

# COLD-WATER CORALS: THE BIOLOGY AND GEOLOGY OF DEEP-SEA CORAL HABITATS

There are more coral species in deep, cold waters than in tropical coral reefs. This broad-ranging treatment is the first to synthesise current understanding of all types of cold-water coral, covering their ecology, biology, palaeontology and geology. Beginning with a history of research in the field, the authors describe the approaches needed to study corals in the deep sea. They consider coral habitats created by stony scleractinian as well as octocoral species. The importance of corals as long-lived geological structures and palaeoclimate archives is discussed, in addition to ways in which they can be conserved. Topic boxes explain unfamiliar concepts, and case studies summarise significant studies, coral habitats or particular conservation measures. Written for professionals and students of marine science, this text is enhanced by an extensive glossary, online resources (www.lophelia.org/coldwatercoralsbook), and a unique collection of colour photographs and illustrations of corals and the habitats they form.

J. MURRAY ROBERTS is a marine biologist at the Scottish Association for Marine Science. His research focuses on the biology and ecology of cold-water corals.

ANDREW J. WHEELER is Senior Lecturer and co-ordinator of marine and freshwater research in the Environmental Research Institute at University College Cork. His research currently focuses on seabed mapping and sedimentology of cold-water coral carbonate mounds.

ANDRÉ FREIWALD is Chair of Palaeontology at the GeoZentrum Nordbayern, Erlangen. His research focuses on cold-water corals, cool-water carbonates and bioerosion.

STEPHEN D. CAIRNS is a Research Zoologist at the Smithsonian Institution, Washington DC. As a systematist he has described approximately 350 new deepwater coral species from around the world.



## COLD-WATER CORALS

The Biology and Geology of Deep-Sea Coral Habitats

#### J. MURRAY ROBERTS

Scottish Association for Marine Science, UK

### ANDREW J. WHEELER

University College Cork, Ireland

## ANDRÉ FREIWALD

Universität Erlangen-Nürnberg, Germany

### STEPHEN D. CAIRNS

Smithsonian Institution, USA





## **CAMBRIDGE**UNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314-321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre, New Delhi - 110025, India

103 Penang Road, #05-06/07, Visioncrest Commercial, Singapore 238467

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning and research at the highest international levels of excellence.

www.cambridge.org
Information on this title: www.cambridge.org/9781009263931

© J. Roberts, A. Wheeler, A. Freiwald and S. Cairns 2009

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2009 Reprinted 2010 First paperback edition 2022

A catalogue record for this publication is available from the British Library

Library of Congress Cataloging in Publication data

Cold-water corals: the biology and geology of deep-sea coral habitats / J. Murray Roberts... [et al.].

p. cm.

Includes bibliographical references and index.

ISBN 978-0-521-88485-3 (hardback)

 Deep sea corals.
 Coral reefs and islands. I. Roberts, J. Murray. II. Title. QL377.C5C647 2009

593.6'1779-dc22 2008050654

ISBN 978-0-521-88485-3 Hardback ISBN 978-1-009-26393-1 Paperback

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.



## To our families:

Lea-Anne, Hannah and David Roberts;
Moira, Nessa, Malachy and Penny Wheeler;
Alexander, Christina, Jannik, Jule, Lea and Angela Freiwald;
Peggy, Peter and Jennifer Cairns.



## Contents

	List	of topic boxes and case studies	page 1X
	Prej	face	xi
	Ack	nowledgements	xiv
1	Hist	1	
	1.1	History	1
	1.2	Research approaches	9
2	Cold-water corals		
	2.1	Ecological categorisation of corals	20
	2.2	The five cold-water coral taxa	24
	2.3	Environmental controls on cold-water coral distribution	43
	2.4	Global patterns of cold-water scleractinian diversity	51
	2.5	Molecular phylogeny of cold-water corals	52
	2.6	Linkages and connectivity	58
3	Biol	67	
	3.1	Anatomy	68
	3.2	Morphology	72
	3.3	Food supply and nutrition	73
	3.4	Growth rates	83
	3.5	Ecophysiology	94
	3.6	Reproduction	100
	3.7	Larval biology and dispersal	104
4	Ree	108	
	4.1	Reef initiation and development	109
	4.2	Reef sedimentation	112
	4.3	Defining coral carbonate mounds	115
	4.4	Mound development	119

vii



V11	1	Contents		
	4.5	Coral carbonate mound morphology	135	
	4.6	Global distribution of coral carbonate mounds	139	
5	Habitats and ecology			
	5.1	Habitats	144	
	5.2	Biodiversity	151	
	5.3	Seamounts, endemism and refugia	158	
	5.4	Species interactions	160	
	5.5	Fish assemblages	163	
	5.6	Predictive mapping	168	
6	Pala	175		
	6.1	Triassic dawn	175	
	6.2	Fossil record of cold-water corals	180	
	6.3	Taphonomy	193	
	6.4	Preservation of the coral-associated fauna	198	
7	Cora	210		
	7.1	Biomineralisation	211	
	7.2	Temperature records	225	
	7.3	Water-mass history	230	
	7.4	Pollution and nutrient records	233	
8	Impacts and conservation			
	8.1	Impacts	237	
	8.2	Conservation	254	
	Glossary		263	
	References		277	
	Inde	ex	324	
	Colour plate section is between pages 144 and 145.			
	Onl	Online appendix www.lophelia.org/coldwatercoralsbook.		



## Topic boxes and Case studies

## **Topic boxes**

1.1	Mapping with sound	page 11
2.1	What makes a reef?	23
2.2	The polymerase chain reaction (PCR)	54
2.3	Hardy-Weinberg equilibrium, the Wahlund effect and null alleles	62
3.1	Stable isotope ratios and delta notation	75
4.1	What is a limestone?	110
4.2	Calcium carbonate mineralogy	130
5.1	Biodiversity	143
5.2	Size classes	152
7.1	Seawater carbonate chemistry	214
7.2	The Younger Dryas	226
8.1	United Nations Convention on the Law of the Sea	259
	Case studies	
4.1	Challenger Mound, northeast Atlantic	122
5.1	Lophelia reef habitats of the Sula Ridge, Norway	147
5.2	Aleutian Island coral gardens, northeast Pacific	150
6.1	The Mediterranean cliff-bound coral habitat	190
8.1	Conservation in national waters: Norway	241
8.2	Conservation in European waters: the Darwin Mounds	242
8.3	The United Nations and vulnerable marine ecosystems	256



## **Preface**

Corals are not restricted to shallow-water tropical seas. Of the approximately 5100 coral species alive today over half are found in deep waters. Cold-water corals can be found over a tremendous range of latitudes from tropical to polar regions and from the shallows to the deep sea. We have known about cold-water corals since the mid-eighteenth century, and pioneering oceanographic expeditions in the late nineteenth century frequently recovered cold-water corals in their dredge nets. But only since the 1970s, and particularly in the last ten years, as acoustic survey techniques have improved and been applied to wider areas of the continental shelf, slope, offshore banks and seamounts have we begun to reveal the true extent of cold-water habitats around the world. In this book we try to summarise what we know about cold-water corals and capture the excitement of a field that is now growing exponentially. For instance, a literature search for the terms 'cold-water coral' and 'deep-sea coral' over the 20 years up to 1996 returned less than 300 publications whereas the same search terms for the following 10 years revealed nearly 700 (see Fig. 1).

The scientific community's fascination with cold-water corals has developed for several reasons. As sessile, suspension feeders that produce complex, sometimes long-lasting, three-dimensional structural habitat they fall at a natural confluence of biology, hydrography and geology. A few species of scleractinian cold-water corals develop elaborate reef frameworks that have spawned many studies into the processes underlying cold-water coral reef and coral carbonate mound formation. Individual cold-water corals, notably species of gold (*Gerardia*) and black (antipatharian) corals may live for over a thousand years, making them by some margin the longest-lived animals in the oceans. The skeletal remains of these corals and long-lasting reef and mound deposits now provide unique palaeoceanographic archives of intermediate water mass temperature and age.

This book's focus is on those cold-water corals that form structural habitat. We will consider how these species function as animals by reviewing what we know

хi



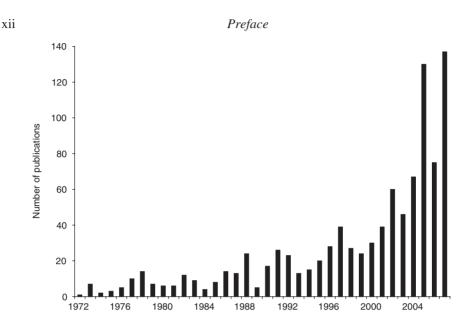


Fig. 1. Histogram showing the number of research papers referring to 'cold-water coral' or 'deep-sea coral' between 1972 and 2007. Special publications devoted to cold-water corals appeared in 2002, 2005 and 2007 explaining the higher number of papers in those years.

of their feeding, growth, reproduction and physiology. In many instances our biological understanding is limited by the practical difficulties of studying any group of animals that live at great depths far from shore. In contrast, our ability to map areas inhabited by cold-water corals is now well advanced and has revealed surprisingly extensive provinces of cold-water coral reefs and huge seabed mounds formed by multiple generations of reef development stacked one upon the other. Long, drilled cores through these coral carbonate mounds are now providing intriguing insights into their geological history and development reaching back over two million years. But corals trace their origins even further back in time and as a group have a chequered history of extinctions and radiations, often in concert with global changes in ocean carbonate chemistry (a critical issue to understand as we enter an era of ocean 'acidification' brought about as anthropogenic carbon dioxide dissolves in the oceans). We consider these long temporal aspects from the fossil record and summarise what we know of cold-water coral palaeontology and the factors underlying preservation of the corals and other animals in the geological record.

Present-day cold-water coral habitats excite interest from all who see them because, like coral habitats in warmer, shallower waters, they are structurally complex and rich with other animal species. Careful surveys with modern submersibles and remotely operated vehicles have brought back stunning images



Preface xiii

of cold-water coral habitats that have captured the imagination not just of research scientists but also members of the public and policy makers. Although work is at an early stage, we are beginning to unravel patterns underlying coldwater coral biodiversity. Some coral habitats seem important to fish populations while others may be less significant. We urgently need properly integrated biodiversity studies related back to sound taxonomy to unlock the patterns controlling species diversity in cold-water coral habitats.

However, the same surveys that brought cold-water corals to public attention have all too frequently revealed that they have been damaged by fishing activity, primarily by bottom trawling. Concern over this damage has led to the creation of several marine protected areas to conserve these habitats. At the time of writing, international discussions on high seas conservation had begun and we consider these issues and how conservation policies can be developed and enforced to protect cold-water corals from future damage. But anthropogenic activities in the deep sea are no longer limited to bottom trawling. Deep-seabed mining, for years the stuff of science fiction, is now becoming a reality and with improved subsea technologies and international demand for metals at an all-time high it seems likely to expand by exploiting mineral deposits within seabed hydrothermal vent systems. Overlying all these activities the effects of climate change may dramatically alter the marine environment. As sea temperatures warm and anthropogenic carbon dioxide is absorbed by the oceans we are witnessing a gradual shift to more acidic ocean pH. Corals, along with all calcareous organisms, face an uncertain future. Corals calcifying in deep, cold waters may be among the first to feel the effects of predicted changes in the carbonate saturation state of the seas. Ocean acidification may shift calcareous marine systems from states of growth to dissolution. Warming seawater temperatures may perturb their physiology and food supplies. It seems that we risk dramatically increasing the stresses on cold-water coral habitats just as we begin to understand and appreciate them.



## Acknowledgements

Many people deserve our thanks for helping with this book. We are grateful to everyone who made time to comment on early drafts of the text including Denis Allemand (Monaco Marine Laboratory, Monaco), Michaela Bernecker (German University of Technology, Sultanate of Oman), Lydia Beuck (Universität Erlangen-Nürnberg, Germany), Sandra Brooke (Marine Conservation Biology Institute, USA), Andrew Davies (Scottish Association for Marine Science, UK), Ben De Mol (University of Barcelona, Spain), Lyndsey Dodds (World Wildlife Fund, UK), Boris Dorschel (University College Cork, Ireland), David Green (Scottish Association for Marine Science, UK), John Guinotte (Marine Conservation Biology Institute, USA), Lea-Anne Henry (Scottish Association for Marine Science, UK), Marie Le Goff-Vitry (University of Cardiff, UK), Matthias López Correa (Universität Erlangen-Nürnberg, Germany), Alberto Lindner (University of São Paulo, Brazil), Francesca Marubini (Joint Nature Conservation Committee, UK), Paolo Montagna (Central Institute for Marine Research, Italy), Cheryl Morrison (US Geological Survey, USA), Liz Neeley (Communication Partnership for Science and the Sea, USA), Sibylle Noé (Universität Erlangen-Nürnberg, Germany), Mary O'Connor (University of North Carolina Chapel Hill, USA), Dennis Opresko (Oak Ridge National Laboratory, USA), Martin Raes (formerly University of Ghent, Belgium), Robert Riding (University of Cardiff, UK), Brendan Roark (Texas A&M University, USA), Steve Ross (University of North Carolina Wilmington, USA), Tim Shank (Woods Hole Oceanographic Institution, USA), Owen Sherwood (Memorial University, Canada), Dan Sinclair (Scottish Association for Marine Science, UK), Alina Szmant (University of North Carolina Wilmington, USA), Mieke Thierens (University College Cork, Ireland), Jürgen Titschack (Universität Erlangen-Nürnberg, Germany), Rhian Waller (University of Hawaii, USA), Max Wisshak (Universität Erlangen-Nürnberg, Germany) and Martin White (National University of Ireland, Galway). Many of the above also provided us with access to their original figures or other graphics to use in this book, please see acknowledgements with each figure or colour plate.

xiv



#### Acknowledgements

χV

Others provided us with access to work currently in press, to unpublished data or with original copies of their graphics. Many thanks to Jess Adkins (Caltech, USA), Amy Baco-Taylor (Florida State University, USA), Tim Beck (formerly Universität Erlangen-Nürnberg, Germany), Alan Blacklock (National Institute of Water & Atmospheric Research, New Zealand), David Clague (Monterey Bay Aquarium Research Institute, USA), Malcolm Clark (National Institute of Water & Atmospheric Research, New Zealand), Stewart Fallon (Lawrence Livermore National Laboratory, USA), Jan-Helge Fosså (Institute of Marine Research, Norway), Kim Fulton-Bennett (Monterey Bay Aquarium Research Institute, USA), Jean-Pierre Gattuso (Observatoire Océanogique de Villefranche sur Mer, France), Susan Gass (formerly Scottish Association for Marine Science, UK), Dennis Gordon (National Institute of Water & Atmospheric Research, New Zealand), Anthony Grehan (National University of Ireland, Galway), Thomas Guilderson (Lawrence Livermore National Laboratory, USA), Julian Gutt (Alfred-Wegener-Institut für Polar- und Meeresforschung, Germany), Karen Hissmann (IFM-GEOMAR, Germany), Rohan Holt (Countryside Council for Wales, UK), Fanny Houlbreque (International Atomic Energy Agency, Monaco), Ellen Kenchington (Department of Fisheries & Oceans, Canada), Pål B. Mortensen (Institute of Marine Research, Norway), Cova Orejas (Instituto de Ciencias del Mar, Spain), John Reed (Harbor Branch Oceanographic Institution, USA), Mike Risk (McMaster University, Canada), Juan Sánchez (Universidad de los Andes, Colombia), Jürgen Schauer (IFM-GEOMAR, Germany), Robert Stewart (Texas A&M University, USA), Melinda Tignor (National Oceanic and Atmospheric Administration, USA), Diane Tracey (National Institute of Water & Atmospheric Research, New Zealand), David van Rooij (University of Ghent, Belgium), Branwen Williams (Ohio State University, USA) and John Wilson (formerly Royal Holloway, University of London, UK).

We would particularly like to thank Andrew Davies (Scottish Association for Marine Science, UK), Boris Dorschel (University College Cork, Ireland), Henk de Haas (Royal Netherlands Institute for Sea Research, the Netherlands), Molly Ryan (Smithsonian Institution, USA) and Jürgen Titschack (Universität Erlangen-Nürnberg, Germany) for help with figures and distribution maps. We are also very grateful to Amadeo Bachar for the illustrations of coral species and habitats he drew especially for this book. Thanks to Moira Ní Loingsigh for help with the glossary and proofreading and to Lea-Anne Henry for vital editorial help in the final stages of completing the manuscript.

We would like to acknowledge the European Commission, European Science Foundation, UK Natural Environment Research Council, Deutsche Forschungsgemeinschaft (DFG), Irish Marine Institute and Geological Survey of Ireland for funding they have provided to advance our understanding of



xvi

#### Acknowledgements

cold-water corals. J. Murray Roberts would also like to thank Steve Ross, Dan Baden and staff at the Randall Library (University of North Carolina Wilmington, USA) for providing research facilities and the European Commission for a Marie Curie fellowship while this book was being written. J. Murray Roberts would also like to remember the late John Gage for introducing him to deep-sea biology and Andrew J. Wheeler would like to remember the late Ray Kearey for making the mapping of the Irish deep sea a reality. Finally, we all thank John Wilson for his enthusiasm and help with the world of cold-water corals.