

The background of the cover is a close-up photograph of seaweed. It features dark, almost black, elongated, leaf-like structures with a slightly textured surface. Interspersed among these are lighter, yellowish-brown, branching structures that resemble the stipes or rhizoids of certain algae. The lighting is dramatic, highlighting the textures and creating deep shadows.

Algae

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Algae

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Preface

This book is designed for use by undergraduate and graduate students in courses on the algae and aquatic ecology, as well as by researchers and professionals in the fields of aquatic ecology and technological applications of algae. This text includes extensive photographic illustrations and provides detailed descriptions of representative algal genera. Professor Paul Silva, University of California-Berkeley, graciously researched the etymologies of the generic names of these representative forms that are included with the descriptions. Terms defined in the glossary appear in boldface in the text.

This book covers freshwater, marine, and terrestrial forms. For the student this provides the widest possible background, and thus greater flexibility in research options and when entering the job market. Our wide ecological treatment allows discussion of some important algal transmigrations. Furthermore, considerations of algal biodiversity and evolutionary topics also require coverage of forms that occupy a wide range of algal habitats.

Distinctive features of this book include a series of five introductory chapters designed to stimulate student interest and to provide an overview of the importance of algae. A survey of algal habitats, general characteristics, nutritional variation, and life-history types constitutes Chapter 1. Chapter 2 is focused on the roles of algae in global biogeochemistry and algal influences on present and past climates and atmospheric chemistry. Chapter 3, which considers biotic associations involving algae, includes discussion of herbivory interactions, algal food quality, predatory algae, pathogens of algae, algae as pathogens, and herbivory- and pathogen-defense adaptations. A chapter on technological applications (Chapter 4) includes discussion of algae grown for use as food and in the production of industrially useful materials, mariculture of economically useful algae, and applications of algae in effluent treatment and space technologies. We have, in Chapter 5, provided a primer on modern approaches to algal systematics, including coverage of major molecular systematic techniques and procedures commonly used to evaluate the significance of phylogenies. Already essential in studies of algal evolution, molecular phylogenetics will increasingly be added to the repertoire of algal ecologists. Operating under the assumption that students may be familiar with major algal groups but not with generic names, we have routinely coupled descriptive modifiers with generic names of algae in the five introductory chapters.

Another distinctive feature of this text is a chapter (Chapter 7) on the topic of endosymbiosis—an extremely widespread and ecologically important natural phenomenon that is the mechanism by which the eukaryotic algal groups arose. We believe knowledge of this subject to be essential for understanding differences in physiological and ecological behavior among protist groups. Chapter 7 provides an introduction to the eukaryotic algae. A core group of 15 chapters (Chapters 6 and 8–21) focuses on one or more groups of related algae. Each chapter includes group-specific structural, physiological, evolutionary, and ecological information. This book concludes with two chapters that provide brief synthetic treatments of phytoplankton ecology (Chapter 22), contributed by Dr. James Graham, and periphyton and seaweed ecology (Chapter 23).

Throughout this book we have included examples of new findings and approaches in algal molecular biology. Many instances of recently discovered algal forms are provided to demonstrate that algal biodiversity is incompletely known and that unknown forms await discovery by the curious and prepared investigator. We have provided somewhat more detail regarding the ultrastructure of flagellar apparatuses of algae than is found in many introductory texts, because such information is often essential (as are pigment and molecular sequence data) for the detection and classification of new forms. There is also an emphasis on algae of extreme habitats, in view of recent widespread interest in exotic biodiversity and its possible relevance to extraterrestrial biology (exobiology or astrobiology).

We have not provided taxonomic keys to the algal genera described due to space constraints and because we believe that the correlative use of more comprehensive, locally relevant taxonomic keys is a better alternative. Further, we have provided class, order, and family classifications only when these are supported by both classical and molecular data. References are provided to classification systems currently in use for the major groups, but we have avoided detailing those that have as yet not been

tested by application of molecular phylogenetic methods. Colloquial names referring to members of phyla (divisions) are given the suffix “phyte” and members of classes, “phycean.”

We have arranged algal groups in order of their phylogenetic divergence (antiquity), as inferred primarily from nuclear SSU rDNA gene sequences. The red algae are a possible exception, their phylogenetic position being currently controversial. We have placed the chapter on red algae between chapters covering brown and marine green algae for the convenience of users in coastal regions where brown, red, and green algae often co-occur. Each chapter is designed to stand alone—the content not depending on that found in other chapters (except Chapter 1)—so that Chapters 2 through 23 may be read in any order.

We have tried to incorporate both very recent and older classic references to research literature from around the world, but have been unable to provide a comprehensive review of the literature due to space limits. Further, we have attempted to reference work accomplished by investigators throughout the world, though few works in languages other than English are cited. Although there is much useful information on algae available on the internet, we have chosen not to include website addresses because of their volatility. We have commonly placed literature citations at the end of a series of relevant sentences to facilitate uninterrupted flow of thought. We would be pleased to receive recommendations of critical literature citations that might be added to a later edition.

Numerous phycologists from around the world graciously contributed original photographs to this project. Contributors are cited in the figure captions. As a token of our appreciation for the use of these images as well as the use of line art, we pledge a substantial contribution arising from book royalties to the International Phycological Congress for use by students for travel to congress meetings.

We are also grateful to Kandis Elliot, UW-Madison Department of Botany artist, who provided technical advice; the staff at Prentice Hall, particularly our editor, Teresa Ryu, and production editor, Kim Dellas; the UW-Madison Biology Library staff; and Professors Jane Gray, University of Oregon, and Ron Hoham, Colgate University, who provided reviews of limited material at our request. The following people were commissioned by Prentice Hall to review one or more book chapters, and we are very appreciative of their helpful efforts:

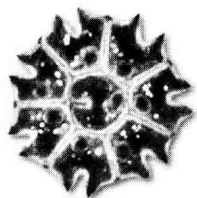
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Brief Contents

Preface	xv
1 Introduction to the Algae—Occurrence, Relationships, Nutrition, Definition, General Features	1
2 The Roles of Algae in Biogeochemistry	22
3 Algae in Biotic Associations	40
4 Technological Applications of Algae	64
5 Algal Diversity and Relationships—Taxonomy, Systematics, and Phylogeny	80
6 Cyanobacteria (Chloroxybacteria)	97
7 Endosymbiosis and the Origin of Eukaryotic Algae—With a Focus on Glaucoephytes, Chlorarachniophytes, and Apicomplexans	132
8 Euglenoids	154
9 Cryptomonads	169
10 Haptophytes	180
11 Dinoflagellates	198
12 Ochrophytes I—Introduction to the Ochrophytes and a Focus on Diatoms	232
13 Ochrophytes II—Raphidophyceans, Chrysophyceans, Synurophyceans, and Eustigmatophyceans	269
14 Ochrophytes III—Pelagophyceans, Silicoflagellates, Pedinellids, and Related Forms	294
15 Ochrophytes IV—Chrysomeridaleans, Phaeothamniophyceans, Tribophyceans, and Phaeophyceans	301
16 Red Algae	343
17 Green Algae I—Introduction and Prasinophyceans	397
18 Green Algae II—Ulvophyceans	420
19 Green Algae III—Trebouxiophyceans	452
20 Green Algae IV—Chlorophyceans	460
21 Green Algae V—Charophyceans	494
22 Phytoplankton Ecology—by <i>Dr. James M. Graham</i>	544
23 Macroalgal and Periphyton Ecology	603
Glossary	G-1
Literature Cited	L-1
Taxonomic Index	TI-1
Subject Index	SI-1

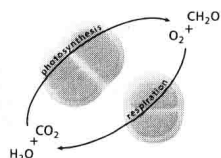
Contents

Preface xv



1 Introduction to the Algae—Occurrence, Relationships, Nutrition, Definition, General Features 1

- An Overview of the Occurrence and Activities of Algae 1
What are the Algae? 8
General Characteristics of Algae 14
Summaries of the Nine Algal Phyla Treated in This Book 19



2 The Roles of Algae in Biogeochemistry 22

- Limiting Factors 23
Algae and the Nitrogen Cycle 25
Cyanobacteria and the Origin of an Oxygen-Rich Atmosphere 26
Algae and the Carbon Cycle 27
Text Box 2-1 Stable Isotopic Measurements 30
Iron Limitation of Algal Growth 37
Algae and the Sulfur Cycle 38
Algal Production of Halocarbons 39



3 Algae in Biotic Associations 40

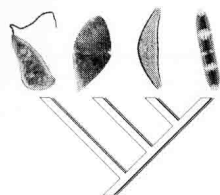
- Types and Importance of Algal Biotic Associations 41
Algal Food Quality 47
Algal Defenses 48
Detrital Food Webs and Pathogens of Algae 54
Algal Defenses Against Pathogens 57
Algal Epibionts 58
Algae as Parasites or Pathogens 58
Algal Symbioses 60
Lichens 61
Cyanobacterial-Plant Associations 63



4 Technological Applications of Algae 64

- Algae as Research Tools 64
Algae as Biomonitoring 66

Use of Fossil Algae in Paleoecological Assessments	67
Microalgae in Animal Aquaculture Systems	68
Microalgal Mass Cultivation for Production of Food Additives, Hydrocarbons, and Other Products	68
Human Uses of Seaweeds	70
The Use of Algal Turf Systems for Removal of Mineral Nutrients in Wastewater Effluents	75
Algae in Space Research	76
Screening of Algae for Production of Antiviral and Antifungal Compounds and Other Pharmaceuticals	77
Genetic Engineering of Algae for Improved Technological Performance	78



5 Algal Diversity and Relationships— Taxonomy, Systematics, and Phylogeny 80

Numbers and Definition of Algal Species	81
The Importance of Algal Species Identifications	82
Phylogeny Reconstruction	84
Choosing Molecular Phylogenetic Approaches	86
Generating, Identifying, and Evaluating Optimal Phylogenetic Trees	92
The Application of Phylogeny	94



6 Cyanobacteria (Chloroxybacteria) 97

The Paleobiology of Cyanobacteria	97
Cyanobacterial Taxonomy and Systematics	101
Cyanobacterial Phylogeny and Evolution	102
DNA Exchange in Cyanobacteria	106
Photosynthetic Light Harvesting	106
Carbon Fixation and Storage	112
Cyanobacterial Motility and Buoyancy	113
Nitrogen-Fixation	115
Akinetes	118
Cyanobacteria of Extreme Habitats	119
Morphological and Reproductive Diversity	121



7 Endosymbiosis and the Origin of Eukaryotic Algae—With a Focus on Glaucophytes, Chlorarachniophytes, and Apicomplexans 132

Precambrian Fossils Attributed to Eukaryotic Algae	135
Molecular and Biochemical Evidence for the Origin of the First Mitochondria and Plastids	136
Glaucophytes and Primary Endosymbiosis	140
Eukaryotic Algal Endosymbionts	143
Acquisition of Plastids by Secondary Endosymbiosis: A Focus on Chlorarachniophytes	147

Tertiary Endosymbiosis and Horizontal Gene Transfer in Dinoflagellates	150
Kleptoplastids	151
Unresolved Issues Surrounding Endosymbiotic Origin of Eukaryotic Algae	152

8 Euglenoids 154

Evolution and Cell Biology of Euglenoids	155
Euglenoid Motility and the Role of the Pellicle	159
Mucilage Production and the Formation of Palmelloid Colonies or Cell Envelopes	161
Euglenoid Reproduction	162
Plastids and Light-Sensing Systems	162
Euglenoid Ecology	163
Euglenoid Diversity	164

9 Cryptomonads 169

Cryptomonad Ecology	170
Cell Biology of Cryptomonads	172
Reproduction	177
Diversity of Cryptomonads	178

10 Haptophytes 180

Fossil Record	181
Phylogeny	182
Cell Biology and Reproduction	184
Diversity, Ecology, and Biogeography of Living and Fossil Haptophytes	190

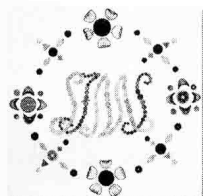
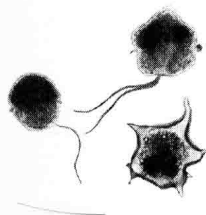
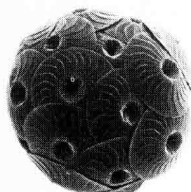
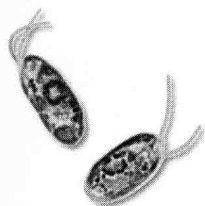
11 Dinoflagellates 198

Fossils and Evolutionary History	200
Dinoflagellate Cell Biology	202
Dinoflagellate Reproduction	211
Ecology	218
Techniques Used in the Identification and Classification of Dinoflagellates	224
Some Examples of Dinoflagellate Diversity	226

12 Ochrophytes I—Introduction to the Ochrophytes and a Focus on Diatoms 232

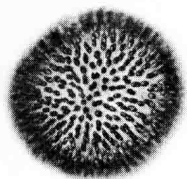
PART 1—INTRODUCTION TO THE OCHROPHYTES 232

Flagella and Flagellar Root Systems	235
Plastids	238
Phylogeny of Ochrophytes	240



PART 2—DIATOMS 241

- Text Box 12-1 Antarctic Sea-Ice Diatoms 243
- Fossil History 244
- Diatom Phylogeny 244
- Diatom Cell Biology 245
- Aspects of Diatom Physiology and Ecology 256
- Diatom Collection, Identification, and Diversity 259



13 Ochrophytes II—Raphidophyceans, Chrysophyceans, Synurophyceans, and Eustigmatophyceans 269

PART 1—RAPHIDOPHYCEANS 270

- Raphidophycean Diversity 272

PART 2—CHRY SOPHYCEANS 273

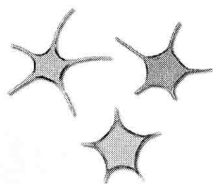
- Pigments 273
- Stomatocysts 274
- Cell Biology 276
- Nutrition 276
- Bloom Formation 277
- Habitat Preferences 277
- Morphology and Diversity 279
- Examples of Chrysophycean Diversity 279

PART 3—SYNUROPHYCEANS 285

- Cell Biology 286
- Synurophycean Ecology 289
- Synurophycean Diversity 290

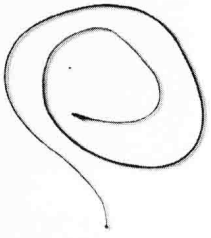
PART 4—EUSTIGMATOPHYCEANS 291

- Eustigmatophycean Diversity 292



14 Ochrophytes III—Pelagophyceans, Silicoflagellates, Pedinellids, and Related Forms 294

- Pelagophyceans and Sarcinochrysidaleans 295
- Silicoflagellates, Pedinellids, and Rhizochromulinids 297



15 Ochrophytes IV—Chrysomeridaleans, Phaeothamniophyceans, Tribophyceans, and Phaeophyceans 301

Fossils and Phylogeny 302

PART 1—CHRYSMERIDALES, PHAEOTHAMNIOPHYCEAE, AND THE XANTHOPHYLL CYCLE 303

PART 2—TRIBOPHYCEAE 305

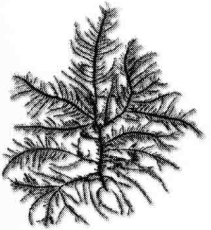
Tribophycean Diversity 306

PART 3—PHAEOPHYCEANS (BROWN ALGAE) 310

Cell Biology 311

Reproduction 316

Phaeophycean Diversity and Systematics 320



16 Red Algae 343

Red Algal Pigments 345

Other Distinctive Features of Red Algae 346

Fossils and Evolutionary Relationships 349

Cell Wall Structure and Biochemical Composition 351

Plastids and Other Cellular Constituents 354

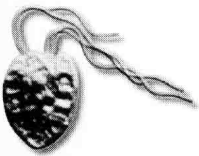
Cell Division, Development, and Primary Pit-Plug Formation 355

Text Box 16-1 Use of DNA Measurements in the Study of Algal Life Histories 358

Reproduction and Life Histories 362

Red Algal Physiology and Ecology 370

Structural and Reproductive Diversity 375



17 Green Algae I—Introduction and Prasinophyceans 397

PART 1—INTRODUCTION TO THE GREEN ALGAE 397

Green Algal Phylogeny and Evolution 400

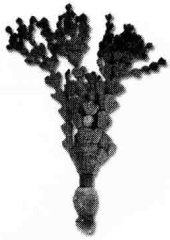
The Major Green Algal Lineages 401

General Characteristics of the Green Algae 403

PART 2—PRASINOPHYCEANS 412

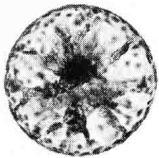
Cellular Features of Prasinophyceans 414

Text Box 17–1 Sexual Reproduction in <i>Nephroselmis olivacea</i>	417
Some Examples of Prasinophycean Diversity	418



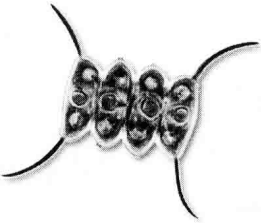
18 Green Algae II—Ulvophyceans 420

Evolution and Fossil History	422
Ulvophycean Diversity and Ecology	424
Text Box 18–1 Mass Spawning by Caulerpalean Algae	446



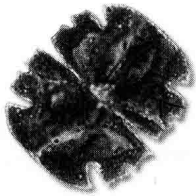
19 Green Algae III—Trebouxiophyceans 452

Phylogenetic Relationships of the Trebouxiophyceans	453
Diversity	454



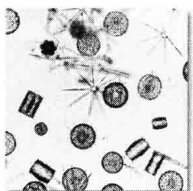
20 Green Algae IV—Chlorophyceans 460

Chlorophycean Thallus Types, Habitats, and Reproduction	461
Chlorophycean Diversity	463
Text Box 20–1 Red and Green Snow	478



21 Green Algae V—Charophyceans 494

Relationships of the Charophycean Algae to Land Plants	496
Text Box 21–1 Molecular Architectural Characters and the Phylogeny of Charophycean Algae	497
Diversity of Charophyceans	498



22 Phytoplankton Ecology— by Dr. James M. Graham 544

The Physical Environment	548
Text Box 22–1 Remote sensing of phytoplankton	555
The Chemical Environment	556
Growth Processes of Phytoplankton Populations	559
Growth and Light	563
Growth and Nutrient Uptake	564
Growth and Uptake of Organic Carbon	571
Loss Processes	571



23 Macroalgal and Periphyton Ecology

603

PART 1—MARINE MACROALGAL ECOLOGY 606

Physical Factors and Macroalgal Adaptations 606

Text Box 23-1 Algae and Coral Reefs 607

Text Box 23-2 Fluorescence Methods for Assessing Photosynthetic Competency and Nitrogen Limitation 615

Biological Factors and Macroalgal Adaptations 619

Macroalgal Biogeography 624

PART 2—MARINE TURF-FORMING PERIPHYTON 630

PART 3—FRESHWATER PERIPHYTON 632

The Influence of Physical Factors on Periphyton 634

Grazing 636

Temporal and Spatial Variation 637

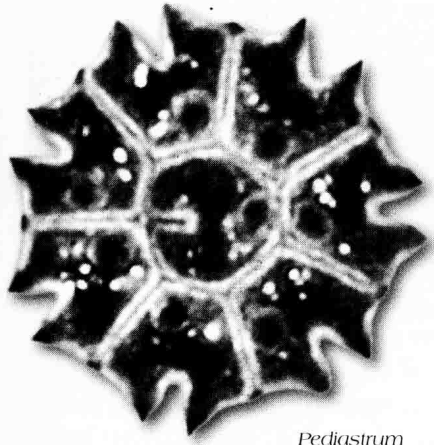
Pollution Effects 639

Glossary G-1

Literature Cited L-1

Taxonomic Index TI-1

Subject Index SI-1



Pedicellula

Introduction to the Algae

Occurrence, Relationships, Nutrition, Definition, General Features

From tiny single-celled species one micrometer in diameter to giant seaweeds over 50 meters long, algae are abundant and ancient organisms that can be found in virtually every ecosystem in the biosphere. For billions of years algae have exerted profound effects on our planet and its biota, and they continue to do so today. Still, in many habitats algae often go unnoticed unless environmental conditions become favorable for the development of conspicuous and sometimes massive proliferations of their numbers—a situation often brought about by human activity. People from many cultures, ancient and modern, have used algae for a variety of purposes. With the advent of biotechnology, algae are poised to play greater, albeit often subtle, roles in the day-to-day lives of human beings. In the following passages we provide a brief overview of algal habitats and activities that demonstrates algae occur in both expected and highly surprising places. This survey will set the stage for a circumscription of the algae, i.e., a definition for this enigmatic group of organisms.

An Overview of the Occurrence and Activities of Algae

Algae in the Marine Habitat

On land the largest and most striking plants are the trees. Together with their herbaceous relatives, their foliage makes green the most conspicuous color of the biosphere. Underwater there are “trees” of similar height that are less widely appreciated because most humans spend little time in their realm. Brown undulating forests of 50-meter-long giant kelps, as tall and crowded as their terrestrial counterparts, dominate significant stretches of submerged temperate coastlines (Fig. 1–1). Like trees, kelps use pho-



Figure 1–1 Kelp forest off the Chilean coast. The predominant alga pictured is *Macrocystis*. (Photograph courtesy R. Searles)

tosynthesis to convert the energy of sunlight into chemical energy, but the green of their chlorophyll is masked by large amounts of brown pigments. These **accessory pigments** aid in the collection of light not absorbed directly by chlorophyll molecules and channel the light

energy to chlorophyll *a*—the only pigment that is able to effectively convert the energy of absorbed light into high energy bonds of organic molecules. This is necessary because as light passes through water, the longer wavelengths are filtered out first, such that eventually all that remains is a faint blue-green light that cannot be absorbed by chlorophyll.

Brown seaweeds are not limited to temperate waters, as they also form luxuriant thickets beneath polar ice sheets rarely noticed by anyone but phycologists or algologists—scientists who study these and other algae. The depth record for algae is held by dark purple-colored crusts of yet unnamed red algae discovered in tropical waters by phycologists using submersibles. These organisms live at depths greater than 250 meters, where the light intensity is only 0.0005% that of surface light. The accessory pigments of these algae—whose role is the same as that for those found in the kelps—are essential for the survival of photosynthetic organisms in such low-irradiance environments. In contrast, algae that live in high-irradiance habitats typically have pigments that help protect against photodamage. It is the composition and amounts of accessory and protective photosynthetic pigments that give algae their wide variety of colors and, for several algal groups, their common names such as the brown algae, red algae, and green algae. (We should caution, however, that attempting to identify a particular alga by color alone could be problematic, since, for example, there are red-colored green algae and brown or purple-colored red algae; other characteristics and features must also be considered.)



Figure 1–2 Nearshore underwater marine algae (primarily the calcified brown alga *Padina*) in the Bahamas. A gorgonian coral is in the foreground.

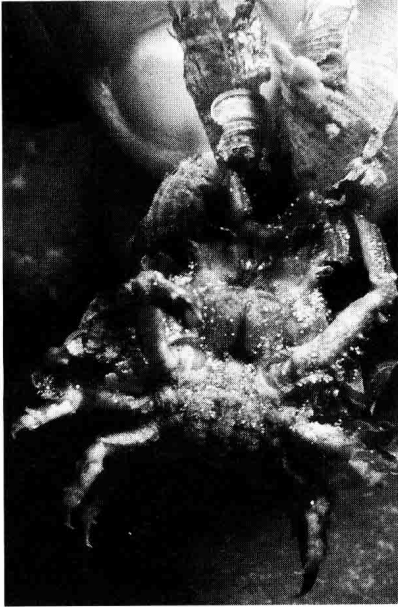


Figure 1-3 A small decorator crab with various attached algae.

The rocky or sandy shallows of temperate and tropical oceans harbor a vast array of brown, red, and green algal growths that may form thin and sometimes slippery films on rocks; diaphanous, lacy, or fleshy forms attached by holdfasts; or miniature jointed shrubs armored with limestone (Fig. 1-2). Myriad smaller algae, like the epiphytes found on rain forest trees, attach themselves to, or actually grow within, larger seaweeds, rocks, corals, and shells. Algae share the tidal zone with numerous invertebrate animals such as barnacles and snails, which often compete with them for space or consume them. Occasionally small clumps of seaweeds may appear to crawl slowly across the ocean floor or along a coral reef—closer inspection reveals “decorator” crabs that have adorned themselves with a fashionable selection of brown, green, or red algae as a camouflage (Fig. 1-3).

Tropical fringes are typically populated with a breathtakingly diverse array of submersed reef-forming corals, whose very existence and form are dependent upon intracellular tenants—microscopic golden algal cells known as **zooxanthellae**—that generate food and oxygen in exchange for metabolic by-products (carbon dioxide and ammonia) released by the coral cells. Zooxanthellae allow corals to thrive in the typically low-nutrient conditions of tropical waters. Because of their obligate association with these photosynthetic algae, reef-building corals are limited to shallow, well-illuminated waters less than 20 meters or

so in depth. Beneficial algae also occur within the cells and tissues of a wide variety of other marine animals such as nudibranchs, anemones, giant clams, ascidians, and sponges, as well as inside the cells of radiolarians and foraminiferans, which are but two types of the multitudinous simple organisms known as **protists**, an informal group to which the algae also belong.

Sandy tropical shallows may also contain extensive microbial mats composed of an interwoven community of cyanobacteria (also known as chloroxybacteria, blue-green algae, or cyanophytes), diatoms, and other microorganisms. In a few places—notably Shark Bay, Australia and tidal channels close to Exuma Island in the Bahamas—generations of calcium carbonate-depositing, sediment-trapping, cyanobacteria have built layered hummocks up to two meters high (Fig. 1-4). These hummocks represent modern versions of more widespread fossil formations known as **stromatolites**, which are commonly associated with the occurrence of earth’s earliest life-forms.

In addition to these conspicuous marine algal communities with their relatively large seaweeds, coral formations, or algal aggregations, the surrounding ocean waters—occupying approximately 70% of the Earth’s surface—teem with some 5000 species of tiny floating or swimming emerald, ruby, topaz, and turquoise jewels known as **phytoplankton** (Fig. 1-5). Although individually visible to humans only with the aid of a microscope, large populations can give ocean waters green or rusty hues. Color variations reflect differences in the types and amounts of blue-green, red, orange, and golden accessory pigments accompanying the green of chlorophyll. Like those giving larger seaweeds their brown, purple, or red coloration, these variously colored pigments also



Figure 1-4 Modern-day stromatolites in Shark Bay, Australia. (Photograph courtesy A. Knoll)

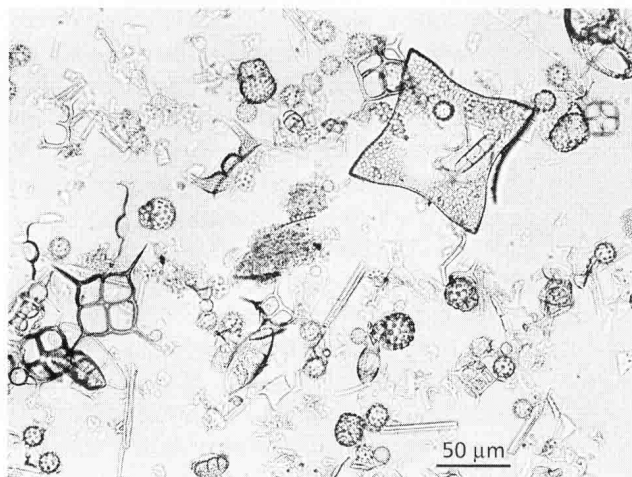


Figure 1-5 Sedimented phytoplankton from the late Cretaceous and early Cenozoic Arctic Ocean, including silicoflagellate and diatom remains. (Specimen courtesy D. Clark)

assist in harvesting light for photosynthesis and in photoprotection. Enormous variation in phytoplankton shape and size has resulted from multiple adaptive solutions to two important problems: sinking to depths where the low levels of light limit photosynthesis and growth, and herbivory—the consumption of algae by animals and protists.

Populations of marine phytoplankton can become so large that they are detectable by satellite remote sensing technology. Such **blooms** are in fact one of the more dramatic vegetational features of the planet when viewed from space (Fig. 1-6). Collectively, marine microalgae have been modifying the earth's atmosphere for more than 2.7 billion years (Buick, 1992), and they continue to exert a powerful influence on modern atmospheric chemistry and biogeochemical cycling of carbon, sulfur, nitrogen, phosphorus, and other elements (Chapter 2). Hundreds of millions of years' worth of past phytoplankton growth and sedimentation have generated important oil and limestone deposits. Algal plankton also form the base of marine food chains, supporting both microbial and animal plankton (zooplankton), upon which economically important marine fisheries and ecologically significant marine mammal and bird populations are dependent.

The Algae of Freshwaters

Freshwater lakes, ponds, and streams contain similar botanical gardens of planktonic microalgae and attached forms (**periphyton**), which are often them-

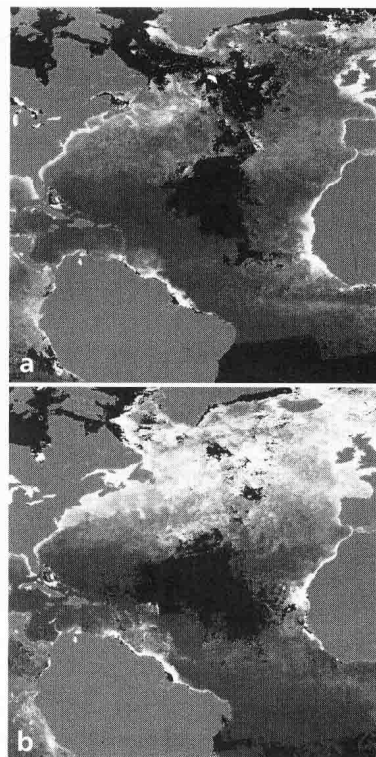


Figure 1-6 Two NASA satellite images of the North Atlantic taken in (a) winter and (b) spring. Brighter areas represent higher concentrations of chlorophyll and, hence, phytoplankton. Totally black areas are regions for which data were not collected.

selves festooned with epiphytes (Fig. 1-7). Although not exhibiting the phenomenal size range of their marine relatives, freshwater algae nonetheless display a wide diversity of form and function. As in the

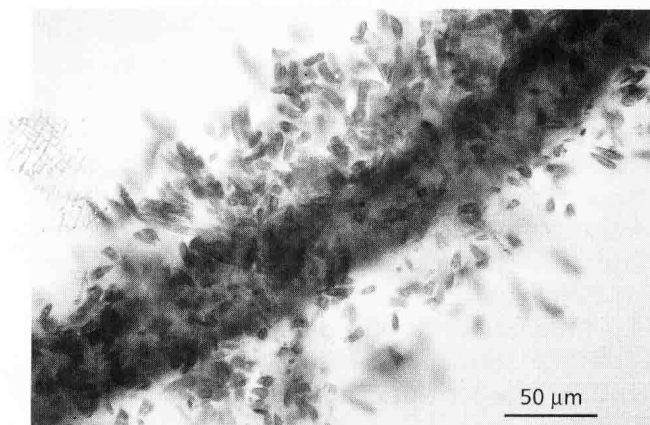


Figure 1-7 A specimen of the freshwater green alga *Oedogonium* with large numbers of epiphytic diatoms.