Photosynthesis in the Marine Environment

Sven Beer, Mats Björk and John Beardall

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Front cover - A thick turf of red and brown algae growing in the high-energy surf zone, Malta. Photo by Mats Björk
Back cover (from left to right) - Colonies of the marine cyanobacteria Trichodesmium (see Figure 2.1b). Photo by Birgitta Bergman - Quantum yield measurement of zooxanthellae in a coral by PAM fluorometry (see Figure 9.7). Photo by Katrin Österlund - Various macroalgae in the Mediterranean, with the brown alga Padina sp. on top. Photo by Katrin Österlund - The seagrass *Cymodocea serrulata*, Zanzibar. Photo by Mats Björk.

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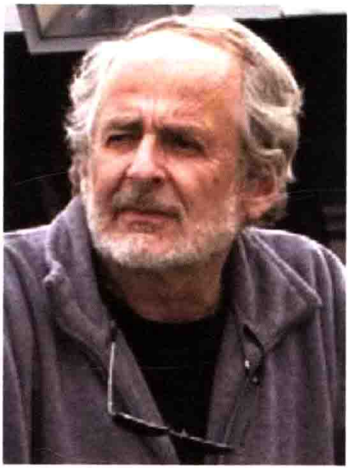

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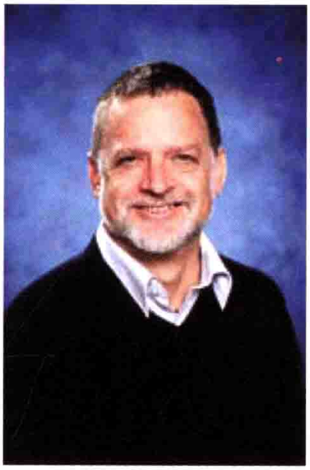

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Prof. Sven Beer was, as his first name indicates, born in Sweden (in 1949), where he also completed his BSc in Biology at Stockholm and Uppsala Universities. After moving to Israel in 1973, he graduated with a PhD (title of dissertation: Photosynthesis of Marine Angiosperms) from Tel Aviv University, where he has worked in teaching and research ever since; he is now a Professor Emeritus at that university, and also holds an affiliated professorship at Stockholm University. During his career, Sven has authored some 120 scientific publications in the field of marine botany and, especially, photosynthesis of marine macrophytes. You can read more about Sven on his home page www.tau.ac.il/lifesci/departments/plant_s/members/beer/beer.html

Prof. Mats Björk, was born in Stockholm, Sweden in 1960. He moved to Uppsala for university studies, and earned his doctorate degree there in 1992. In 1996 he took up a research position at Stockholm University, where he currently is Professor of Marine Plant Physiology. His research focuses on marine plants and their productivity in both tropical and temperate environments, and how they are affected by environmental change such as pollution and ocean acidification. He has worked extensively with academic institutions in Africa, where he has co-ordinated various educational and research projects and guided many graduate students.

Prof. John Beardall was born in the UK in 1951. He studied Microbiology at Queen Elizabeth College, University of London, prior to moving across town to University College (also University of London) for his PhD. Following post-doctoral studies at University College of North Wales, then at University of Dundee, John moved to Australia in 1982, taking up a Lecturer position at La Trobe's Department of Botany. He and his team moved to Monash in 1988 when John was appointed Senior Lecturer in the, then, Department of Botany. He currently holds a Professorial position in the School of Biological Sciences. John has published 130 papers and over 20 book chapters. His research group focuses on the physiology of algae in relation to environmental factors. A major interest is related to understanding the ways in which marine and freshwater microalgae, including the cyanobacteria responsible for toxic blooms in inland and coastal waters, will be influenced by global change. John's home page is http://monash.edu/science/about/schools/biological-sciences/staff/beardall/

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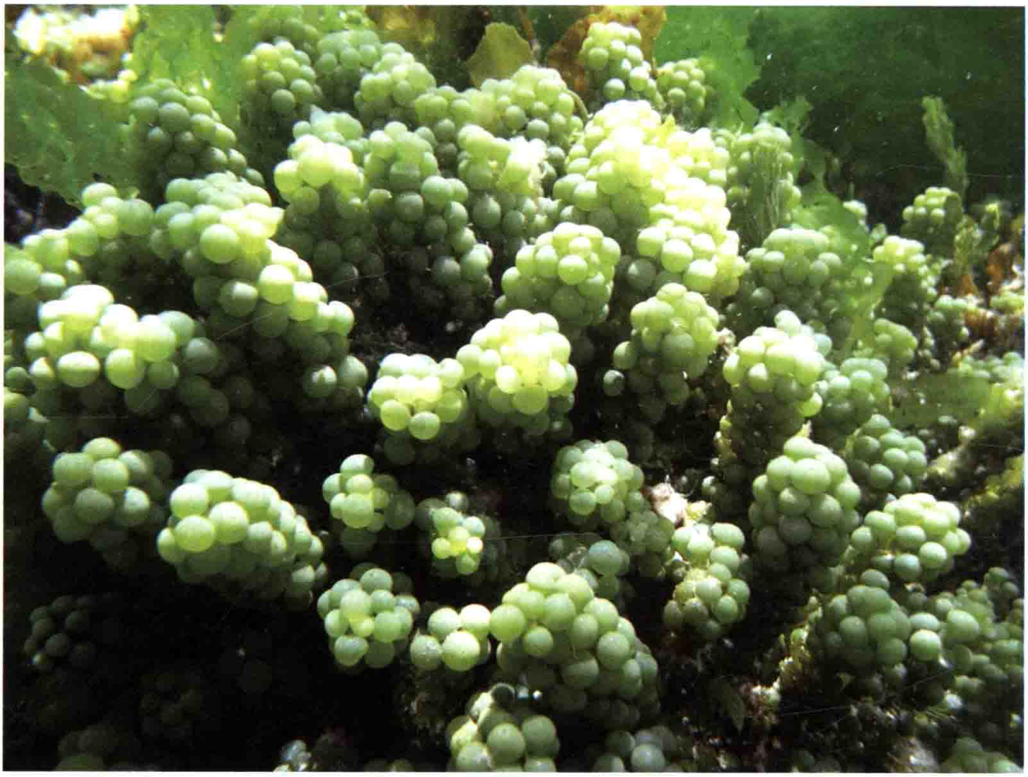
Preface

When we started to write this book, there were already a few excellent textbooks on the market describing photosynthesis in aquatic, including marine, environments. Noteworthy among them are the graduate-level books Aquatic Photosynthesis by our friends and colleagues Paul Falkowski and John Raven and the equally high-level book Light and Photosynthesis in Aquatic Ecosystems by our more recent acquaintance John Kirk. In addition, Anthony Larkum, Susan Douglas and John Raven had edited a multi-authored volume in the series Advances in Photosynthesis and Respiration entitled Photosynthesis in Algae. So why, then, yet another book on marine photosynthesis? First, the present text is suitable also for under-graduate level university and college students (BSc and equal levels) of biology or marine sciences, and parts can also be used for high-school science students who wish to brush up on photosynthesis and connect it with marine studies. Secondly, while the previous books describe marine photosynthesis and light as its driving force in great detail, the present book takes a more general look upon our oceans as an important habitat for plant growth (using the broad definition of marine 'plants' as including all photosynthetic organisms in the oceans), and we try in our text to link photosynthesis to the very special and different-from-terrestrial milieus that marine environments provide. Thus, researchers in the fields of terrestrial plant, or more general marine, sciences may here also be introduced to, or complement their knowledge in, the expanding field of marine plant 'ecophysiology' as related specifically to photosynthesis as the basis for marine plant growth. In this context we treat acclimations not only to light and the inorganic carbon composition of seawater, but also, e.g. to desiccation in the intertidal and pH in rockpools. Also, there is a chapter on how some marine plants can, through their photosynthetic characteristics, change the environment for other plants. Further, the present book fills in some gaps not covered extensively in the other volumes. These include subjects such as photosymbiosis in marine invertebrates, significantly larger portions devoted to marine macrophytes (macroalgae and, especially, seagrasses) and a background to common methodologies used for marine photosynthetic research. Lastly, but most importantly, however, the present book came about because we felt the need to convey our experiences in teaching and working on various aspects of marine plant photosynthesis to a larger audience than those peers and graduate students that (occasionally) read our scientific papers. The fact that much of this book reflects those experiences also goes hand in hand with the fun we had writing it; we hope you will enjoy reading it too!

Sven Beer, Mats Björk and John Beardall
Tel Aviv, Stockholm and Melbourne

PS: This is a First Edition and, so, mistakes are unavoidable. In order to make forthcoming editions better, we would be happy for any advice on improvements. Therefore, please do e-mail us any comments you may have on the contents of this book.

Cover photo: A thick turf of red and brown algae growing in the high-energy surf zone, Malta. Photo by Mats Björk.



The green alga *Caulerpa racemosa* at Zanzibar. Photo by Katrin Österlund.

About the companion website

This book is accompanied by a companion website:

www.wiley.com/go/beer/photosynthesis

The website includes:

- Powerpoints of all figures from the book for downloading
- PDFs of tables from the book

The brown alga *Fucus serratus* at the Swedish west coast. Photo by Mats Björk.

Contents

Part I
Plants and the Oceans

Introduction

Our planet as viewed from space is largely blue. This is because it is largely covered by water, mainly in the form of oceans (and we explain why the oceans are blue in Box 3.2, i.e. Box 2 in Chapter 3). So why then call this planet **Earth?** In our view, Planet Ocean, or **Oceanus**, would be a more suitable name; since the primary hit on Google for 'Planet Ocean' is a watch brand, let's meanwhile stick with Oceanus. Not only is the area covered by oceans larger than that covered by earth, rocks, cities and other dry places, but the volume of the oceans that can sustain life is vastly larger than that of their terrestrial counterparts. Thus, if we approximate that the majority of terrestrial life extends from just beneath the soil surface (where bacteria and some worms live) to some tens of metres (m) up (where the birds soar), and given the fact that, on the other hand, life in the oceans extends to their deepest depths of some 11 000 m, then a simple multiplication of the surface areas (~70% for oceans and ~30% for land) with the average depth of the oceans (3800 m), or height of terrestrial environments, gives the result that the oceans constitute a life-sustaining volume that is some 1000 times larger than that of the land. If we do the same calculation for plants only under the assumptions that the average terrestrial-plant height is 1 m (including the roots) and that there is enough light to drive **diel positive apparent** (or **net**) **photosynthesis**[1] down to an average depth of 100 m, then the 'life volume' for plant growth in the oceans is 250 times that provided by the terrestrial environments.

It has been estimated that photosynthesis by **aquatic plants**[2] **provides roughly half of the**

[1]Diel (= within 24 h, i.e. during the day AND the night) apparent (or net) photosynthesis is the **metabolic gas exchange of CO_2 or O_2** resulting from photosynthesis and respiration in a **24-h cycle** of light (where both processes take place) and darkness (where only respiration occurs). Net photosynthesis is positive if, during these 24 h, there is a net consumption of CO_2 or a net production of O_2.

[2]The word '**plant(s)**' is used here in the wider sense of encompassing all photosynthetic organisms, including those algae sometimes classified as belonging to the kingdom Protista (in, e.g. Peter Raven's et al. textbook Biology of Plants) and, unconventionally, also those photosynthetic prokaryotes referred to as cyanobacteria. The latter are of course not included taxonomically in the kingdom Plantae (they belong to the Eubacteria), but can, just like the algae, functionally be considered as 'plants' in terms

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global primary production[3] of organic matter (see, e.g. the book Aquatic Photosynthesis by Paul Falkowski and John Raven). Given that the salty seas occupy much larger areas of our planet than the freshwater lakes and rivers, there is no doubt that the vastly greater part of that aquatic productivity stems from photosynthetic organisms of the oceans. Other researchers have indicated that the marine primary (i.e. photosynthetic) productivity may be even higher than the terrestrial one: Woodward in a 2007 paper estimated the global marine primary production to be 65 Gt[4] carbon $year^{-1}$ while the terrestrial one was 60 Gt $year^{-1}$. This, and recently increasing realisations of the important contributions from very small, cyanobacterial, organisms previously missed by researchers (see Figure I.1a), lends thought to the realistic possibility that photosynthesis in the marine environment contributes to the major part of the primary productivity worldwide. Some of the players contributing to the marine primary production are depicted in Fig. I.1, while many others are described in Chapter 2.

Because marine plants are the basis for generating energy for virtually every marine food web[5], and given that the oceans may be even more productive than all terrestrial environments together, it is logical that the process of marine photosynthesis should be of interest to every biologist. But what about non-biologists? Why should the average person care about marine photosynthesis or marine plants? One of SB's in-laws has never eaten algae or any other products stemming from the sea; he hates even the smell of fish! However, after telling him that the oxygen (O_2) we breathe is (virtually, see Box 1.2) exclusively generated by plants through the process of photosynthesis, and that approximately half of the global photosynthetic activity takes place in the seas, even he agreed that any interference with the oceans that would lower their photosynthetic production would indeed also jeopardise his own wellbeing. And for those who like fish as part of their diet, the primary production of **phytoplankton**[6] is directly related to global fisheries' catches. So, for whatever reason, the need to maintain a healthy marine environment that promotes high rates of photosynthesis and, accordingly, plant growth in the oceans should be of high concern for everyone, just as it is of more intuitive concern to maintain healthy terrestrial environments.

This book will in this, its first, part initially review what we think we know about the evolution of marine photosynthetic organisms.

of their (important) role as primary (photosynthetic) producers in the oceans.

[3]Since photosynthesis is the basic process that produces energy for the life and growth of all organisms, its outcome is often called **primary production**; the rate at which the process of primary production occurs is called **primary productivity**.

[4]In the article by Woodward, the amounts of carbon is given in Pg (petagrams, $=10^{15}$ g). However, here we will adhere to the equally large unit Gt (gigatonnes, $=10^{9}$ tonnes) for global production rates of plants.

[5]The word 'virtually' is inserted as a caution from making too broad generalisations, and there are exceptions (which is true for almost every aspect of biology): It is for instance possible that runoff containing organic matter from land could partly sustain some near-shore ecosystems. Also, non-photosynthetic formation of organic matter (in a process called chemolithotrophy, where, e.g. energy to drive CO_2 assimilation is obtained from the oxidation of hydrogen sulphided to sulphur) near hydrothermal vents in the deep ocean has been found to feed entire, albeit quite space-limited, ecosystems.

[6]**Phytoplankton** (phytos = plant; plankton = 'drifters') refers here to all photosynthetic organisms that are carried around by the waves and currents of the oceans, be it small, often unicellular, cyanobacteria, eukaryotic microalgae or the occasional larger alga drifting in the water body. In the animal kingdom, the analogues to phytoplankton are the zooplankton; those animals that can direct their way by swimming against the currents are called nekton (e.g. most adult fish and other larger forms).

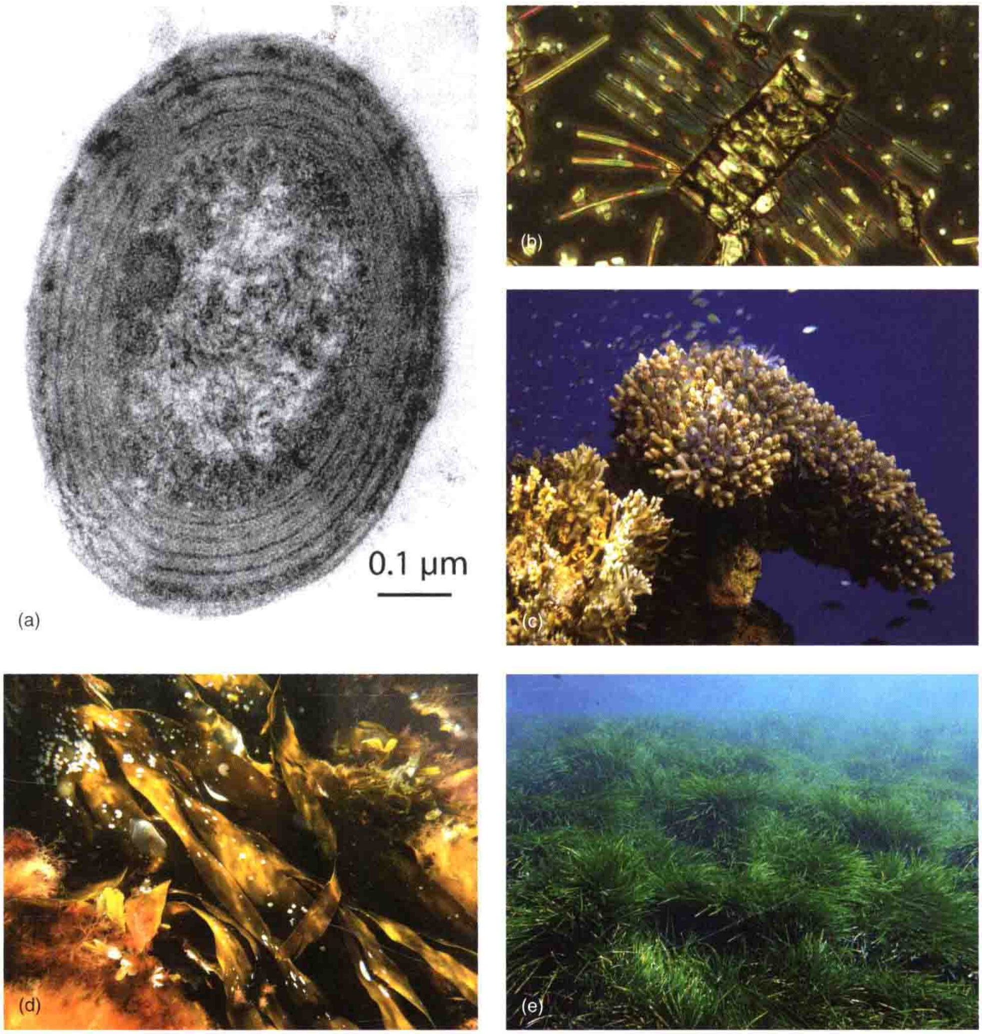

Figure I.1 Some of the 'players' in marine photosynthetic productivity. (a) The tiniest cyanobacterium (*Prochlorococcus marinus*) – the cyanobacteria may provide close to half of the oceanic primary production, at least in nutrient-poor waters. (b) A eukaryotic phytoplankter (the microalga *Chaetoceros* sp.) – the microalgae are probably the main primary producers of the seas. (c) Two photosymbiont- (zooxanthellae-)containing corals from the Red Sea (*Millepora sp.*, left, and *Stylophora pistillata*, right) – while quantitatively minor providers to global primary production, these photosymbionts keep the coral reefs alive. (d) The temperate macroalga *Laminaria digitata* – macroalgae provide maybe up to 10% of the marine primary production. (e) A meadow of the Mediterranean seagrass *Posidonia oceanica* – even though their primary productivity is amongst the highest in the world on an area basis, the contribution of seagrasses to the global primary production is small (but they form beautiful meadows!). Photos with permission from, and thanks to, William K. W. Li (Bedford Institute of Oceanography, Dartmouth, NS, Canada) and Frédéric Partensky (Station Biologique, CNRS, Roscoff, France) (a), Olivia Sackett (b), Sven Beer (c), Katrin Österlund (d) and Mats Björk (e).

Personal Note: Why algae are important

Most of the students taking my (JB) Marine Biology class are more interested in the animals (especially the 'charismatic' mega-fauna like dolphins, turtles and whales) than in those plants that ultimately provide their food. Indeed, when I first started my PhD, my supervisor advised me to "...never admit at parties to what you are studying (i.e. algae), or no-one will talk to you...". However, algae (as a major proportion of the marine flora) are far more important than 'just those things that cause green scum in swimming pools'. I deal with this in the very first lecture of my course by asking the students to put down their pens (or these days their laptops) and take a deep breath. They do this and I then I ask them to take a second deep breath – by this time they are wondering if I've finally lost it, but then I explain that the second breath they have just taken is using oxygen from photosynthesis by marine plants and that if it wasn't for this group of organisms, not only would our fisheries be more depleted than they already are, but also we'd only have half the oxygen to breath! This tends to focus their attention on those organisms at the bottom of the marine food chain and the fact that algae are responsible for around half of the biological CO_2 draw-down that occurs on our planet. As a consequence, algae get more of their respect.

—John Beardall.

Then, the different photosynthetic 'players' in the various marine environments will be introduced: the cyanobacteria and microalgae that constitute the bulk of the phytoplankton in sunlit open waters, the photosymbionts that inhabit many marine invertebrates, and the different macroalgae as well as seagrasses in those benthic[7] environments where there is enough light during the day for dielly positive net (or 'apparent', see, e.g. Section 8.1) photosynthesis to take place. Finally, the third chapter of this part will outline the different properties of seawater that are conducive to plant photosynthesis and growth, and in doing so will especially focus on what we view as the two main differences between the marine and terrestrial environments: the availability of **light** and **inorganic carbon**[8]. In doing so, this first part will, hopefully, become the basis for understanding the other two parts, which deal more specifically with photosynthesis in the marine environment.

[7] Benthic refers to the environments close to the bottom of water bodies (as opposed to the water column itself); the flora and fauna of the **benthos** are those organisms living in that environment and they include all sessile (bottom-attached) plants, the **phytobenthos**, as well as sessile and other bottom-dwelling animals such as cod.

[8] Unlike terrestrial plants, which use only atmospheric CO_2 for their photosynthesis, **marine plants can also utilise other inorganic carbon (Ci) forms** dissolved in seawater (see Chapters 3 and 7).