BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) was a unique, large-scale, long-term international research programme established in 1977 to investigate the ecology of the Southern Ocean. Its main aim was to gain a greater understanding of the biological systems and stocks in the marine Antarctic environment, thereby providing a sound basis for the future management of the living resources within this immense ocean. The programme was drawn to a close in 1991 and its completion marked by a colloquium which brought together key researchers to summarize and review the results obtained.

This volume, arising from that colloquium, provides a succinct, up-to-date account of the ecology of the Southern Ocean and serves as a comprehensive record of this unique and successful international project.
Southern Ocean ecology: the BIOMASS perspective
Southern Ocean ecology: the BIOMASS perspective

Edited by

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Glossary of acronyms

AAAS  American Association for the Advancement of Science  
AABW  Antarctic Bottom Water  
ACC  Antarctic Circumpolar Current  
ACMRR  Advisory Committee on Marine Resources Research  
ADBE  Antarctic Division BIOMASS Experiment  
AZ  Antarctic Zone  
BAS  British Antarctic Survey  
BIOMASS  Biological Investigations of Marine Antarctic Systems and Stocks  
BOFS  Biogeochemical Ocean Flux Study  
BSBBW  Bransfield Strait Basin Bottom Water  
BWPF  BIOMASS Working Party on Fish Ecology  
CCAMLR  Commission for (or Convention on) the Conservation of Antarctic Marine Living Resources  
CCSZ  Coastal and Continental Shelf Zone  
CDW  Circumpolar Deep Water  
CPUE  catch per unit effort  
CSW  Continental Shelf Water  
DEE  Daily Energy Expenditure  
DMS  dimethylsulphide  
DMSP  β-dimethylsulphonio-propionate  
DOM  dissolved organic matter  
EASIZ  Ecology of the Antarctic Sea-Ice Zone  
EEZ  Exclusive Economic Zone  
ENSO  El Niño – Southern Oscillation  
EPOS  European Polarstern Study  
FAP  fluorescent age pigment  
FIBEX  First International BIOMASS Experiment  
FRAM  Fine Resolution Antarctic Model  
GEOSECS  Geochemical Ocean Sections Study  
GLOBEC  Global Ocean Ecosystem Dynamics Programme  

ix
# Glossary of Acronyms

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Definition</th>
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<tbody>
<tr>
<td>GOSEAC</td>
<td>Group of Specialists on Environment and Conservation</td>
</tr>
<tr>
<td>HNLC</td>
<td>high-nutrient, low-chlorophyll (waters)</td>
</tr>
<tr>
<td>IABO</td>
<td>International Association for Biological Oceanography</td>
</tr>
<tr>
<td>ICES</td>
<td>International Council for the Exploration of the Sea</td>
</tr>
<tr>
<td>IFZ</td>
<td>Ice-Free Zone</td>
</tr>
<tr>
<td>IGBP</td>
<td>International Geosphere–Biosphere Programme</td>
</tr>
<tr>
<td>IGY</td>
<td>International Geophysical Year (1956–7)</td>
</tr>
<tr>
<td>IOC</td>
<td>Intergovernmental Oceanographic Organization</td>
</tr>
<tr>
<td>ISU</td>
<td>International Council of Scientific Unions</td>
</tr>
<tr>
<td>ISAS</td>
<td>International Survey of Antarctic Seabirds</td>
</tr>
<tr>
<td>IUCN</td>
<td>International Union for the Conservation of Nature</td>
</tr>
<tr>
<td>IWC</td>
<td>International Whaling Commission</td>
</tr>
<tr>
<td>IWSOE</td>
<td>International Weddell Sea Oceanographic Expedition</td>
</tr>
<tr>
<td>JARE</td>
<td>Japanese Antarctic Research Expedition</td>
</tr>
<tr>
<td>JGOFS</td>
<td>Joint Global Ocean Flux Study</td>
</tr>
<tr>
<td>LOICZ</td>
<td>Land–Ocean Interactions in the Coastal Zone</td>
</tr>
<tr>
<td>LME</td>
<td>large marine ecosystem</td>
</tr>
<tr>
<td>MIZ</td>
<td>Marginal Ice Zone</td>
</tr>
<tr>
<td>MVBS</td>
<td>mean volume backscattering strength</td>
</tr>
<tr>
<td>NMDS</td>
<td>non-metric multidimensional ordination</td>
</tr>
<tr>
<td>NOAA</td>
<td>National Oceanic and Atmospheric Administration</td>
</tr>
<tr>
<td>PF</td>
<td>Polar Front</td>
</tr>
<tr>
<td>PFZ</td>
<td>Polar Frontal Zone</td>
</tr>
<tr>
<td>POM</td>
<td>particulate organic matter</td>
</tr>
<tr>
<td>POOZ</td>
<td>Permanently Open Ocean Zone</td>
</tr>
<tr>
<td>PPIZ</td>
<td>Permanent Pack-Ice Zone</td>
</tr>
<tr>
<td>PSU</td>
<td>Practical Salinity Unit</td>
</tr>
<tr>
<td>RACER</td>
<td>Research on Antarctic Coastal Ecosystem Rates</td>
</tr>
<tr>
<td>SACW</td>
<td>South Atlantic Central Water</td>
</tr>
<tr>
<td>SAF</td>
<td>Sub-Antarctic Front</td>
</tr>
<tr>
<td>SAZ</td>
<td>Sub-Antarctic Zone</td>
</tr>
<tr>
<td>SCAR</td>
<td>Scientific Committee on Antarctic Research</td>
</tr>
<tr>
<td>SC-CAMLR</td>
<td>Scientific Committee for the Conservation of Antarctic Marine Living Resources</td>
</tr>
<tr>
<td>SC-CCAMLR</td>
<td>Scientific Committee of the Commission for the Conservation of Antarctic Marine Living Resources</td>
</tr>
<tr>
<td>SCOR</td>
<td>Scientific Committee on Oceanic Research</td>
</tr>
<tr>
<td>SIBEX</td>
<td>Second International BIOMASS Experiment</td>
</tr>
<tr>
<td>SIBW</td>
<td>South Indian Basin Bottom Water</td>
</tr>
<tr>
<td>SIZ</td>
<td>Seasonal Ice Zone</td>
</tr>
<tr>
<td>SL</td>
<td>standard length</td>
</tr>
<tr>
<td>SPIZ</td>
<td>Seasonal Pack-Ice Zone</td>
</tr>
<tr>
<td>STF</td>
<td>Subtropical Front</td>
</tr>
<tr>
<td>SSW</td>
<td>Summer Surface Water</td>
</tr>
<tr>
<td>SW</td>
<td>Surface Water or Shelf Water</td>
</tr>
<tr>
<td>TAAF</td>
<td>Terres Australes et Antarctiques Francaises</td>
</tr>
<tr>
<td>UML</td>
<td>upper mixed layer</td>
</tr>
<tr>
<td>WCRP</td>
<td>World Climate Research Programme</td>
</tr>
<tr>
<td>WDW</td>
<td>Warm Deep Water</td>
</tr>
<tr>
<td>WEBW</td>
<td>Weddell–Enderby Basin Bottom Water</td>
</tr>
<tr>
<td>Acronym</td>
<td>Description</td>
</tr>
<tr>
<td>---------</td>
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<tr>
<td>WG-CEMP</td>
<td>Working Group for the CCAMLR Ecosystem Monitoring Programme</td>
</tr>
<tr>
<td>WG-FSA</td>
<td>Working Group on Fish Stock Assessment</td>
</tr>
<tr>
<td>WG-Krill</td>
<td>Working Group on Krill</td>
</tr>
<tr>
<td>WOCE</td>
<td>World Ocean Circulation Experiment</td>
</tr>
<tr>
<td>WSC</td>
<td>Weddell–Scotia Confluence</td>
</tr>
<tr>
<td>WW</td>
<td>Winter Water</td>
</tr>
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</table>
Foreword

The BIOMASS Colloquium, held in Bremerhaven, Germany, in September 1991, was the culmination of the major programme of Biological Investigations on Marine Antarctic Systems and Stocks, formulated in 1976, and directed to improving understanding of the ecology of the vast Southern Ocean. The origins of the programme lie in the establishment, in 1972, of a Subcommittee of the SCAR Working Group on Biology, on Marine Living Resources of the Southern Ocean. In 1975 this Subcommittee was upgraded by SCAR to a Group of Specialists on Living Resources of the Southern Ocean, which was later renamed the SCAR Group of Specialists on Southern Ocean Ecosystems and their Living Resources, in co-sponsorship with SCOR (as Working Group 54), IABO and ACMRR.

A keystone species of the Antarctic marine ecosystem is a small shrimp-like organism called krill (Euphausia superba), potentially a major human food source that may provide an important supply of protein for the future. Krill are crucial to the Antarctic pelagic food chain, providing food for the higher species including whales, seals, penguins, fishes and squid.

The BIOMASS Programme was a major collaborative effort of scientists from many nations; one of its main objectives was to provide an adequate body of knowledge for the wise management of the living resources of the Southern Ocean surrounding the continent of Antarctica. It grew out of the scientific community's concern for maintaining the underlying ecological relationships between the living organisms in this ocean. The BIOMASS Programme facilitated the achievement of an international convention – the 1980 Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) – as part of the Antarctic Treaty System. It has been an important source of information for the Scientific Committee of CCAMLR; the BIOMASS investigators were commissioned to produce two key reports for CCAMLR, on the Biology and Status of Exploited Antarctic Fish Stocks, and on the Biology and Ecology of the Antarctic Krill, both published as BIOMASS Scientific Series 6 and 9, respectively.

BIOMASS was one of the first international collaborations of scientists attempting to provide information for the formulation and application of multispecies management policies, before an ecosystem is seriously threatened or destroyed by commercial exploitation. Because of the immensity of the circumpolar Southern Ocean – some fifty million square kilometres – and its participating membership of eleven countries, the programme was truly international in character.

The overall programme initiated, promoted and drew together marine scientific studies by the participating nations. Scientists standardized methodology, planned programmes, exchanged information in workshops, coordinated the work of joint expeditions and made provision for data archiving and...
management by setting up the BIOMASS Data Centre. Two multiship, multinational cruises – FIBEX and SIBEX (First and Second International BIOMASS Experiments) – took place in 1981 and 1984–5. Some 32 international workshops were held around the world. The BIOMASS Programme also led to an impressive number of publications, including many valuable contributions in scientific journals, in addition to 68 Reports in the BIOMASS Report Series, 23 BIOMASS Handbooks, 10 volumes in the BIOMASS Scientific Series, and 25 issues of the BIOMASS Newsletter. The Programme transformed knowledge of the ecology and oceanography of the Southern Ocean, but has also had an impact on scientific research far beyond that region.

In the process the BIOMASS Programme trained and encouraged many young scientists from a variety of nations, disciplines and backgrounds, bringing them together in workshops, as invited participants in the Group of Specialists’ meetings, and at the Colloquium.

The administrative costs of this major programme extending over fifteen years totalled less than US$600,000, that is less than $40,000 a year, contributed predominantly by the Antarctic Operating Agencies, but also by the International Council of Scientific Unions (ICSU) and its Scientific Committees on Antarctic (SCAR) and Oceanic (SCOR) Research. The leadership of this intensive and extensive international programme was in the hands of Professor S. Z. El-Sayed (with a tiny Secretariat at Texas A&M University) and the members of the BIOMASS Executive, to whom, and to the many Chairmen, Convenors and contributing scientists, we offer our appreciation and thanks.

In this volume, arising from the contributions to the BIOMASS Colloquium, some of the many accomplishments of the Programme are described, including aspects of physical oceanography; estimates of krill stocks, advances in krill biology, physiology and biochemistry; contributions to the knowledge of organisms at higher trophic levels, particularly fish and birds; and the operation and achievements of the BIOMASS Data Centre. There was remarkable unanimity among those attending the Colloquium that the BIOMASS Programme had been a resounding success and that related programmes, such as the International Geosphere–Biosphere Programme (IGBP) and its core programme the Joint Global Ocean Flux Study (JGOFS), now under way, as well as others now being planned (e.g. the Global Ocean Ecosystem Dynamics Programme, GLOBEC), could build on the BIOMASS data and experience. SCAR and SCOR are proud to have been closely involved in this success story.

Richard M. Laws
President, SCAR

Jarl-Øve Stromberg
President, SCOR
Preface

This book is the proceedings of the BIOMASS Colloquium held at the Alfred Wegener Institute, Bremerhaven, Germany, in September 1991. It is a record of accomplishments of the international BIOMASS programme during the decade of the 1980s. It traces the historical context and circumstances that led to the establishment in 1972 of the subcommittee on the Marine Living Resources of the Southern Ocean (of the SCAR Working Group on Biology), and the subsequent upgrading, in 1976, of that subcommittee to the SCAR Group of Specialists on Southern Ocean Ecosystems and Their Living Resources. That group was charged with planning, developing and implementing the BIOMASS Programme.

The book consists of 22 peer-reviewed chapters in six sections. The chapters' arrangement follows closely the organizational structure of the Colloquium. The opening chapter gives a short narrative of the history of BIOMASS, which is followed by description of the physical and chemical settings of the two regions of the Southern Ocean that were the main foci of the BIOMASS field work, namely, the Southwest Atlantic Ocean and the Prydz Bay area (in the Indian Sector). This is followed by chapters on the phytoplankton and zooplankton (not including krill). Because of the great attention given to krill research during BIOMASS, the several papers presented at the Colloquium underscore the preoccupation of the BIOMASS investigators with the Antarctic's keystone organism. The chapters on higher trophic levels, namely fish and birds, document BIOMASS accomplishments in ichthyo- and avifauna research. The interactions among these trophic levels are highlighted in the chapters presented on the subject.

The final chapters are intended as a look to the future. Speakers were asked to respond to the challenge presented by the Convenor, who asked 'Is there life after BIOMASS?' Predictably, the speakers rose to the challenge and provided thought-provoking and stimulating commentaries.

For each of the Colloquium's six sessions, discussants were invited to present their impressions on the papers presented, and to evaluate their strengths and shortcomings. They were later asked to summarize their evaluations, which we are pleased to include under the heading 'Discusant's report' at the end of each section.

As is the case in similar multinational, multidisciplinary programmes whose lifespans extend more than a decade, and in which hundreds of researchers are involved, it is natural to expect that most of the chapters in the book are essentially review papers of the state-of-the-art knowledge in the various disciplines at the end of BIOMASS. This was the charge given beforehand to the authors, all of whom made special effort to comply with that charge.

It is indeed a pleasure to acknowledge with deep gratitude the valuable contributions to this volume.
made by the authors and discussants. I am very much indebted to the several reviewers for their diligence and thoroughness, and for making helpful suggestions and thoughtful comments for improvement of the manuscripts.

Grateful acknowledgements should be extended to those members of the BIOMASS community at large, to the members of the SCAR Group of Specialists on Southern Ocean Ecosystems and Their Living Resources, to the Chairmen and members of the BIOMASS Technical Groups, Working Parties and ad hoc Groups. Without their interest, enthusiasm and devotion to the cause of BIOMASS, the programme would not have become the reality and the success we believe it was.

Finally, The British Antarctic Survey deserves our appreciation for housing and supporting the operational aspects of the BIOMASS Data Centre. Special thanks are extended to the two main sponsors of BIOMASS, SCAR and SCOR, and to the contributors to the BIOMASS Special Fund, who over the long duration of the programme have given generously to finance almost all aspects related to BIOMASS: its workshops, meetings and publications, including subsidy of the present book.

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