processes from the microscopic to the global scale.

> Nearly 40% of the world's population live close to the coastline.

> The world's oceans are heavily exploited for mineral and biological resources even though much of the ocean remains unexplored.

The evolution of marine ecology

The development of marine ecology can be charted through three major eras. Early naturalists worked in an age when seafarers' stories of sea monsters abounded and authors such as Jules Verne romanticized exploration of the deep and the battle with the leviathan. The observations of early naturalists, such as Darwin, were mostly restricted to the shoreline, while scientific sampling of the abyss was performed by lowering crude sampling devices to the distant seabed. This must have been (and remains) an incredibly exciting time, as every sample probably contained an organism viewed for the first time by human eyes. Exploration of the oceans continues to be an ongoing task, with the discovery of a new phylum in the last few decades (Chapter 1). Then in the early to mid-twentieth century, ecologists such as Petersen and Thorson began to consider ecological rules that determined the distribution and abundance of marine species and communities (Chapters 3, 7, 8, and 13). This coincided with the early beginnings of fisheries science and concerted efforts to understand the processes affecting population variability in fish populations.

> The history of marine ecology can be divided into three main eras: (1) exploration and description; (2) experimental manipulation; (3) integration and application.

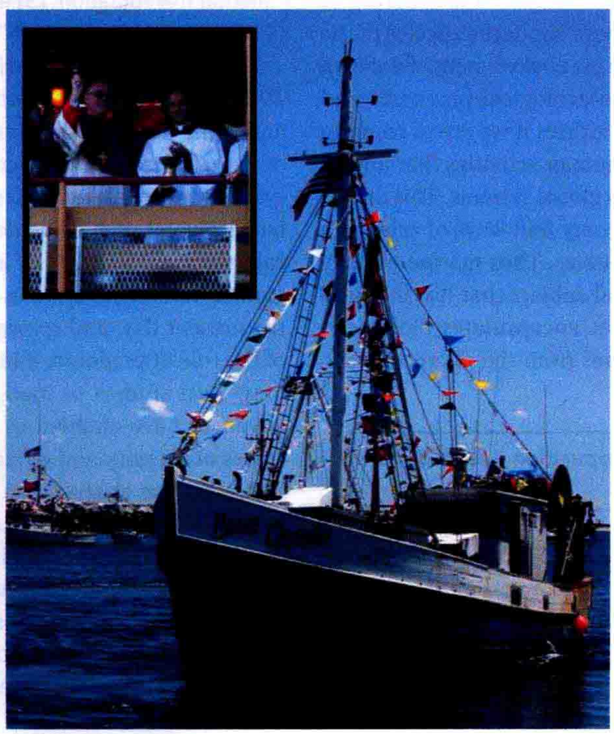
The second era of marine ecology began in the late 1960s and early 1970s, when ecologists such as Connell and Paine undertook their seminal research on the effects of disturbance and competition in ecology, using marine systems as models for their studies (Chapter 6). Their work had a pivotal role in the development of general ecological theory, which then springboarded into the more easily studied terrestrial systems. This theme has developed to the present day, and spawned many manipulative studies of the role of predators and grazers in marine systems and long-term studies of food-web dynamics. Technological advances have enabled us to understand better the processes of primary and microbial production; the advent of stable isotope analysis has provided a common means to assess the trophic status (i.e. top predator, forage species, detritivore, secondary producer) of species in marine communities from around the world (Chapters 7, 8, and 10) and the development of remote sensing methods to describe the distribution and dynamics of primary production on global scales provided unprecedented insights into the ecology of the global oceans. Novel molecular tools have offered new insights into the diversity of species complexes that previously were the source of debate amongst taxonomists (Chapter 1).

While we still have a lot to learn about marine ecosystem processes, we have entered a new phase (the third era) in which research has become more urgently focused on the ecological ramifications of an ever-increasing list of human impacts (Chapters 13, 14, and 15). This new focus still firmly relies upon ecological theory (Chapters 1, 3, 4, 7, 13, and 15) to understand how communities respond to exploitation and disturbance. These impacts occur against a background of climate change that is occurring at a rate faster than previously recorded in our time. Changes in water temperature, storm activity, and precipitation are now compounded by the potential of ocean acidification altering biochemical processes in the ocean. Activities such as commercial fishing have occurred for hundreds of years, but have sometimes reached such intensive levels that they have driven fundamental changes in ecosystem status. An increasingly complex range of contaminants is pouring into many coastal waters, and their pernicious sub-lethal effects may cause reduced survival of larval stages and alteration of sexual characteristics in adult organisms. The incidences of deoxygenation in coastal waters have increased in recent years with catastrophic implications for the associated fisheries and aquaculture activities, not to mention degradation of ecosystem functioning, goods, and services (see box below). The latter provide a clue to the direction of marine ecology of the future. While there are still many gaps to be filled, the latest exciting advances are being made by studies that are multidisciplinary, combining oceanography, biogeochemistry, and sedimentology together with marine ecology, a trend that is set to continue into the future.

Human impacts on the marine environment are set against a background of an increasing rate of global climate change.

Ecosystem goods and services

The concept of ecosystem goods is fairly easy to grasp in tangible economic terms; for example, the value (US$) of fish or other commodities extracted or farmed in the ocean. Perhaps less obvious are the values attributed to the regulating functions, such as flood control and coastal defence, and the cultural non-material benefits derived from marine ecosystems. Cultural values are often deeply embedded within human society, as typified by the blessing of the fleet by the local Roman Catholic Bishop in Provincetown Harbour, New England (inset), where a large proportion of the fishing community can trace their roots to Portugal or the Azores. (Photographs: M. J. Kaiser.)



Provisioning	Regulating	Cultural
Products obtained from:	Benefits obtained from:	Non-material benefits obtained from:
ecosystems	regulation of ecosystem processes	ecosystems
food	climate regulation	spiritual
freshwater	disease control	recreational
fuel	flood control	aesthetic
biochemicals	detoxification	inspirational
genetic resources	pollination	educational
		communal
		symbolic

Supporting
Services necessary for the production of all other ecosystem services
Soil formation
Nutrient cycling
Ecological processes/functioning

These are exciting times, but even the multidisciplinary approach is constrained within the boundaries of 'marine science'. This has been the typical approach of scientists, to offer up our findings to the wider public and governmental bodies, at which point we have fulfilled our duty. This approach is rapidly being replaced by the realization that marine ecosystems have tangible value to society, not only in terms of the goods (fish, aggregate, oil) that are yielded, but also in terms of the services that they provide (carbon sequestration, coastal defence, waste repositories). Degradation of biodiversity is thought to reduce the capacity of the ecosystems to deliver goods and services, thus biodiversity loss has real economic, societal, and cultural costs for human society. For example, living marine systems, such as coral reefs and mangrove forests, provide an important buffer between the ocean and the land. This role was brought sharply into focus with the 2004 tsunami that struck the Indian Ocean leaving over 5000 dead in Thailand alone, with the extent of damage often correlating with the extent of coastal defence.

> Marine ecology is beginning to break out of traditional scientific boundaries and is beginning to interface with economics and the social sciences to understand the wider societal importance of marine biodiversity.

Most experimental manipulations of biodiversity indicate some relationship between biodiversity and ecosystem processes; however, few have drawn out the links between biodiversity change and the output of goods and services. A good example would be the loss of the cultural services that occurs when a pristine flora and fauna is degraded (e.g. loss of whales from Arctic waters deprives Inuit peoples of the cultural aspect of hunting whales, regardless of the practical need to acquire food) (see box above). Different biodiversity change scenarios (e.g. habitat fragmentation, contamination, over-exploitation) are likely to affect processes to a varying extent, because different kinds of taxa (large or small, primary producers or top predators) are lost under the different scenarios. A good example of the latter is the over-harvesting of bottom-dwelling fish and incidental removal of other seabed animals (**benthos**) on the Scotian Shelf off Canada. This has led to a decoupling of the ecosystem link between water column and seabed processes (**benthopelagic coupling**) and ultimately resulted in a system dominated by mid-water (**pelagic**) fishes. In addition, specific goods and services may be supported by several different processes, further convoluting their relationship with biodiversity.

> While ecosystem goods are reasonably simple concepts to grasp, e.g. the acquisition of food or minerals, the cultural value of biodiversity is a more abstract concept.

Using this book to study marine ecology

Marine Ecology: Processes, Systems, and Impacts has been written to address the current need to understand the application of marine ecology in a marine environment strongly influenced by human activities. The structure of the book reflects the integrated approach to marine ecology that is necessary to answer many of today's key marine environmental and conservation problems, which form the focus of the last section of the book. The book is divided into 16 chapters arranged in four distinct sections. The opening chapter deals with the processes that affect patterns at a variety of spatial and temporal scales, diversity, community organization, and structuring processes, and provides a palaeoecological perspective on present-day marine systems. As a marine ecologist, it is important to have a grasp of the relevant time-scales that impact upon the systems in which we work. While much of the ecology we encounter deals with either instantaneous or relatively short-term (1–3 years in duration) processes, evolutionary ecologists think in terms of thousands to millions of years. Some environments, such as the deep sea, have remained relatively stable on an evolutionary time-scale, whereas coastal and shelf habitats have experienced far more frequent changes. This dynamic flux in the near coastal habitat is brought into focus by present-day findings, at sites currently 40 m beneath the sea to the west of Florida in the Gulf of Mexico, of human artefacts and animal bones from the early Holocene with evidence of butcher cuts and other implement shaping.

Processes contains three chapters that address the fundamental global processes of primary and microbial production that fuel marine systems and the ecology of the organisms responsible. Chapter two describes primary processes, while Chapter three has been revised extensively to better convey its biological context. These two chapters lead into a new chapter that deals with secondary production. **Systems** then addresses in more detail estuaries, rocky and sandy shores, the pelagic environment, continental shelf seabed, the deep sea, mangroves, and seagrass meadows, coral reefs, and polar seas. **Impacts** tackles some of the most pressing environmental issues relevant to the marine environment that span the systems described beforehand, with chapters on fisheries, aquaculture, disturbance, pollution, and climate change, and finally marine conservation. The penultimate chapter also includes a consideration of the experimental approach needed to determine the effects of human impacts and deals with common pitfalls made by students undertaking field and laboratory projects.

This second edition has been revised extensively throughout and the feedback from users of the first edition has helped us identify new areas for inclusion. As requested, we have supplemented the online supporting materials with worked examples (e.g. how to calculate secondary production) and advice on improving exam performance.

Other textbooks have traditionally dealt with key physical and chemical environmental processes as a discrete unit, usually towards the beginning of the book. This section can be overlooked or its importance not appreciated at the time of reading or forgotten by the time it becomes relevant in the text. In *Marine Ecology: Processes, Systems, and Impacts*, we have integrated the environmental processes at key points that are cross-referenced throughout the text, so that their relevance is immediate and the learning process enhanced. Some of these key processes are reiterated from a slightly different perspective or even repeated in a number of chapters so that learning is reinforced. Key words and concepts are highlighted in bold throughout the text to aid learning and revision. In addition to the definitions and explanations given in the text, an excellent online glossary of important marine biological terms can be found at the website of the Marine Life Information Network for Britain and Ireland (MARLIN; see www.marlin.ac.uk for more information). Boxes are used to expand specific points, and offer interesting examples and case studies that illuminate the concepts being introduced. In this second edition we have highlighted in each chapter key **techniques** that are important to the contemporary marine ecologist and **current focus** boxes that we feel are likely to be of major interest in coming years. Finally, we have provided a short list of further reading, trying wherever possible to recommend widely accessible literature and have provided a list of websites that will enable you to learn more about specific subjects or disciplines. Full citations for all references given in the chapters can be found at the end of the book.

Marine ecology is a highly relevant and challenging subject that is fascinating to amateur, student, and professional alike. We hope that students using this textbook will gain a real feeling for the excitement of marine ecology as a subject of interest, a hobby, and a potential career.

Michel Kaiser

Online Resource Centre

Marine Ecology: Processes, Systems, and Impacts is supported by an Online Resource Centre, which holds various supplementary materials for students and registered adopters, including figures from the book available to download, videos, and a web link library including all the URLs cited in the book. Visit: www.oxfordtextbooks.co.uk/orc/kaiser2e/.

New to this Edition

This 2nd edition has been revised by 30%, including an entirely new chapter on secondary production. Two new authors have been added to the team, and all chapters have been updated to include key works, issues, and topics published since 2005. Coverage of socioeconomic issues and climate change has been enhanced in this edition and two new box types—Current Focus and Techniques—have been introduced to highlight important issues facing ecologists today and showcase contemporary research methods, respectively.

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Outline Contents

Detailed Contents

Patterns in the Marine Environment

1

Chapter Summary

Most space for life on Earth is in the vast oceans and seas. Life began in the oceans and remained confined to this environment for hundreds of millions of years. Most major groups (phyla) of animals never left it. The wide expanse of the oceanscape changes dramatically, from undersea mountain ranges to sediment plains and coral reefs, to forests of kelp. Patterns of organisms, so obvious at the shore, are also evident from the poles to the tropics, from coasts to ocean centres, from the shallows to the deep abyss, and from millions of years ago to the present day. Patterns occur in species' richness, abundance, ancientness, or size, all of which are indicators of powerful changes on the planet surface in time and space. Oceans have widened or been compressed, risen and fallen, heated and cooled, and remain dynamic places; most will have changed drastically in just the lifespan of the reader of this book. Examining some of the major patterns in organisms and their biology gives a strong insight into the processes that determine success and evolution of life on Earth.

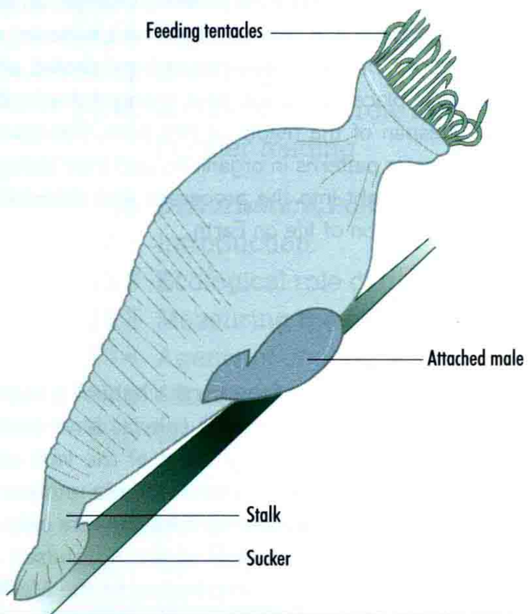
1.1 Introduction

Humans are a land-living species and consequently most familiar with the terrestrial environment, yet the Earth is a blue planet and the oceans cover >70% of its surface. Close to the continents this aquatic ecosystem takes the form of shallow seas just a few hundred metres deep known as the **continental shelf**. However, around Antarctica the mass of the huge (3-km thick) icecap has depressed the shelf to be as deep as 1000 m in places. Most of the oceanic habitat (and 51% of the earth's surface) is nearly 4000 m deep. This three-dimensional environment is populated throughout its depth by many organisms. The steep rises up to the continental shelf contrast with the large sediment-covered basins that span tens of thousands of square kilometres, broken only by the undersea mountain ranges of **mid-ocean ridges**. At these locations oceanic crust is formed and gradually moves outwards, pushing continents apart, and eventually disappears down beneath continental crust, forming deep oceanic trenches. Considering its volume, the vast majority (*c*.99%) of the Earth's habitat is marine, where most major types of animal (phyla) have evolved and continue to live exclusively. Most of the vast water column and seabed (**benthic**) habitat remain unobserved by human eyes. The first biological samples were only collected from the continental shelf of the Amundsen Sea (which spans 40° longitude—equivalent to the Mediterranean) in 2008. New species are still routinely found in deep-sea samples and even some of the larger animals on Earth which live there, megamouth sharks and giant squid, have only recently been seen alive in their natural habitat.

Our impoverished knowledge of the ocean's inhabitants is emphasized by the fact that it is not just new species that are described, but that even some of those that are high-profile and common, such as the crown-of-thorns starfish, now appear to be several species (like giraffes on land). Furthermore, entirely new classes or phyla (the highest taxonomic levels of animal types) have been discovered in just the last couple of decades.

Box 1.1: A new phylum

In 1995 an entire new phylum of tiny animals, the Cycliophora, was reported from a discovery two years earlier. As it is only 350 ∝m in size and superficially resembles individuals of several other phyla of small animals (Gastrotricha, Rotifera, and Entoprocta), it could be considered unsurprising that such animals are still being discovered. Surprisingly, though, the single species (***Symbion pandora***) lives on the mouthparts of ***Nephrops norvegicus***—a very common, well studied, and widely consumed species, often referred to as scampi. ***S. pandora***, or the 'Pandora', attaches to its host using a sucker and suspension feeds on particles in the water, a small parasitic male (whose sole purpose seems to be for breeding) is also shown attached in the picture below.



Standing at the edge of a forest looking out over a prairie, lake, or into the tree canopy, it is easy to see how fragmented the land can be. Furthermore, even a simple climb up a mountain can reveal altitudinal changes and, though few have experienced it, most people understand that polar regions are deserts compared to the generally species-rich tropics. In contrast, the water column and wide ocean basins might be envisaged as fairly monotonous, uniform ecosystems. However, there are many features that punctuate them abruptly or gradually into many different environments. Changes in time, topography, chemistry, and oceanography allow for the development of patterns across a wide range of scales in time and space, and form the subject of this first chapter and are themes that reoccur throughout this book.

1.1.1 Zonation

Patterns in the marine environment are often beyond our immediate perception; we cannot always see them. Often, patterns are only revealed through sampling and subsequent interpretation. The number and size of samples collected and the type of equipment used will have a profound effect on what is found. Strong differences in opinion exist about even the most basic marine biotic patterns, each defined by evidence from a discrete set of samples (see also sampling in Chapter 8). In many respects, patterns in the sea resemble those on land; for example, at a large scale along gradients of solar radiation (latitudinal gradients), altitudinal (which in the marine environment is depth, thus bathymetry), from the coast to ocean/continent centres, and from young to old areas (e.g. from the mid-Atlantic ridge (new) to the far eastern or western Atlantic sea-floor (oldest)). In the shallowest parts of the sea there are plenty of places where the type or nature of the organisms changes over tens of centimetres or metres, which we term **zonation** (Chapter 6). In warm tropical waters, the type and dominance of corals changes quickly with depth (Chapter 11). In polar seas the abundance and richness of marine life alters equally sharply in response to decreasing physical disturbance by floating icebergs that scour the seabed (Chapter 12). In certain types of environment, such as estuaries (Chapter 5), rapid changes in biological constituents occur along the length of the estuary in response to a suite of changing environmental variables; patterns that are repeated at virtually all latitudes. Zonation is most apparent where the land meets the sea and it is here that it has been studied in most detail (Fig. 1.1a). Zonation is not just driven by tolerance to physical conditions (though this is most important at the high shore level). Connell's (1961a, 1961b) work on barnacles demonstrated that interspecific competition and differential predation pressures strongly influence the location where species survive. In temperate regions across the globe different species and colours of algae and lichens indicate the gradient of immersion on the lower and upper regions of the shore. Shore zonation is equally apparent in some muddy shores in changing saltmarsh vegetation or, at tropical latitudes, in mangrove trees and their associated fauna. Only towards the polar regions does shore zonation become increasingly constrained and ultimately disappear altogether at very high latitudes (Fig. 1.1b). At high polar latitudes (Fig. 1.1c), very few organisms can survive the constant abrasion by floating ice during the summer, coupled with encasement in winter ice