

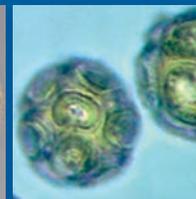
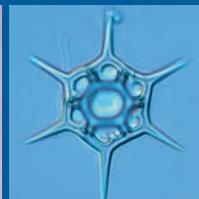
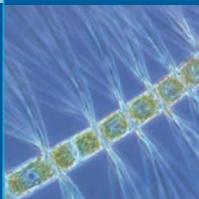


Kleine Senckenberg-Reihe 49

Mona Hoppenrath, Malte Elbrächter & Gerhard Drebes

# Marine Phytoplankton

Selected microphytoplankton species from the North Sea  
around Helgoland and Sylt



E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller) Stuttgart

Mona Hoppenrath, Malte Elbrächter & Gerhard Drebes

# Marine Phytoplankton

**Selected microphytoplankton species from the North Sea  
around Helgoland and Sylt**

senckenberg  
forschungsinstitut und naturmuseum



AWI   
Alfred-Wegener-Institut  
für Polar- und Meeresforschung  
in der Helmholtz-Gemeinschaft

# Impressum

## Herausgeber

Prof. Dr. Dr. h.c. Volker Mosbrugger,  
Senckenberg Gesellschaft für Naturforschung,  
Senckenberganlage 25, 60325 Frankfurt am Main, Germany

## Autoren des Bandes

Dr. Mona Hoppenrath,  
Forschungsinstitut Senckenberg,  
Deutsches Zentrum für Marine Biodiversitätsforschung,  
Südstrand 44, D–26382 Wilhelmshaven, Germany,  
E-Mail: mhoppenrath@senckenberg.de;

Dr. Malte Elbrächter,  
Forschungsinstitut Senckenberg,  
Deutsches Zentrum für Marine Biodiversitätsforschung,  
Wattenmeerstation Sylt, Hafenstrasse 43,  
D–25992 List/Sylt, Germany;

Dr. Gerhard Drebes,  
Wattenmeerstation Sylt,  
Alfred Wegener Institut für Polar- und Meeresforschung,  
Hafenstrasse 43,  
D–25992 List/Sylt, Germany;  
derzeitige Adresse: Magnussenstr. 15,  
D–24837 Schleswig, Germany

## Umschlag

Die Abbildungen auf dem Umschlag zeigen eine kleine Auswahl von Phytoplanktonarten, die in der Nordsee leben. Die abgebildeten Arten präsentieren die unterschiedlichen Gruppen: Kieselalgen, Dinoflagellaten, Silikoflagellaten und Prymnesiophyten – alle detailliert in diesem Band beschrieben.

## Satz, Layout und Lithografie

Petra Schwarzmann, Wiesbaden, Germany

## Druck und buchbinderische Verarbeitung

Druckerei Hubert & Co GmbH & Co, Göttingen, Germany

## Vertriebsverlag

E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller)  
Johannesstraße 3A, 70176 Stuttgart, Germany  
www.schweizerbart.de  
E-Mail: mail@schweizerbart.de  
© 2009 E. Schweizerbart'sche Verlagsbuchhandlung

Die Autoren sind für den Inhalt des Bandes verantwortlich.

Alle Rechte, auch das der Übersetzung, des auszugsweisen Nachdrucks, der Herstellung von Mikrofilmen und der Übernahme in Datenverarbeitungsanlagen vorbehalten.

Dieses Buchprojekt wurde in Kooperation und mit Unterstützung des Alfred-Wegener-Institut für Polar- und Meeresforschung in der Helmholtz-Gemeinschaft realisiert.

[www.senckenberg.de](http://www.senckenberg.de)

ISBN 978–3–510–61392–2  
ISBN ebook (pdf) 978-3-510-65519-9

## Bibliografische Information Der Deutschen Bibliothek

Die Deutsche Bibliothek verzeichnet diese Publikation in der Deutschen Nationalbibliografie; detaillierte bibliografische Daten sind im Internet über <http://dnb.ddb.de> abrufbar.



Bildbearbeitung: Brockmann Consult © 2009, Datenquelle: Landsat 7 ETM, Eurimage © 2002

# Contents

<b>Greetings</b>		8
<b>Foreword</b>		9
<b>Acknowledgements</b>		10
<b>Introduction</b>	Hoppenrath, Elbrächter & Drebes	12
<b>Diatoms / Bacillariophyceae</b>	Hoppenrath & Drebes	22
Centric diatoms		28
<b>Centric looking centric diatoms</b>		28
Genus: <i>Coscinodiscus</i>		28
Genus: <i>Stellarima</i>		32
Genus: <i>Actinocyclus</i>		33
Genus: <i>Roperia</i>		35
Genus: <i>Actinoptychus</i>		35
Genus: <i>Auliscus</i>		37
Genus: <i>Aulacodiscus</i>		39
Genus: <i>Cerataulus</i>		39
Genus: <i>Podosira</i>		39
Genus: <i>Melosira</i>		40
Genus: <i>Paralia</i>		40
Genus: <i>Stephanopyxis</i>		42
Genus: <i>Skeletonema</i>		44
Genus: <i>Detonula</i>		45
Genus: <i>Lauderia</i>		47
Genus: <i>Porosira</i>		47
Genus: <i>Thalassiosira</i>		49
Genus: <i>Minidiscus</i>		62
Genus: <i>Cyclotella</i>		62
<b>Rod-like looking and cylindrical chain forming centric diatoms</b>		62
Genus: <i>Rhizosolenia</i>		62
Genus: <i>Proboscia</i>		66
Genus: <i>Dactyliosolen</i>		68
Genus: <i>Cerataulina</i>		68
Genus: <i>Guinardia</i>		70
Genus: <i>Leptocylindrus</i>		71
<b>Centric, mainly chain-forming, diatoms with spines and setae</b>		71
Genus: <i>Corethron</i>		71
Genus: <i>Bacteriastrum</i>		73
Genus: <i>Chaetoceros</i>		73
<b>Leaf-like looking centric diatoms</b>		85
Genus: <i>Neocalyptrella</i>		85
Genus: <i>Helicotheca</i>		87
Genus: <i>Mediopyxis</i>		87

<b>Not “centric”-looking centric diatoms</b>	<b>89</b>
Genus: <i>Lithodesmium</i>	89
Genus: <i>Ditylum</i>	89
Genus: <i>Bellerochea</i>	91
Genus: <i>Odontella</i>	91
Genus: <i>Biddulphia</i>	97
Genus: <i>Triceratium</i>	98
Genus: <i>Eucampia</i>	98
Genus: <i>Eunotogramma</i>	98
Genus: <i>Brockmanniella</i>	100
Genus: <i>Cymatosira</i>	100
Genus: <i>Minutocellus</i>	100
Genus: <i>Plagiogrammopsis</i>	102
<b>Pennate diatoms</b>	<b>102</b>
Genus: <i>Plagiogramma</i>	102
Genus: <i>Subsilicea</i>	103
Genus: <i>Fragilaria</i>	103
Genus: <i>Asterionellopsis</i>	103
Genus: <i>Asteroplanus</i>	105
Genus: <i>Rhaphoneis</i>	105
Genus: <i>Delphineis</i>	105
Genus: <i>Thalassionema</i>	106
Genus: <i>Achnanthes</i>	106
Genus: <i>Meuniera</i>	106
Genus: <i>Bacillaria</i>	108
Genus: <i>Ceratoneis</i>	108
Genus: <i>Pseudo-nitzschia</i>	110
Genus: <i>Nitzschia</i>	112
<b>Dinoflagellates / Dinophyceae</b>	<b>Elbrächter &amp; Hoppenrath</b>
<b>Unarmoured (athecate) species</b>	<b>114</b>
Genus: <i>Gymnodinium</i>	120
Genus: <i>Syltodium</i>	123
Genus: <i>Akashiwo</i>	125
Genus: <i>Karenia</i>	125
Genus: <i>Karlodinium</i>	126
Genus: <i>Gyrodinium</i>	127
Genus: <i>Sclerodinium</i>	130
Genus: <i>Spatulodinium</i>	131
Genus: <i>Actiniscus</i>	131
Genus: <i>Togula</i>	133
Genus: <i>Amphidinium</i>	133
Genus: <i>Katodinium</i>	134

Genus: <i>Torodinium</i>	135
Genus: <i>Cochlodinium</i>	135
Unarmoured Dinophytes with a conspicuous ocelloid	136
Genus: <i>Warnowia</i>	136
Genus: <i>Nematodinium</i>	138
Genus: <i>Proterythroopsis</i>	138
Species forming pseudocolonies	138
Genus: <i>Polykrikos</i>	138
Species with a tentacle, see also mature cells of <i>Spatulodinium</i>	140
Genus: <i>Noctiluca</i>	140
Aberrant dinoflagellates	142
Genus: <i>Pronoctiluca</i>	142
Genus: <i>Oxyrrhis</i>	142
Armoured (thecate) Dinophytes	143
<b>Order Peridiniales</b>	143
Genus: <i>Protoperidinium</i>	143
Group: <i>Scrippsiella</i>	162
Genus: <i>Scrippsiella</i>	163
Genus: <i>Pentapharsodinium</i>	164
Genus: <i>Ensiculifera</i>	164
Genus: <i>Heterocapsa</i>	164
Group: <i>Diplopsalis</i>	166
Genus: <i>Diplopsalis</i>	167
Genus: <i>Preperidinium</i>	167
Genus: <i>Diplopelta</i>	169
Genus: <i>Diplopsalopsis</i>	169
Genus: <i>Oblea</i>	172
<b>Order Gonyaulacales</b>	172
Genus: <i>Ceratium</i>	172
Genus: <i>Gonyaulax</i>	179
Genus: <i>Protoceratium</i>	182
Genus: <i>Amylax</i>	183
Genus: <i>Alexandrium</i>	184
Genus: <i>Fragilidium</i>	188
Genus: <i>Pyrophacus</i>	188
Genus: <i>Thecadinium</i>	190
<b>Order Dinophysiales</b>	191
Genus: <i>Dinophysis</i>	191
<b>Order Prorocentrales</b>	194
Genus: <i>Prorocentrum</i>	195
Genus: <i>Mesoporus</i>	198

Parasitic dinoflagellates	199
Genus: <i>Dissodinium</i>	199
Genus: <i>Paulsenella</i>	202
Genus: <i>Oodinium</i>	204
Genus: <i>Dubosquella</i>	204
Genus: <i>Amoebophrya</i>	206
<b>Prymnesiophytes</b>	<b>Hoppenrath &amp; Elbrächter</b>
<i>Phaeocystis</i>	207
<i>Corymbellus</i>	209
<i>Acanthoica</i>	209
<i>Coccolithus</i>	209
<i>Emiliana</i>	209
<b>Raphidophyceae</b>	<b>Elbrächter &amp; Hoppenrath</b>
<i>Fibrocapsa</i>	211
<b>Dictyochophyceae</b>	<b>Hoppenrath &amp; Elbrächter</b>
<i>Dictyocha</i>	213
<i>Pseudochattonella</i>	213
<i>Verrucuphora</i>	213
<b>Other selected protists</b>	<b>Hoppenrath &amp; Elbrächter</b>
<i>Ebria</i>	215
<i>Hemistasia</i>	215
<i>Mesodinium</i>	215
<i>Halosphaera</i>	217
<i>Paulinella</i>	217
<i>Calycomonas</i>	217
<b>Plankton parasites</b>	<b>Hoppenrath, Elbrächter &amp; Drebes</b>
<i>Lagenisma</i>	218
<i>Ectrogella</i>	218
<i>Rhizophydium</i>	218
<i>Chytridium</i>	218
<i>Phagomyxa</i>	218
<i>Pseudaphelidium</i>	220
<i>Rhizamoeba</i>	220
<i>Amoeba</i>	220
<i>Pirsonia</i>	220
<i>Pseudopirsonia</i>	222
<i>Cryothecomonas</i>	223
<i>Victoriniella</i>	223
<b>References</b>	224
<b>Scientific movies</b>	246
<b>Taxonomic index</b>	248

## Greetings

As far as we know, the earth is the only “living planet”. Its biosphere is not just a nice epiphenomenon but a most relevant and active part of earth system dynamics. Life has conquered all surface environments of our planet, the deep biosphere even a relatively thick layer of the earth’s crust. It controls biogeochemical cycles, influences weathering, erosion and climate and thus shapes the environment of our planet. And last but not least, we humans are part of this biosphere and live of it. However, in spite of all our scientific efforts we still know relatively little about this biosphere. Presently 1.8 million species are known, but experts estimate that an unknown diversity of 5 to 50 times as many species are actually living on our planet and that we are constantly losing about 100 unknown species per day due to human activities. This clearly illustrates the relevance of inventories of life!

Hence, this book is a welcome, timely and in fact an utmost needed contribution to our understanding of the marine biosphere and more specifically of the marine phytoplankton representing the basis of the marine ecosystems inhabiting the world ocean. It describes

almost 300 phytoplankton species from the North Sea around Helgoland and Sylt. With its excellent illustrations it will certainly find the broad readership it is designed for and help in assessment and management processes of North Sea ecosystems. The book also illustrates that systematics and compiling inventories of life is a most demanding and complex science requiring long-term field observations as well as most advanced laboratory techniques.

Our congratulations go to the three authors, all internationally renowned experts in the field of marine biodiversity, for this monograph which certainly will serve as a standard work for many years to come. Our institutions, i.e. the Alfred Wegener Institut and Senckenberg, are proud of having hosted and supported this great project.

Volker Mosbrugger  
Senckenberg

Joern Thiede  
Retired from AWI

## Foreword

The world of marine phytoplankton is both fascinating and beautiful. We present it here to a broad audience of users: hobby-microscopists, students of biology and biological oceanography and persons doing phytoplankton monitoring and administrators using the results of the phytoplankton assessment. We hope that scientists will use this book either as an identification-help, as a starting point for their own research, or as a means of documentation of the species diversity of a special region that contributes greatly to current biogeographic knowledge.

The first edition of this book (Drebes 1974) aimed to present phytoplankton taxa in their living form and to contribute to the knowledge of their life cycles. It was written with a focus on living cells, in contrast to the usual taxonomic publications of that time, that emphasized dead parts of the cells (silica frustules, cellulosic thecal plates, calcareous coccoliths). Because the first edition was continuously “mis”-used for species identification and taxonomic work, we changed the focus of the present edition in this respect. While still focusing on living cells and their life cycle stages in the light microscope, the book has been expanded

by adding ultrastructural data (scanning electron microscopy = SEM), by updating and expanding on taxonomic information and by the comparison with similar species. As a consequence, the content of the book has increased somewhat, reflecting the increased knowledge about the species present in the investigated area and about their taxonomy. We present 288 species in 129 genera [141 diatoms (57 genera), 113 dinoflagellates (47 genera), 6 prymnesiophytes (5 genera), 1 raphidophyte, 3 dictyochophytes (2 genera), 6 others (6 genera), and 18 plankton parasites (11 genera)], in comparison to about 170 species in the first edition (Drebes 1974). They are illustrated with around 1100 images and 70 line drawings on 85 plates. Many of the original light micrographs presented in the first edition (Drebes 1974) are shown here again, and we are grateful to the GEORG THIEME VERLAG for agreeing to transfer the copyright.

Wilhelmshaven, List/Sylt & Schleswig,  
Januar 2009

Mona Hoppenrath, Malte Elbrächter &  
Gerhard Drebes

## Acknowledgements

This book is one of the major outcomes of a postdoctoral project financed by the Alfred Wegener Institut für Polar- und Meeresforschung (AWI) and MH thanks for the position, which gave her the chance to reinvestigate the phytoplankton taxonomically. ME, as permanent guest scientist at the AWI, acknowledges the generous support he got during all these years by the director of the AWI, Prof. Dr. Jörn Thiede, and the staff of the Wadden Sea Station Sylt.

We are grateful to the following colleagues, who contributed in one or the other way to this book. First of all Mrs Hannelore Halliger (AWI, Wadden Sea Station Sylt, Germany), she accompanied the phytoplankton biodiversity-monitoring many years as technical assistant, and is now continuing the work, keeping the phytoplankton long-term series at Sylt alive. Special thanks to her from MH for the first introduction to the phytoplankton diatom identification, the discussions about actual observations, the help with specimen isolations, culturing, preparation for the SEM, literature, and additional light micrographic documentation of many species. Dr. Linda Medlin (AWI Bremerhaven, Germany) kindly

helped identifying some *Thalassiosira* species and used molecular tools to verify the identity of *Pseudo-nitzschia* and *Skeletonema* isolates. Prof. Dr. Grethe R. Hasle (University of Oslo, Norway) is thanked for the information about *Pseudo-nitzschia* identifications from Helgoland samples and the many reprints. Prof. Dr. Jan Rines (University of Rhode Island, USA) kindly gave her opinion about our *Chaetoceros* identifications and helped naming some, thank you very much for that. Dr. Richard Crawford (AWI Bremerhaven, Germany) is thanked for the discussions about taxonomic and nomenclatural issues and Mrs Friedel Hinz (AWI Bremerhaven, Germany) for the many “literature- and information-e-mails” while MH was working in Canada. Dr. Rolf Klee (Bayerisches Landesamt für Umwelt, Germany) helped with the *Cyclotella* identification. Dr. Sabine Agatha and Prof. Dr. Wilhelm Foissner (University of Salzburg, Austria) gave their opinion about the *Mesodinium/Myrionecta rubrum/a* taxonomy and helped with literature. Dr. Erik Hagmeier’s (Helgoland) “informative stories”, his constant interest in the topic and the discussions have been very much appreciated by MH. We thank Prof. Dr. Eberhard Schnepf (University of Heidelberg, Germany), Prof. Dr. Karsten Reise

(Wadden Sea Station Sylt, AWI, Germany), Dr. Michael Schweikert PD (University of Stuttgart, Germany), Mr. Gerrit Sahling (Biologische Anstalt Helgoland, AWI, Germany), Dipl.-Biol. Kerstin Pick (University of Göttingen, Germany), Dr. Andrew Alverson (University of Texas at Austin, USA), and René van Wezel (Koeman en Bijkerk BV, The Netherlands), who all provided images (of species) from the North Sea. Dr. Tatiana Morozova scanned many negatives of the archive from MH and helped processing some of these especially for the in parallel initiated and produced database Plankton\*net@AWI. A very special note of appreciation goes to the teams of the research vessels “Mya” (Sylt) and “Aade” (Helgoland) for the uncountable net-plankton samples and to all the “Bios” at the Wattenmeerstation Sylt and the Biologische Anstalt Helgoland who were interested in and supported our work. Finally, Dr. Juan Saldarriaga’s (University of British Columbia, Canada) improvement of our English is very much appreciated. Without the great patience of Prof. Dr. Brian Leander (University of British Columbia, Canada) while this book was in a crucial phase of writing, this work would not have been possible for MH. ME cordially acknowledges the more of three decades last-

ing period in which Alexa patiently shared her husband with the dinoflagellates.

We want to thank the reviewers for their attentive feedback which has improved the manuscript.

Financial support was given by the Senckenberg Gesellschaft für Naturforschung and by the Alfred Wegener Institute for Polar and Marine Research by the mediation of Prof. Dr. Allan Cembella and Dr. Ragnhild Asmus. Dr. Peter Königshof, Senckenberg Forschungsinstitut und Naturmuseum, had the editorial responsibilities and Mrs Isabell Clasen and colleagues, Senckenberg Forschungsinstitut und Naturmuseum, patiently answered many questions and did the editing.

Johannes Müller to the young  
Ernst Haeckel at Helgoland in 1854:  
“As soon as you have entered into this pelagic  
wonderland you will see that you cannot  
leave it.”

(Haeckel 1890, transl. G.W. Field 1893, p. 573;  
cited from Taylor 1980)

## Introduction

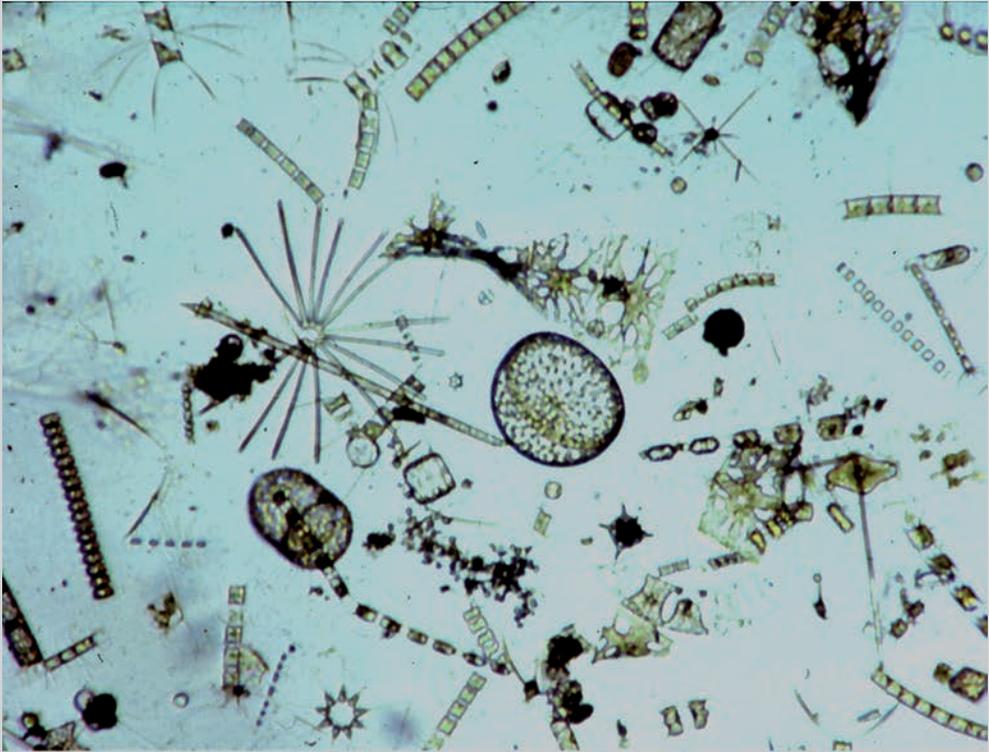
The term “plankton” was introduced by Viktor Hensen (1887), and originally described “everything that drifts in the water, whether shallow or deep, living or dead” (from Taylor 1980). The term is used today only for living organisms, a change in meaning that may have been caused by Ernst Haeckel’s “Plankton-Studien” (1890), where he discussed only plants and animals (Taylor 1980).

Here we deal mainly with phytoplankton, the small “plants” / ”algae” / photosynthetic protists that drift in the water column in spite of often being able to swim on their own. We focus on the microphytoplankton, cells 20–200 µm in size. However, any classification of plankton by size is artificial and a few larger taxa and some smaller ones (nanoplankton, 2–20 µm in size) are also included. The term “phyto”-plankton is also misleading in some respects, because some groups like the dinoflagellates include many species that are non-photosynthetic, and are thus members of the micro-zooplankton (see also the introduction to dinoflagellates below). So the functional definition of phyto- versus zoo-plankton gets mixed up when dealing with taxonomical groups. A broad variety of higher taxa are represented in the marine phytoplankton, including cyanobacteria, Prochlorophyta, Chloro-

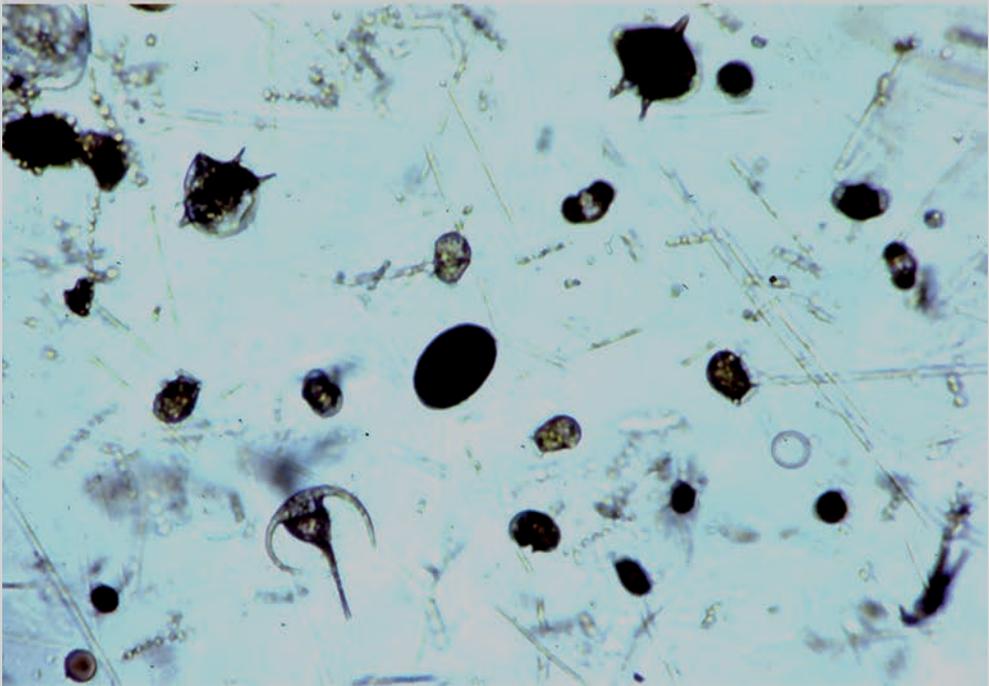
phyta, Euglenophyta, Dinophyta, Cryptophyta and, Chromophyta (Bacillariophyceae, Chrysophyceae, Raphidophyceae and Prymnesiophyceae). Our emphasis is on diatoms and dinoflagellates, because they represent the largest species diversity in this habitat and they are the only groups where morphological characters are relatively easy to observe in the LM; but some species of other higher taxa are also described to bring attention to the other groups as well.

Primary production is one of the most important ecological aspects of the phytoplankton. The biomass built through photosynthesis is the nutritional basis for all higher trophic levels of consumers (e.g., zooplankton). The widely accepted notion that these consumers are larger in size than their prey is challenged in our last chapter: predators can be much smaller than their prey, and when dealing with these small feeders the borderline between predator and parasite is blurred. Interactions within the planktonic community are complex, therefore an exact knowledge about the actors involved is very important. These interactions should not be understood as chains anymore, but as complicated networks (food webs) that involve both biotic and abiotic factors. Understanding just parts of the processes are challenging ecological tasks today. In very general terms the phototrophic phytoplankton biomass production is controlled by at least two factors: physical-chemical conditions (bottom up control) and feeding pressure by the predators (top down control). The “microbial loop”, originally described for benthic communities, is also important in plankton communities.

Often neglected in the past but increasingly recognized today is the role of phytoplankton viral infections. Phytoplankton taxa have different “strategies” to defend their populations



a: Diatom dominant plankton community - spring and autumn bloom.



b: Dinoflagellate dominant plankton community - summer plankton.

Fig. 1. Phytoplankton succession.

from predation or viral attacks that can be based on several types of features: morphological (e.g., bulky shape - chain formation and setae in the diatom genus *Chaetoceros*, colony formation of the prymnesiophycean genus *Phaeocystis*), mechanical (e.g., slime production - in the diatom genus *Coscinodiscus*), or chemical (e.g., toxin production by dinoflagellates or raphidophytes; pheromone production by many protists). These shortly listed ecological aspects of phytoplankton life should give an idea about the many interesting questions surrounding every single species/population. It is not just the species diversity by itself that is exciting to be explored but that is the basic unit, which needs to be known to study the interactions going on. It is far beyond the scope of this book to deepen the ecological knowledge about the described species but for the attentive reader there are hints to these topics scattered throughout the whole text.

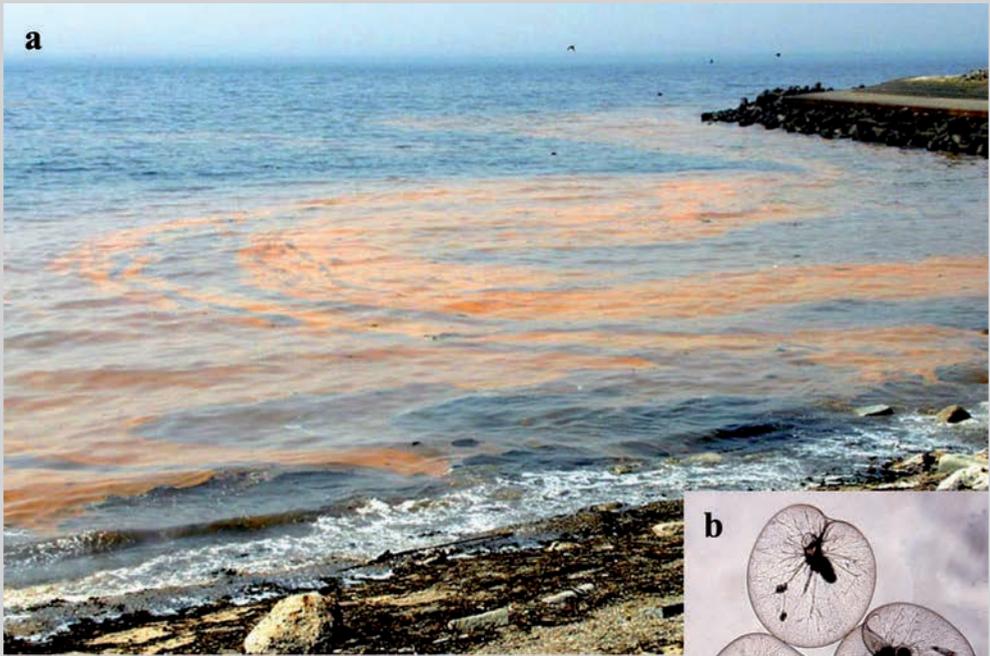
### **The yearly phytoplankton succession**

Two phytoplankton blooms tend to develop in the temperate climate zone of the North Sea per year. With increasing water temperatures in spring, the North Sea waters stabilize, and the light intensities entering the upper water layers get higher. Calm weather favours water stratification and a fast and intensive phytoplankton growth commonly dominated by diatoms (Fig. 1a). In coastal zones, stratification only occurs rarely due to strong tidal currents, and so light penetration is reduced and the start of this spring bloom normally happens between March and May. The date, intensity and composition of the bloom vary from year to year. The phytoplankton growth goes on as long as nutrients are available. Decreased silicate levels will limit diatom growth, and herbivores, usually predators in the zooplankton, may also decrease the phytoplankton biomass.

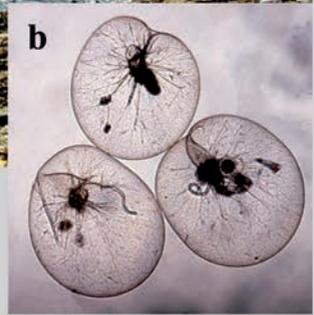
This causes the spring diatom bloom to brake down. At this stage, nitrogen and phosphate levels are usually still not exhausted, and *Phaeocystis* tends to take over, at least in coastal zones. Phytoplankton populations in the summer tend to be small and dominated by dinoflagellates (Fig. 1b). In late summer and autumn, with light intensities still high and nutrients becoming available again because of mixing (wind turbulence bring up degraded and dissolved material), a second smaller bloom occurs, usually dominated by diatoms again. Due to strong winds causing turbulence in late autumn and winter the phytoplankton biomass production decreases drastically because of limiting light conditions. The complete mixing of the water column during winter brings back the high nutrient levels needed for the next spring bloom.

Many phytoplankton species occur all year round in different concentrations, others occur only in particular seasons (species adapted to cold or warm waters). The temporal succession of planktonic species or communities in a given region can occur within one water body or because of a sequence of different water bodies passing the site. Usually the phytoplankton is not dispersed evenly within the water, but forms a mosaic of “population clouds” that expands more or less intensively horizontally and vertically. This phenomenon is called patchiness.

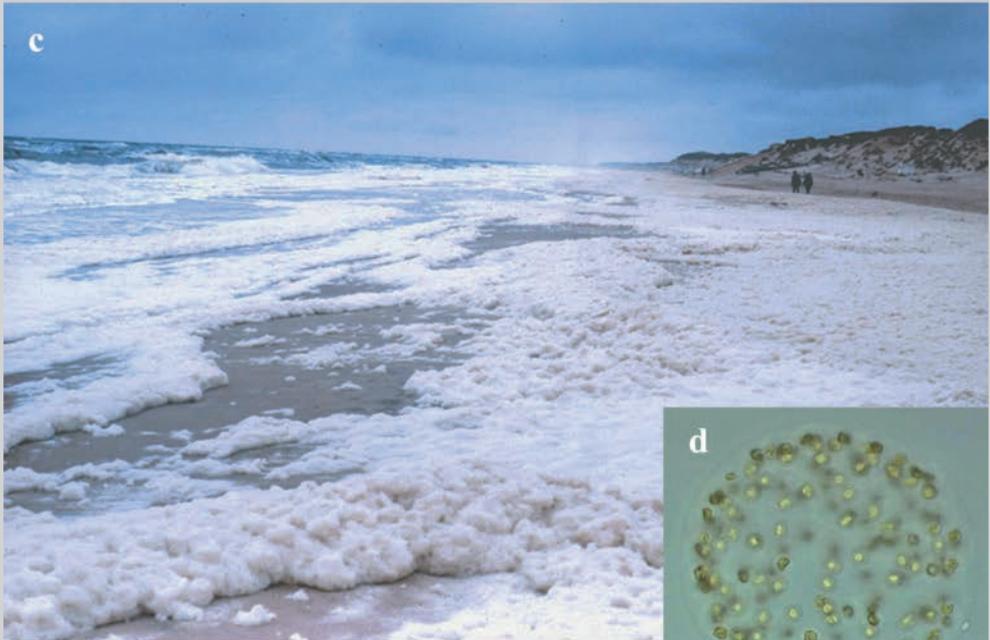
**Harmful algal blooms** Blooms of phytoplankton species are a natural and not unusual event. Some species can discolour the water when their biomass/cell numbers are high. In the North Sea these coloured tides, generally named red tides, are caused by several species. *Noctiluca scintillans*, a dinoflagellate, shows mass occurrences nearly every year and discolours the water a very spectacular red



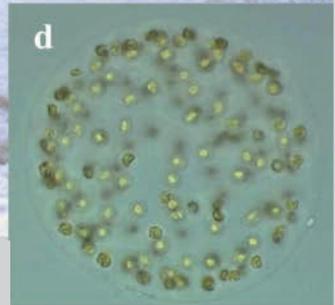
**a**



**b**



**c**



**d**

Fig. 2. Red tides – harmful algal blooms.

a: Red tide (photo courtesy G. Sahling) caused by *Noctiluca scintillans* (b).

c: Massive foam production at the coast of Sylt (photo courtesy K. Reise) caused by *Phaeocystis globosa* (d).

(Figs. 2a, b). Species of the dinoflagellate genus *Ceratium* can discolour the water brown. A *Gymnodinium chlorophorum* (dinoflagellate) bloom looks green. The ciliate *Mesodinium rubrum* also discolours the water purple-red. These mass developments are not toxic but can be harmful, as in the case of *Noctiluca* blooms, because of oxygen depletion. Other blooms can be recognized by massive foam production (e.g., the prymnesiophycean *Phaeocystis globosa*, Figs. 2c, d) or slime formation (e.g., by the diatom *Coscinodiscus wailesii*). Sometimes, the term “red tide” has been used as synonym for “harmful algal bloom” (HAB). Most of the harmful algal blooms are caused by species producing some kind of toxin, and they do not discolour the water in an obvious way (e.g., *Dinophysis* and *Pseudo-nitzschia* species). Some species can be toxic even at very low cell concentrations and therefore monitoring these species is essential to prevent harm to humans. Around 20 of the North Sea phytoplankton species produce toxins. Toxin-producing species are known in the diatoms (*Pseudo-nitzschia*), the dinoflagellates (e.g., *Alexandrium*, *Dinophysis*, *Prorocentrum*), the prymnesiophyceans (*Chrysochromulina*), and the raphidophytes (*Fibrocapsa*). It needs to be emphasized that species that are known to be toxic at another sites in the world are not necessarily toxic in the North Sea. This is often signalled in the literature by the phrase “potentially toxic”. Information on toxin-producing species (Moestrup et al. 2004) and the problems associated with their occurrence are summarized in GEOHAB (2001) and can be found at <http://ioc.unesco.org> (under „Fisheries and Ecosystems“). General information about techniques and taxonomy can be found in Hallegraeff et al. (2003) and papers cited therein. Other interesting web pages dealing with this

topic are: <http://issha.org>, and <http://www.who.edu/redtide/>.

**Introduced (exotic) species.** It is very difficult to distinguish between real exotics and erroneously ‘misinterpreted’ native species (pseudo-exotics) that were discovered late but may have been around long before without being noticed (Reise et al. 1999). This is especially true for small organisms like phytoplankton taxa. Methodological problems and extrinsic factors make it difficult to prove the exotic status of protists (Elbrächter 1999). There are only a few examples of well-documented introductions of planktonic diatoms in the North Sea, e.g. *Odontella sinensis* (as *Biddulphia sinensis* in Ostenfeld 1908), *Thalassiosira punctigera* (Dürselen and Rick 1999) and *Coscinodiscus wailesii* (Boalch and Harbour 1977, Dürselen and Rick 1999, Rick and Dürselen 1995, Robinson et al. 1980). Flagellates have rarely been documented as introduced species and the only known examples are *Karenia mikimotoi* (as *Gyrodinium aureolum* in Braarud and Heimdal 1970, Hickel et al. 1971) and *Alexandrium leei* Balech (Koeman 1997). A recently established member of the North Sea dinoflagellate community is *Thecadinium yashimaense* (Hoppenrath et al. 2007). The possible mechanisms for the dispersal of non-indigenous species are diverse, and include aquaculture, migratory birds, ballast water of ocean going vessels. There is also the possibility that species may expand their range via ocean currents.

**Biogeography.** Phytoplankton species can have particular geographic distributions, and we added this information in the taxonomic part of this book, as it was available. But these data need to be treated cautiously. Not even the cosmopolitan status of a species seems to be

certain in all cases, because of the risk of misidentifications and cryptic speciation. Generally one should keep in mind, what Hargraves wrote in respect of diatoms: “In the biogeography of diatoms, distribution is often a function of concentration of diatom taxonomists, and where they have gone on field trips.” (Hargraves 1990). Still a lot has to be done on this topic.

**The habitat** of the marine phytoplankton comprises an off shore, oceanic, and a near shore (shelf sea), neritic zone. Specific phytoplankton taxa may or may not prefer one of these zones. The North Sea is a neritic biotope. The very shallow Wadden Sea areas, which are closest to the coast and somehow separated by the islands situated off the coast, may be regarded as a specific biotope itself. Oceanic species (holoplankton) usually have no contact to the sea floor, they live permanently in the water column. In shallow sea regions meroplankton dominates, species that live only part of their life cycle in the pelagic zone and the rest of the time occur in the benthic area. Benthic species can also occur as tychoplankton (also named pseudoplankton or accidental plankton) temporarily in the pelagic zone. They are occasionally carried into it by chance factors such as turbulence. The influence of the sea bed (sublittoral) is very apparent, for example in the Wadden Sea region. In the Frisian Wadden Sea phytoplankton benthic, sand-dwelling diatom or dinoflagellate species (littoral plankton) can often be observed (e.g., *Actinocyclus roperi*, *Togula britannica*, *Thecadinium yashimaense*).

The habitat of the plankton species from Helgoland is the open North Sea (Figs. 3a–c), a relatively shallow shelf sea off the Northeast Atlantic with a complicated current system of different water bodies. The North Sea is main-

ly characterized by the following water bodies (Hagmeier and Künne 1951): (1) Atlantic, oceanic water coming from the north, characterized by high salinities (> 35) and high winter temperatures; (2) Channel current water coming through the English Channel from the southwest, also oceanic with high salinity and high winter temperatures; (3) varying amounts of coastal water, lower in salinity because of river water influence, with low winter and high summer temperatures; (4) mixed water from the central North Sea, hydrographically in-between coastal and oceanic water; and (5) Baltic Sea water of low salinity from the Skagerrak, flowing in western to north western direction. In detail the hydrographical conditions are much more complicated (e.g., Huthnance 1991, Charnock et al. 1994).

As simplified here Helgoland is situated in the mixed water area, close to the area of coastal water influence. The salinity range there is between 28 and 33, and the water temperature can be between 22 °C in summer and just below zero (-2 °C) during winter (Wiltshire and Manly 2004).

Sylt is situated in the Northfrisian Wadden Sea (Figs. 3b, d), a shallow, tidally influenced coastal sea. Tides are semidiurnal with a mean range of 2 m. Salinity ranges on average between 27.5 and 31. Long-term average temperatures range between 2.7 °C in winter and 18.1 °C in summer, but can drop below zero and get higher in summer.

**The methods.** The species presented here were captured in the waters around the islands of Helgoland and Sylt (Figs. 3a–d), mainly from research vessels at two “fixed” stations, but also from the docks. Net samples from near-surface water from the Helgoland Reede Station (54° 11.30'N, 7° 54.00' E, Fig. 3c) and from a station close to List/Sylt (55° 01.30'N;

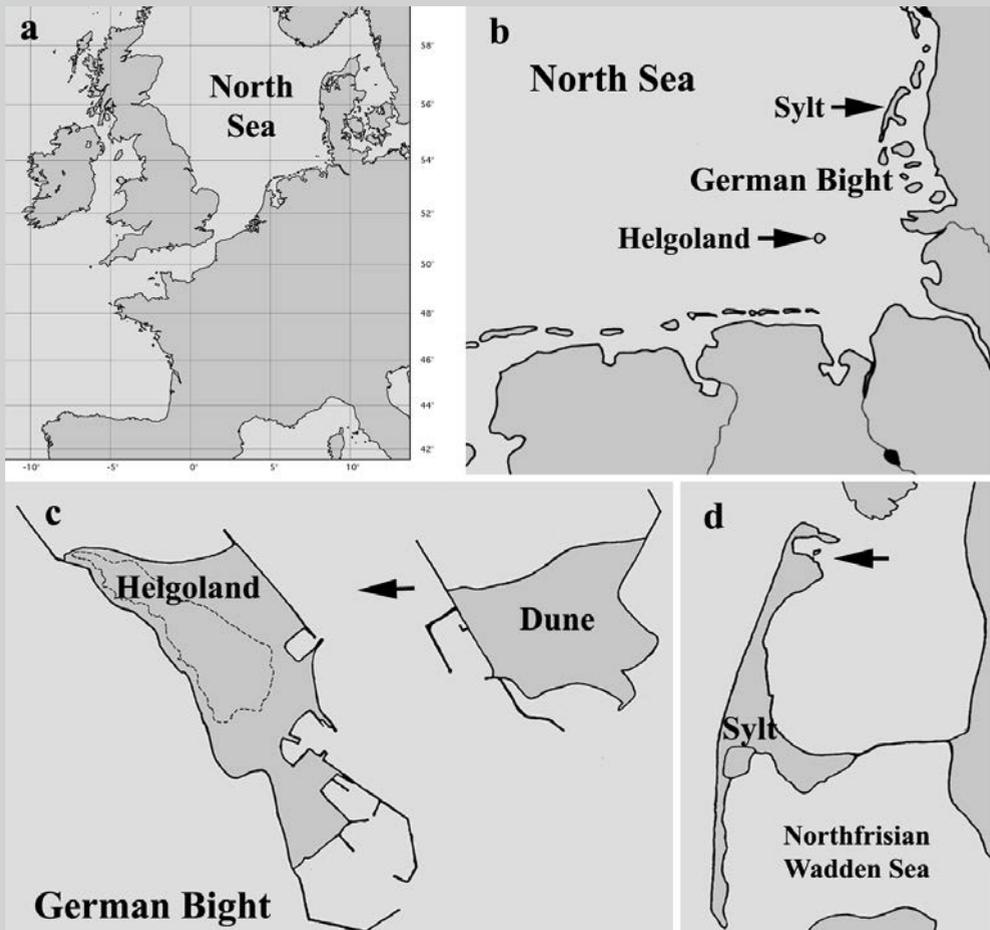


Fig. 3. Maps of the sampling area. a: The North Sea. b: The German Bight as part of the North Sea with the two islands Helgoland and Sylt. c: Detail of the island of Helgoland with the neighbouring Dune, the monitoring sampling site is indicated by an arrow. d: Detail of the island of Sylt, the monitoring sampling site is indicated by an arrow.

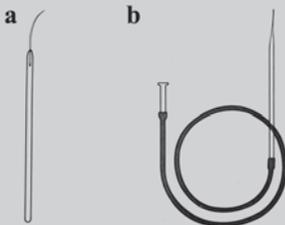


Fig. 4. Tools for cell isolation.  
 a: Dissecting needle made of tungsten-wire.  
 b: Capillary glass pipette connected with a rubber-hose.

08° 27.10'E, Fig. 3d) were investigated at least once a week. Nets of different mesh size, 20 µm and 80 µm, were used. The samples were stored in white plastic bottles and brought directly to the laboratory. These living samples stay in a good condition only for some hours (depending on the biomass concentration and zooplankton content). To save some living material for the next day, smaller subsamples can be stored in Petri dishes in a culture cabinet at about 15–18 °C with light, or at a place near a window without direct sunlight. Samples with high cell densities should be diluted with fine-filtered seawater of the sampling site or with culture medium. Subcultures with a small inoculum supplied with medium and stored in culture cabinets can be investigated for some days and can provide species that occur only in low numbers in the sample. Living organisms were identified in small Petri dishes with a dissecting-, an inverted- and a normal light microscope equipped with seawater-immersion objectives. Starting with low magnifications (16–64x) at the binocular, skilled investigators are able to identify many large to medium sized species. Afterwards more detailed observations and identifications of smaller species were done with seawater immersion objectives. Alternatively cells can be micropipetted and placed on microscope slides, covered with cover slips and observed at high magnifications under a compound microscope with bright field illumination, differential interference contrast or phase contrast. Prior to cell isolation the desired specimen should be freed from other organisms and detritus by removing them with a dissecting needle made of tungsten-wire (Fig. 4a). Self-made capillary glass pipettes connected with a rubber-hose (Fig. 4b) were used for cell isolation by mouth-pipetting. For long-time observations of wild material or cultures (e.g., of life cycle stages and

transformations), cover slips should be sealed. All species observed and identified were listed and documented photographically over the years. Single isolated and washed cells sometimes can be cultured, depending of course on the species and their nutritional strategy. There are several different approaches for establishing cultures of different kinds (unialgal, clonal, axenic, etc.) for phototrophic, mixotrophic, and even heterotrophic species. But there are species that can't be cultured. For detailed instructions and media compositions read in Andersen (2005). An identification to species is sometimes impossible in living cells, and cultures and/or special cell preparations are needed. Protocols for the treatment of diatoms and their frustules for light microscopy (LM), transmission (TEM), and scanning electron microscopy (SEM) are published in e.g., Barber and Haworth (1994), Cox (1996), Hasle and Syvertsen (1996), and Hoppenrath (2009). In the case of dinoflagellates, tabulational details are often needed to identify species. Procedural descriptions for dinoflagellate preparations for LM and SEM can be found in Steidinger and Tangen in Tomas (1997) and in Taylor et al. in Hallegraeff et al. (2003).

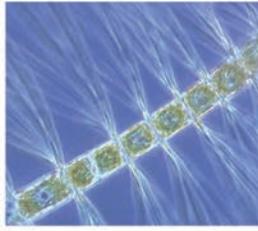
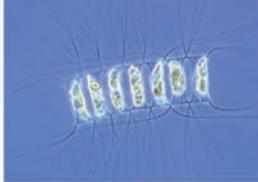
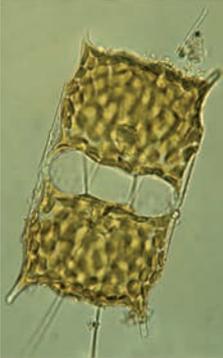
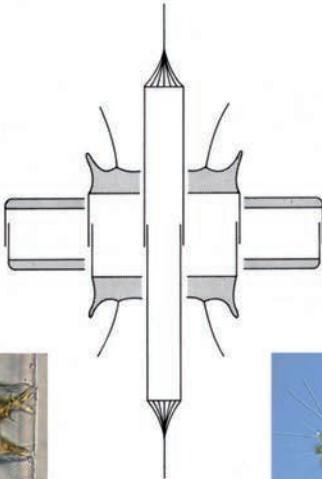
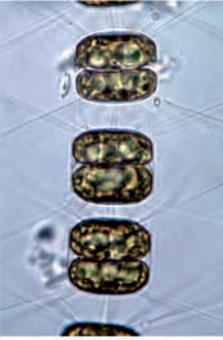
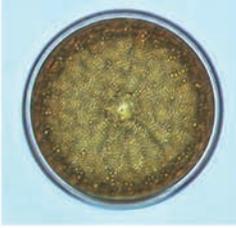
This book concentrates on a particular geographic region – the German Bight of the North Sea. The data presented are part of the phytoplankton research at the former Biologische Anstalt Helgoland – now Alfred Wegener Institute for Polar and Marine Research. A unique long-term phytoplankton data series (counts on a workday basis) exists for Helgoland (e.g., Wiltshire and Dürselen 2004 and references therein). Drebes surveyed the phytoplankton species at Helgoland from 1966 to 1971 (Drebes 1974), but afterwards the species composition has not been recorded continuously. More recently, the taxonomy of the

Helgoland phytoplankton was reinvestigated (Hoppenrath 2004). There are continuous phytoplankton species composition records for the German Wadden Sea at Sylt (Drebes and Elbrächter 1976, and unpublished data) from 1972 until today. The accumulated taxonomic knowledge about the species occurring at both sites is reflected in this book. The original introductory account of the marine phytoplankton of Helgoland (Drebes 1974) has been expanded into a taxonomic account that should help everyone to identify the most frequently occurring species. It is still a selection focussing on diatoms and dinoflagellates. Other groups like cryptophytes and others are excluded even though they are often very abundant in the samples due to methodological restrictions and lack of taxonomic expertise for these groups. We make here no claim of completeness. Within a protist group (e.g., diatoms) no strict systematic order has been used for the species presentation, instead a more “practical” grouping has been favoured to simplify the search for non-specialists. Identification keys were beyond the scope of this book and can be found elsewhere (e.g., Tomas 1997). We deliberately left out magnifications (scale bars) from the illustrations, partly because there are considerable problems in obtaining absolute magnifications when old

and also new negative and slide photo material is scanned and processed electronically, without knowledge of the cell sizes of the photographed specimens; and because diatoms and to a lesser extent dinoflagellates vary enormously in size during their life cycle. Size should not be overemphasized as a taxonomic criterion. The images should show the general appearance of the living cells, sometimes their morphological variability and life cycle stages as they will be observed in living net-plankton samples. They are intended to be used as “search”- or “identification-pictures”. Scanning electron micrographs (SEM) help to understand the structures visible in the light microscope (LM), show special ultrastructural features, aid in identifying species unrecognizable under the LM, and of course show the diversity and beauty of the morphology of these tiny organisms. Some of the images presented here, especially coloured ones, can be found in the database Plankton\*net @ AWI (<http://planktonnet.awi.de>).

We were careful and tried to avoid mistakes, but in spite of this there might be unintentional errors in the text. The reader is encouraged to notify us of these errors, as well as of differences in taxonomic opinions.

# Diatoms



## Diatoms / Bacillariophyceae

There are between 10.000 and 100.000 living diatom species (estimates differ) in over 250 genera, and of those, approximately 1400 to 1800 species are from marine plankton. They vary in size between ~ 5 µm and up to 2 mm. Diatoms have their place in the botanical system as the algal class Bacillariophyceae within the division Chromophyta. Diatoms are one of the main components of the marine phytoplankton, in addition to dinoflagellates and some other flagellates like the prymnesiophytes (see general Introduction). As the main component of the microplankton they constitute the nutritional basis for much of the other marine life, which is directly or indirectly dependent on their primary production. In the North Sea they reach highest abundances in spring (diatom spring-bloom), but a second smaller peak occurs in autumn.

The diatom cell is characterized by a unique type of cell wall, the silica frustule. It is shaped in its basic form like a Petri dish consisting of two halves, the epitheca (upper part) and the hypotheca (lower part). Each theca consists of two parts, a flat part, the valve, and a ring-like side wall, the cingulum or girdle (Fig. 5). Additionally there can be a few to several girdle bands, or the girdle can be composed of numerous segments. In their guide to the morphology of the diatom frustule Barber and Haworth (1994) explained the naming of the complex and very diverse ultrastructural features. To get a first impression of some features have a look at Figs. 5 and 6. The morphogenesis of diatom valves has been investigated (see Pickett-Heaps et al. 1990 for a review). The chloroplasts are brownish because of the accessory pigment fucoxanthin, which masks the chlorophylls *a* and *c*, and they have pyrenoids. Their ultrastructure is typically Heterokontophyte-like. The large nucleus often lies centrally in the cell in a cytoplasm bridge. Mitochondria

have cristae of the tubular type. Photosynthates are stored in the form of chrysolaminaran and lipid drops that sometimes can be seen in the cells. Diatom cells occur solitary or in different types of colonies. For a general introduction to diatoms please read the textbooks of Van den Hoek et al. (1995), Lee (1999), and/or Graham and Wilcox (2000), Round et al. (1990), Hasle and Syvertsen (1996).

The vegetative reproduction of diatoms is by binary fission. The two new cells both receive one half of the original cell theca and form a new second half, which is always a hypotheca. This type of division leads to the progressive decrease of the average cell size (Fig. 7) in most species (exceptions exist where species divide without size reduction). This is the reason for the large variation in the size ranges recorded for most diatom species. Size-dependent morphological changes of the frustule have to be considered when dealing with small specimens of a species. There is a species-specific minimum size. Before reaching it, the original maximal cell size can be restored by auxospore formation (Pfitzer-MacDonald's law) (Fig. 7). This size-dependent process occurs when cells reach about one third of its maximal size (Drebes 1977). Usually auxospores are distended zygotes of a previous sexual act but can also be the result of a vegetative event. The initial cell – the first cell formed inside the auxospore envelope – can differ in morphology from a normal vegetative cell. If diatoms pass the critical cell size without triggering auxospore formation, they will continue to divide until they reach their minimal size and die.

The sexual reproduction of the diplontic cells is different in centric and pennate diatoms. Gametogenesis occurs generally at the end of the meiosis and zygotes develop into auxospores. Centric diatoms reproduce by oogamy with unflagellated male gametes (Figs. 7–9), and pennate diatoms without flagellated stages mostly by

isogamy but also by anisogamy (Drebes 1977). Detailed descriptions of the sexual reproduction in diatoms can be found in, e.g., von Stosch (1954), von Stosch and Drebes (1964), Drebes (1974, 1977), and Round et al. (1990). If likely to be observed in living net-samples, we mention sexual stages in the following species descriptions.

Resting spore formation is a reaction to environmental stress situations like nutrient depletion, changes in temperature and/or light, etc., and is common in centric marine diatoms (Fig. 10). Planktonic resting spores fall to the sea bottom, until restored to the surface during more favourable growing conditions (e.g., Hargraves and French 1983). The spores show a special morphology with thick walls, which can either resemble the vegetative cells or differ drastically from them (e.g., Hargraves 1976, Syvertsen 1979, 1985). Resting spore morphology is valuable for taxonomy and is shown for some species in the following descriptions. Three resting spore types are known, exogenous, semiendogenous, and endogenous ones. Resting cells (physiological resting stages) do not have a special morphology (e.g., *Odontella aurita*), they look like vegetative cells but perhaps with a little thicker cell wall, but are prepared to resume metabolism as soon as more favourable conditions return.

To identify diatom genera and species from living material one should look at cell shape and size first. Both views – valve view and girdle view – are important and the investigator must pay attention to size variability in diatoms in connection with the life cycle. Lengths (apical axis) and widths (transapical axis) are maximum dimensions in most cases. Usually the width of a valve is maximal in the centre, but there are exceptions, especially in heteropolar diatoms. The cell depth is the distance between the valve faces of a cell. Pay attention to colony type and

morphological details of the valves like raphe, spines, setae, costae, septa, striae and patterns of alveolae. Some genera have specially named morphological features that distinguish them from other genera, and the variations of these features are often species specific (Figs. 5, 6). Chloroplast number, position, and shape as well as other distinctive cellular inclusions are also useful for the identification of living specimens. Some species are often attached to fine sediment particles (e.g., *Delphineis surirella* and *Auliscus sculptus*) or broken frustules of larger diatoms (e.g., *Rhaphoneis amphiceros*) floating in the water column. For an introduction on how to investigate and identify marine planktonic diatoms see Hasle and Syvertsen (1996) and Hoppenrath (2009). The taxonomic treatment presented here is focused on the identification of species in living net samples, but for species unidentifiable in that condition, ultrastructural details visible in the SEM are also given. Methods for chemical cleaning of diatom frustules can be found in Cox (1996), Barber and Haworth (1994) or Hasle and Syvertsen (1996). Here, taxa are not presented in a strict systematic context (still under discussion and in change), only centric and pennate diatoms have been distinguished. The centric diatoms are grouped in a non-systematic manner according to their overall appearance, for example “rod-like and cylindrical chain forming” or “leaf-like”, to help the non-taxonomists to find the taxa without systematic background. Keys to the genera and species have not been included but can be found for most taxa in Hasle and Syvertsen (1996). For systematics see Round et al. (1990) and Hasle and Syvertsen (1996). For further species descriptions and identification help see Hasle and Syvertsen (1996), Thronsdon et al. (2003), Horner (2002), Hustedt (1930, 1959, 1961), and Cupp (1943). Size ranges given for the species are maximum ranges known from the literature.

## General morphology of the diatom frustule

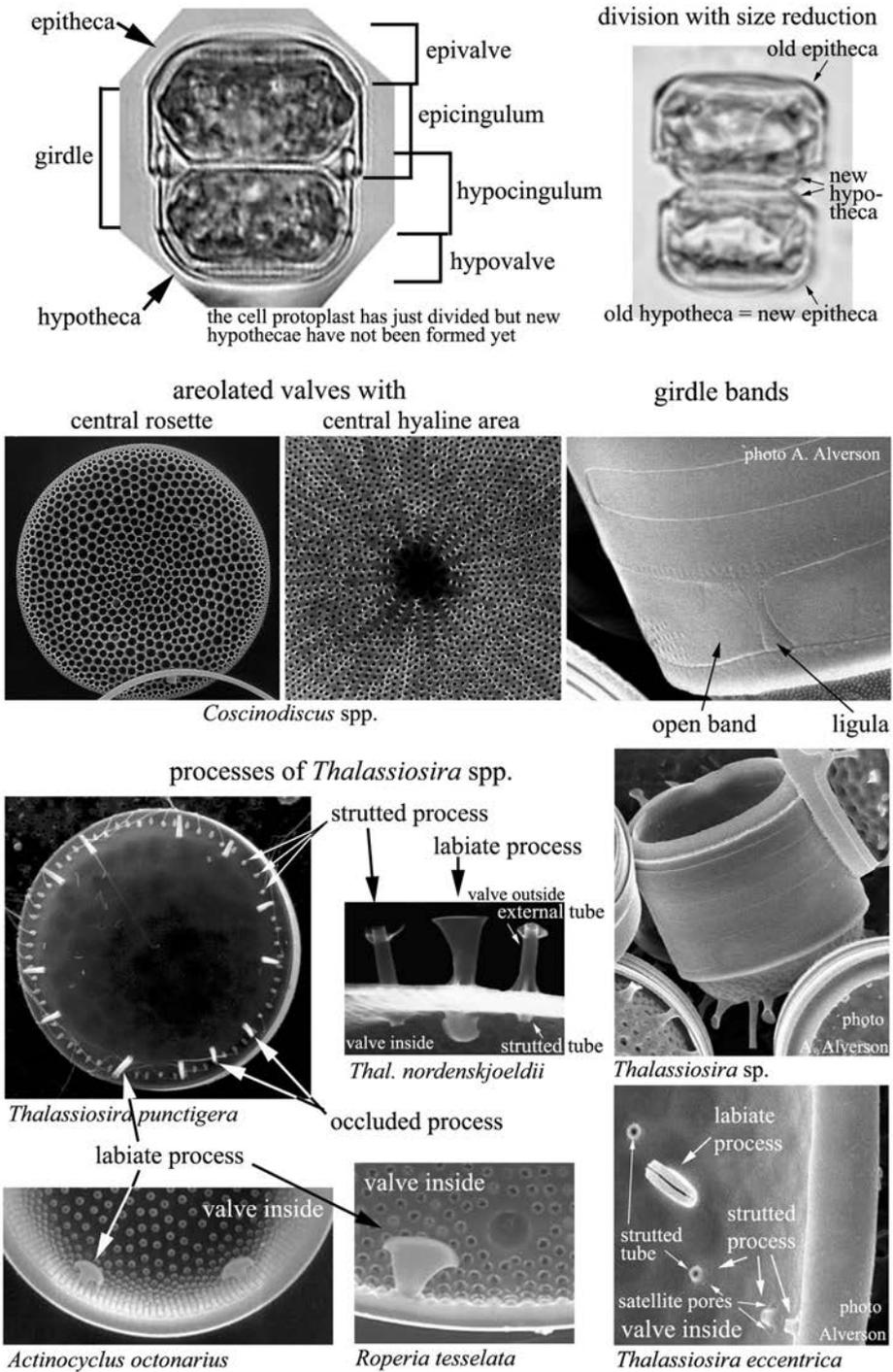
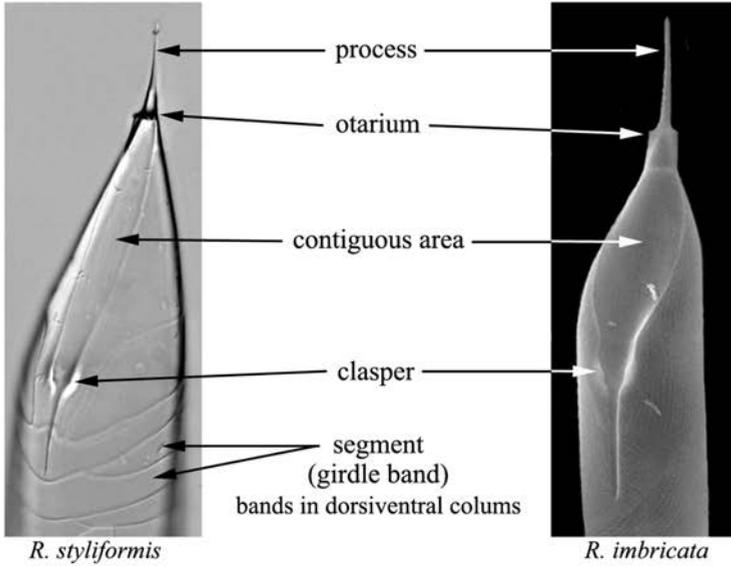


Fig. 5. General morphology of the diatom frustule.

**Rhizosolenia spp. morphology**



**Chaetoceros spp. morphology**

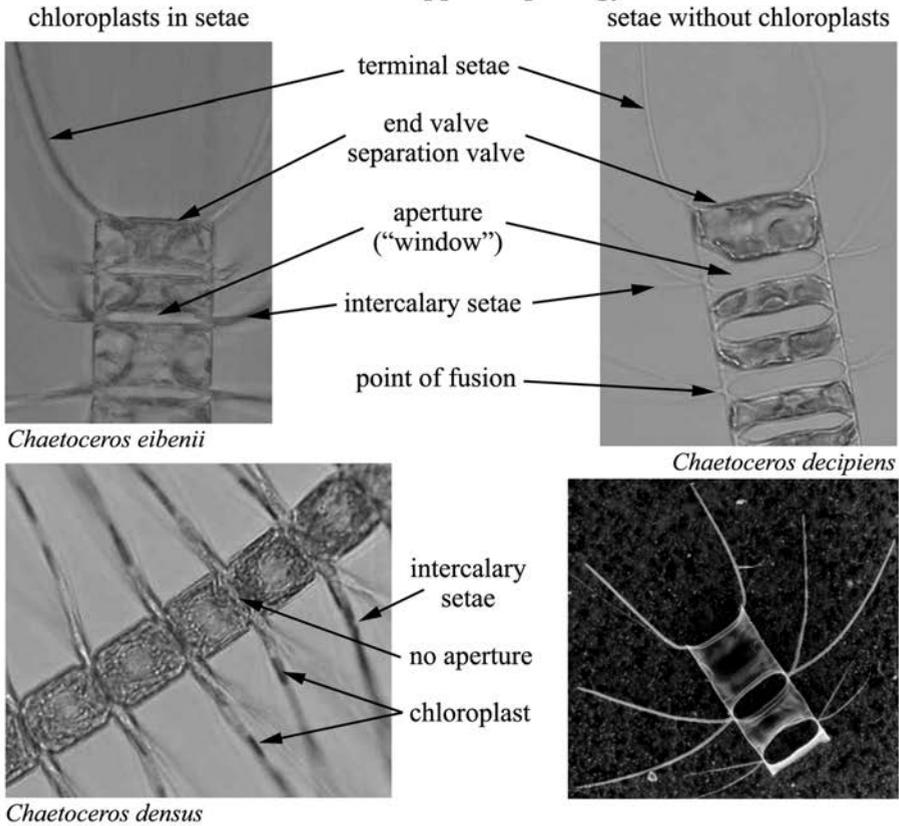


Fig. 6. Terms describing the morphology of the genera *Rhizosolenia* and *Chaetoceros*.

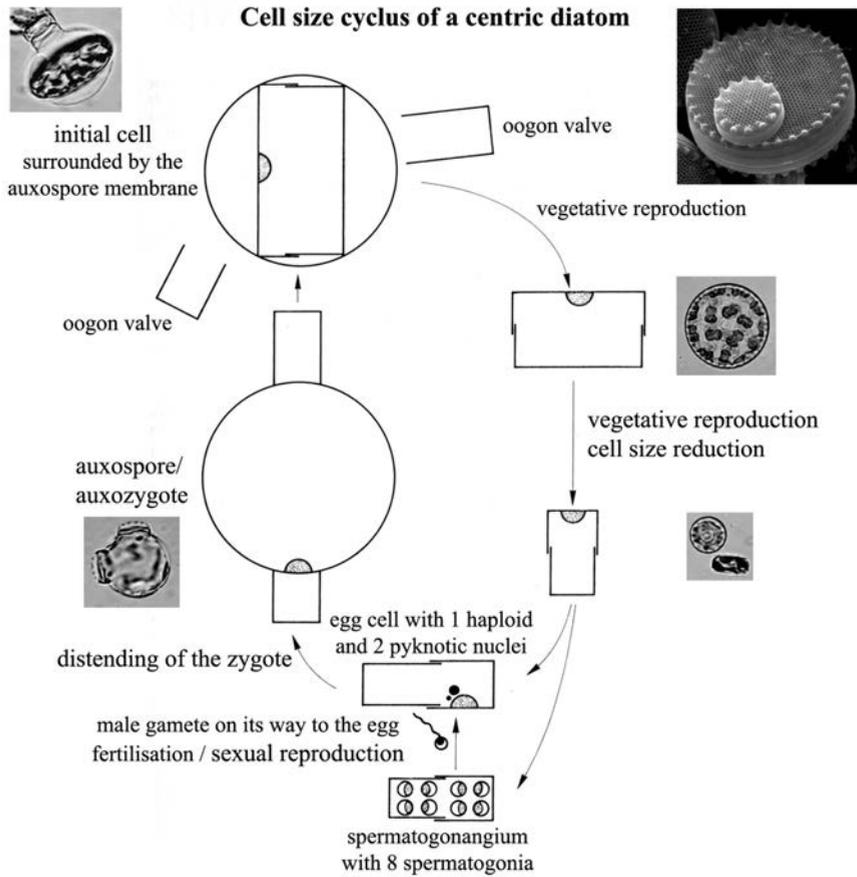


Fig. 7

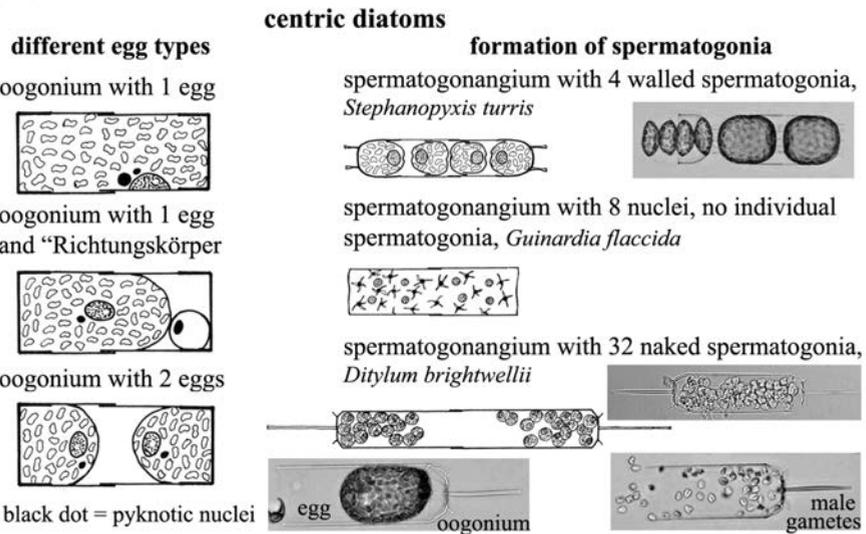


Fig. 8