MARINE ECOLOGY

A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters

Editor
OTTO KINNE
Biologische Anstalt Helgoland
Hamburg, West Germany

VOLUME I
Environmental Factors
Part 1

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INTRODUCTION
to the
TREATISE

No words can introduce a Treatise on Marine Ecology more adequately than those by JOHANN WOLFGANG VON GOETHE[1] (1749–1832). I am quoting here the German text, as well as a favourite English translation by JOHN ANSTER:

'Alles ist aus dem Wasser entsprungen!!
Alles wird durch das Wasser erhalten!
Ozean, gönn uns dein ewiges Walten.
Wenn du nicht Wolken sendetest,
Nicht reiche Bäche spendetest,
Hin und her nicht Flüsse wendetest,
Die Ströme nicht vollendetest,
Was wären Gebirge, was Ebnen und Welt?
Du bist's, der das frischeste Leben erhält.'

'In Water all hath had its primal source;
And Water still keeps all things in their course.
Ocean, still round us let thy billows proud
Roll in their strength—still send up mist and cloud.
If the rich rivers thou didst cease to spread—
If floods no more were from thy bounty fed—
And the thin brooklet died in its dry bed—
Where then were mountains—valleys? Where would be
The world itself? Oh! thou dost still, great Sea,
Sustain alone the fresh life of all things.'

To modern science, the field of ecology comprises studies of organisms in relation to their environment, abiotic and biotic. Marine ecology is a branch of ecology dealing with the vast multiplicity of organisms living in oceans and coastal waters. The present treatise attempts to cover all major aspects of marine ecology. It consists of several volumes which, for convenience, in some cases have been subdivided into parts. At present 5 volumes are envisaged:

Volume I —Environmental Factors
Volume II —Physiological Mechanisms
Volume III—Cultivation
Volume IV —Dynamics
Volume V —Ocean Management

Environmental Factors is introduced on the following pages (Foreword). Volumes II to V are presently being organized and are scheduled to be published in the next few years.

Physiological Mechanisms will deal with support mechanisms, such as photosynthesis, respiration, reproduction; timing mechanisms, e.g. biological clocks, rhythms; orientation mechanisms; regulatory mechanisms, e.g. volume-, ion-, turgor-, osmo- and thermo-regulation; mechanisms of adaption; and communication mechanisms, such as sound production and perception, as well as visual and chemical communications.

Cultivation will be concerned with maintaining, raising, rearing and breeding marine and brackish-water organisms in laboratories, ponds, under-sea farms, restricted sea areas, etc., both for scientific and economic purposes; this volume will also include sections on technical aspects and diseases.

[1] Werke (Hamburger Ausg., 4th ed.) Vol. 3. Faust. Part 2, p. 255. Wegner, Hamburg, 1959.

Dynamics will focus on production, transformation and decomposition of organic matter in the marine environment; population dynamics; food-chain relations; nutritional requirements; as well as on flow and balance of energy and matter.

Ocean Management—a rather ambitious term for a young and virgin aspect of marine ecological research—will present a brief synopsis of important taxonomic groups, zonations, organismic assemblages; sea-water pollution (sources, biological consequences, avoidance, control, conventions); organic resources of the seas (distribution, use, control, conservation); and a general discussion concerning possible ways and means for management of important sea areas.

A comprehensive, integrated treatise on life in oceans and coastal waters cannot be written by a single author; it must draw from a multitude of talents and sources, and hence requires interdisciplinary and international co-operation. Neither a compendium nor an encyclopaedia, the treatise is intended to be an exhaustive systematic exposition summarizing and evaluating information obtained thus far on living systems in the seas and littoral areas. It has been conceived with the growing number of individuals in mind who are professionally concerned with life in the marine environment, especially investigators, engineers, teachers, students, administrators and businessmen. Although, for the benefit of the reader, integrated into a methodically arranged general concept, each contribution is intended to represent a detailed, authentic critical account in its own right; all contributors are free in choice of material and emphasis.

The first tentative outline of the treatise was circulated among several hundred marine ecologists in November, 1965. The warm response received from the international scientific community and the stimulating support from the publishers have encouraged me to proceed with my plans. Criticism, advice and assistance of numerous colleagues have greatly affected and improved the first proposal. I gratefully acknowledge all this support. It is not possible to list here the names of even the most active supporters; they will be mentioned in the forewords to the respective volumes.

A treatise such as this needs continued criticism and advice. Any comments—especially on outline, coverage and new points of view—will be most welcome.

July 21, 1969 O. KINNE

FOREWORD
to
VOLUME I: ENVIRONMENTAL FACTORS

'Environmental Factors' summarizes and evaluates all important information available to date on the responses of ocean and coastal-water living organisms to intensity variations of the major abiotic and biotic ecological factors. It is subdivided into 3 parts which contain the following chapters:

Part 1

Chapter 1 : Oceans and Coastal Waters as Life-supporting Environments
Chapter 2 : Light
Chapter 3 : Temperature

Part 2

Chapter 4 : Salinity
Chapter 5 : Water Movement
Chapter 6 : Turbidity

Part 3

Chapter 7 : Substratum
Chapter 8 : Pressure
Chapter 9 : Dissolved Gases
Chapter 10: Organic Substances
Chapter 11: Ionizing Radiation
Chapter 12: Factor Combinations

Chapter 1 considers oceans and coastal waters as life-supporting environments. It describes briefly the ocean basins, their principal water masses and circulation, the sea-land boundary, the properties of sea water and the chemical cycles in the seas.

Chapters 2 to 11 deal with responses to environmental factors. Of course, only factors about which enough information is available can be treated. Each chapter begins with a general introduction informing the reader about (1) general aspects of the environmental factor concerned, (2) methods of measuring its intensities, and (3) its intensity patterns in oceans and coastal waters. The chapter outline, suggested to all contributors, distinguishes between functional and structural responses. Functional responses are subdivided into tolerance, metabolism and activity, reproduction, and distribution; structural responses are dealt with under the subheadings size (body length, width, volume), external structures (shape, differentiation, etc. of external body parts) and internal structures (organs, tissues, cells or parts thereof). The monofactorial approach used in Chapters 2 to 11 has been chosen because of the insufficient amount of information at hand on multifactorial relationships, and because organisms—whether bacteria, plants or animals—frequently exhibit comparable responses to intensity variations of environmental entities such as light, temperature or salinity. A monofactorial (univariable) design facilitates comparison, evaluation and generalization of reactions to a given environmental factor by members of different taxa. It is realized, of course, that in natural habitats organisms respond to their total environment rather than to single factors (selected by man for methodological, conceptual or historical reasons). Factor interactions, known or expected to be of special importance, are therefore referred to briefly in each chapter.

Chapter 12 presents a special, detailed account on organismic responses to factor combinations. There can be no doubt: investigation of responses to intensity variations of environmental factors acting in concert must be given priority if man wants to understand ecological dynamics and to achieve forecasting and controlling capacities in regard to life in the marine environment. There is great need for (i) conducting large-scale research projects based on multivariable designs and including all life-history stages of important food-web representatives, (ii) developing appropriate analyzing and evaluating techniques (computation, mathematical models and concepts of abstraction, formalization and generalization). Chapter 12 represents a pioneer effort to stimulate progress in this modern branch of ecological research.

Our intention to provide the reader with a well-organized source of information which enables him to find and compare facts and problems of interest to him quickly and easily created several difficulties. The first difficulty was to achieve general agreement in regard to gross taxonomic subdivisions. The subdivisions 'bacteria, fungi and blue-green algae', 'plants', and 'animals' have been adopted after long discussions; they are the result of a compromise between the need to keep the number of taxa as small as possible and to choose groups of organisms which can be conveniently treated by single authors; whenever necessary these groups are subdivided further, e.g. 'animals' into 'invertebrates' and 'fishes'. The second difficulty concerned the treatment of 'nutrition'. In bacteria, nutrients and substratum (Chapter 7) are hardly separable; in plants, nutrients overlap to a certain degree with salinity (Chapter 4), in animals with organic substances (Chapter 10). While some aspects of nutrition have been considered under various headings, nutritional aspects will be treated in detail in Volumes III and IV. The third difficulty was created by differences in thematic emphasis and in the usage of certain scientific terms in the fields of marine microbiology, botany or zoology. An example is the connotation of the term 'growth', which means increase in individual numbers in microbiology, but increase in organic matter of individuals in botany and zoology. Such terminological problems were solved by providing definitions or explanations.

The policy of placing the conceptual grid of the chapter outlines on the body of knowledge available and reviewing the material found near each 'point of intersection' (rather than following, as usual, the meandering path along which information happens to have accumulated) made us aware that many important areas of marine ecological research have hardly been touched upon, while others have attracted unparalleled attention; such disproportions are reflected in the lengths of the respective contributions. The Chapter 'Water Movement: bacteria, fungi and blue-green algae' had to remain unwritten because of insufficient knowledge available.

Lack of information also created a serious gap in regard to biotic factors (e.g. behavioural and biochemical interactions between organisms of a given ecosystem) which may affect, or even govern, intra- and interspecific patterns of organismic co-existence. Little pertinent information is at hand on marine mammals and birds; their responses to environmental stress often depend on endogenous homeostatic mechanisms.

'Environmental Factors' concentrates on responses of intact organisms. However, if considered relevant, information obtained at the individual level is complemented by findings at the sub- or supra-individual levels. Functional and structural responses are primarily considered under the aspect of quantitative variability, i.e. in terms of changes in rates or intensities of performance. The physiological mechanisms involved will be dealt with in Volume II. General trends that have become apparent are documented by referring to one or a few well worked out examples rather than by presenting a long list of parallel findings. All literature cited appears in alphabetical order at the end of each chapter; it is hoped that such a procedure will help to strengthen interdisciplinary contacts between the fields of marine microbiology, botany and zoology and to facilitate a fast and convenient survey of important pertinent literature.

While an effort has been made to concentrate on marine and brackish-water organisms, in some instances information obtained on limnic forms has been included, especially in situations where knowledge on salt-water living organisms is scarce, or in which it appears safe to assume that both groups of aquatic organisms would exhibit comparable responses.

Much of our present knowledge on responses of marine and coastal-water living organisms to environmental stress has been obtained during casual observation or in insufficiently equipped and staffed laboratories. More complete studies require modern scientific dimensions: more space, better facilities and teams of scientists and technicians.

I am deeply indebted to all contributors for their patience, dedication and willingness to co-operate far beyond the usual demands; despite technical difficulties it was possible in most cases to adhere closely to the outlines proposed. The publishers have supported me wholeheartedly and considerably reduced the many problems by not imposing any space or time limits; I am grateful for this confidence and for excellent co-operation. It is a pleasure to acknowledge support, advice and criticism received by many colleagues, especially by D. F. Alderdice, J. R. Brett, A. W. Collier, M. Gillbricht, E. Hagmeier, M. Hoppenheit, H. W. Jannasch, R. I. Smith, R. W. Taylor and B. P. Ushakov. During the years of organizing and preparing Volume I, Mrs. J. M. Christian, Miss V. J. Clark and Miss F. C. Crouse have served as reliable and highly capable editorial secretaries and assistants. Mr. J. Marschall has given generously of his time and talent in altering or improving illustrations and Mr. W. Meiss was an indispensable and conscientious helper in all matters related to bibliographical problems. It is with a deep sense of gratitude that I acknowledge all this assistance.

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CONTRIBUTORS
to
VOLUME I, PART 1

BLAXTER, J. H. S.,	*Marine Research Laboratory, P.O. Box 3; Oban, Argyll, Scotland.*
BRETT, J. R.,	*Fisheries Research Board of Canada, Biological Station; Nanaimo, British Columbia, Canada.*
COLLIER, A. W.,	*Department of Biological Science, The Florida State University; Tallahassee, Florida 32306, USA.*
GARSIDE, E. T.,	*Biological Department, Dalhousie University; Halifax, Nova Scotia, Canada.*
GESSNER, F.,	*Institut für Meereskunde an der Universität Kiel, Niemannsweg 11; 23 Kiel, West Germany.*
GUNKEL, W.,	*Biologische Anstalt Helgoland (Meeresstation); 2192 Helgoland, West Germany.*
HELLEBUST, J. A.,	*Department of Botany, University of Toronto; Toronto 5, Canada.*
JERLOV, N. G.,	*Institute of Physical Oceanography, University of Copenhagen, Sølvgade 83; Copenhagen K, Denmark.*
KINNE, O.,	*Biologische Anstalt Helgoland (Zentrale), Palmaille 9; 2000 Hamburg 50, West Germany.*
OPPENHEIMER, C. H.,	*The Florida State University; Tallahassee, Florida 32306, USA.*
SEGAL, E.,	*Department of Biology, San Fernando Valley State College, 18111 Nordhoff Street; Northridge, California 91324, USA.*

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of
VOLUME I, PART 1

1. OCEANS AND COASTAL WATERS AS LIFE-SUPPORTING ENVIRONMENTS

A. W. COLLIER

(1) Introduction

The marine ecologist strives for maximum comprehension of a biota which has been immersed in a saline medium since primeval times. The myriads of species composing the contemporary flora and fauna have been derived through the many failures and successes of opportunistic evolution (SIMPSON, 1949) from the biological primordium of ancient seas. The marine biota of today is the product of: (1) the tendency of living matter (and non-living matter) to assume every possible form compatible with the environment, (2) the capacity of living matter to utilize non-living and living matter as a source of energy and materials for survival and multiplication, and (3) nature's most abundant commodity: time.

The above paragraph offers a perspective which spans the appraisal of the oceans and their ancillary bodies as life-supporting environments. The purpose of this chapter is to describe briefly the oceans' basins and the pertinent attributes of the waters which they contain.

The attributes of sea water and the physical characteristics of the oceans have special meaning when they are viewed as parts of a system supporting an infinite variety of forms and functional specializations. The challenge of understanding an infinite variety of living organisms in a medium which has changed but little over many millions of years is one of the great fascinations of marine ecology.

(2) The Ocean Basins

The world ocean, as a responsive fluid, is subject to the remote but violent sun through the intermediary of the atmosphere; it is also a receptacle for organic and inorganic residues from a relatively small area of land which rises above it (slightly more than one quarter of Earth's total surface). The dissection of the hydrosphere by the land masses has been one of the important determinants in the development and distribution of both aquatic and terrestrial taxa. An examination of the general plan of articulation of the primary ocean basins and their ancillary bodies is fundamental to an evaluation of the marine environment.

In this section, I have chosen to organize the treatment of the basins to begin with the Arctic Ocean and to end with the Southern Ocean. Each major or primary ocean is presented with its adjoining secondary branches in geographical order.

The Arctic Ocean

The Arctic Ocean may be viewed as an inland sea with restricted communication with the world ocean. This ocean lies astride the North Pole as the continent of

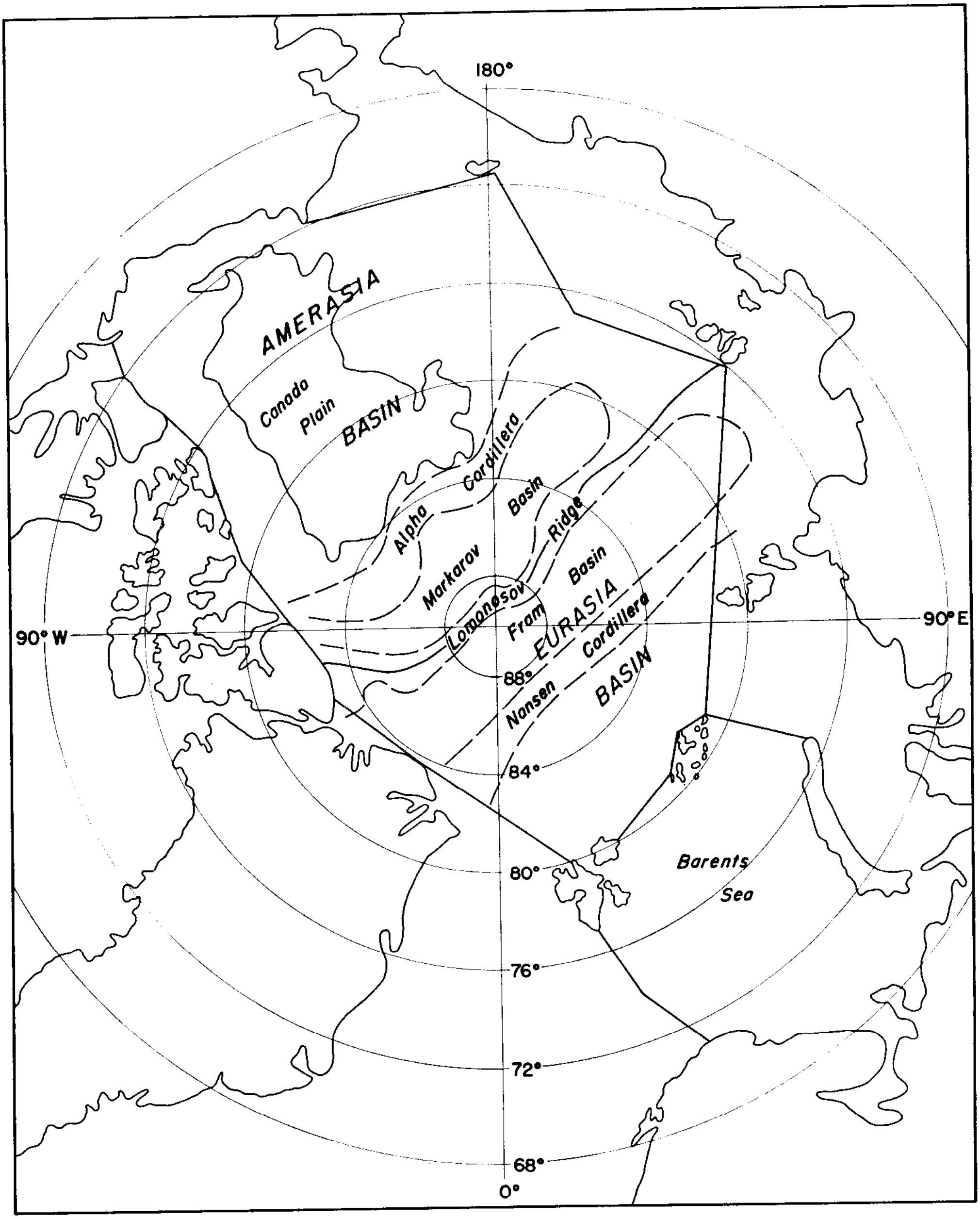

Fig. 1-1: The basins and the dominant bathymetric features of the Arctic Ocean. (After BEAL and co-authors 1966, and other sources.)

Antarctica embraces the South Pole. As an inland sea receiving continental drainage, Arctic waters are responsive to the balance of oceanic and terrestrial factors. By contrast, the Southern Ocean, peripheral to Antarctica, affects the character of a major part of the world ocean.

Arctic Basin

In this brief description of the Arctic Basin we shall follow the commentary on geographic names of the floor of the Arctic Ocean presented by BEAL and co-authors (1966). Beginning in the west, the Arctic Basin is divided into three easily identifiable segments: the Amerasia Basin, the Eurasia Basin, and Barents Sea (Fig. 1-1). Along the Eurasian continent there are the secondary seas, east to west: Chukchi Sea, East Siberian Sea, Laptev Sea, and Kara Sea. On the opposite side, from Greenland to Alaska, there are no secondary seas. 'Beaufort Sea' is given no hydrographic or geographic grounds for standing as a place name by BEAL and co-authors (1966).

The dividing line between the Amerasia Basin and the Eurasia Basin is the Lomonosov Ridge. It very nearly subtends the meridian 140° E to the North Pole; at a point just south of the pole, the ridge takes a turn to the west and parallels the meridian 85° W. Flanking the Lomonosov Ridge we find a series of parallel folds and correlated basins on either side. These features have been named, respectively, the Fram Basin and its dextrally-lying Nansen Cordillera in the Eurasia Basin, and the Markarov Basin with its sinistrally-lying Alpha Cordillera in the Amerasia Basin.

West of the Alpha Cordillera lies the Canada Plain bounded by a portion of the East Siberian Shelf, the Chukchi Shelf, and the Alaskan and Canadian coasts. The smaller details of the Arctic Basins are shown in Fig. 1-2.

Water Masses and Circulation of the Arctic Ocean

With respect to vertical distribution, three distinct water masses are recognized in the Arctic Ocean; they are related to the sources of water feeding into the ocean. The principal sources of water affecting the composition and differentiation of the masses are: Atlantic Ocean, Bering Sea, Norwegian coast and continental drainage from Asia. Horizontally, there is also differentiation. The vertically distributed masses are divided between the Amerasia and the Eurasia Basins.

COACHMAN and BARNES (1962) described the surface stratum, the Arctic Water Mass, as being composed of three layers: (1) from near the surface to 25 to 50 m, (2) from 25 to 50 m to 100 m, and (3) from 100 m to the Atlantic Water Mass, whose core lies at 250 to 300 m.

The deep Arctic is covered with an ice blanket which keeps the surface layer near the freezing point. An increase in density in the water just below prevents seasonal convection from being manifest to depths greater than 25 m, rarely to 50 m. This layer has a comparatively broad salinity range: 28 to 33·5 $^0/_{00}$.

The subsurface layer is characterized by a halocline reaching a maximum salinity of 34 $^0/_{00}$ at its lower limit of 100 m. The origin of this is postulated as arising from a mixture of Atlantic Water and continental drainage through an estuarine-like mechanism inherent in the canyon structures along the Eurasian continental slope (COACHMAN and BARNES, 1962).

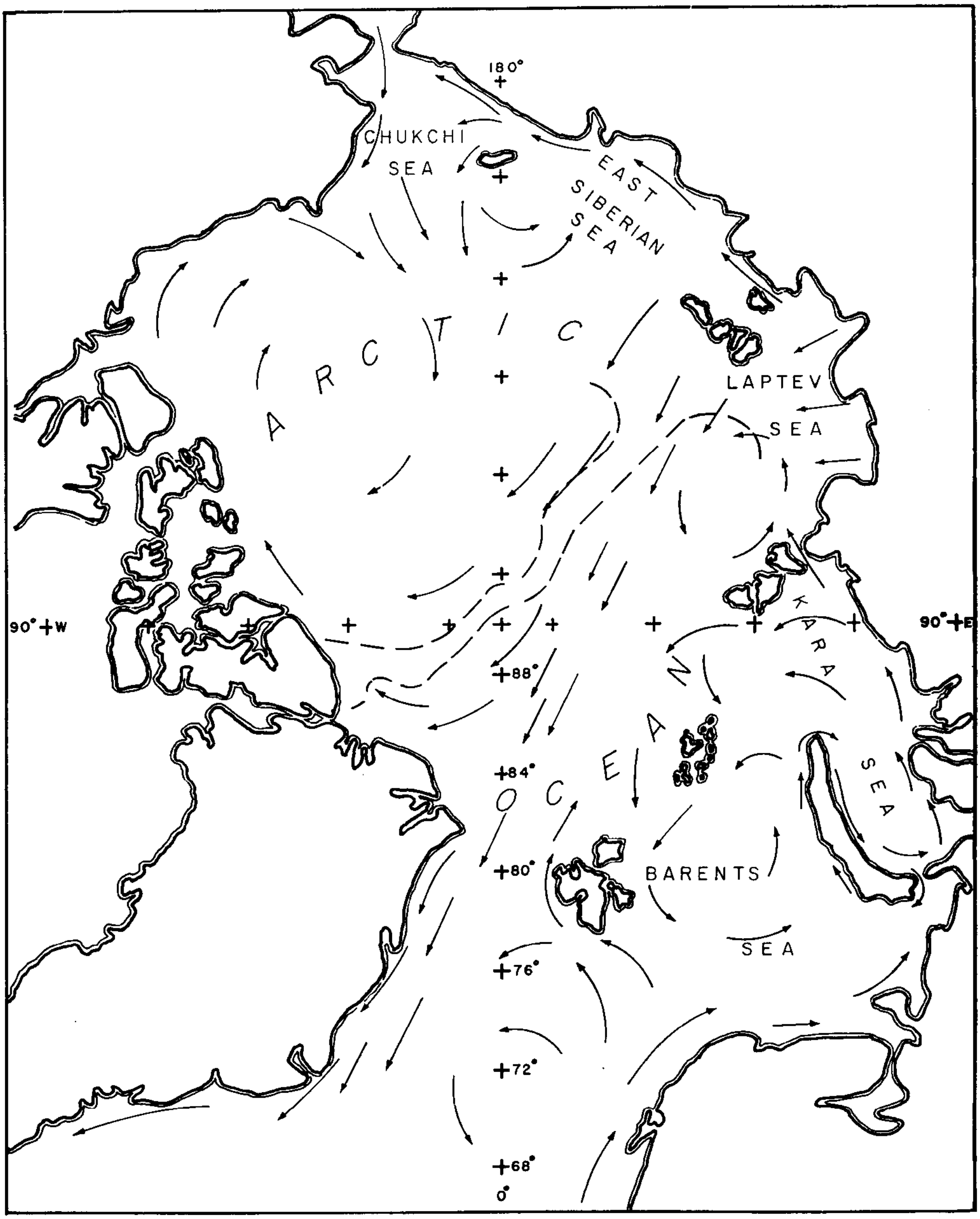

Fig. 1-2: The Arctic Ocean, its secondary seas and the principal routes of water circulation. (After various Sources.)

The third subdivision of the Arctic Water Mass extends from 100 m to the Atlantic Water Mass and is actually a mixture of the latter and the subsurface layer described above. Its properties are intermediate between the two.

It appears that Bering Sea water flows into the Amerasia Basin through Bering Strait and mixes with Siberian Shelf water after which it becomes a part of the Arctic circulation at a point northwest of Point Barrow (COACHMAN and BARNES, 1961). It is estimated that about 20% of this water comes from the Bering Sea. That water which passes through the Bering Strait in the summer causes a shallow temperature maximum and that which is brought in during the winter is believed to be associated with a deeper minimum temperature. It is these characteristics which differentiate the Amerasian Arctic Mass from the Eurasian Mass, the latter showing no shallow temperature maximum.

Using the core method of WÜST (1964), COACHMAN and BARNES (1963) made a study of the movement of the Atlantic Water in the Arctic Ocean. This water enters the Arctic near Spitsbergen and flows along the Eurasian continental slope to a point north of the Laptev Sea. Along this route segments of the mainstream curl off and flow back in a southwesterly direction towards the main exit of the Arctic—the current along East Greenland. This return movement aids in the rapid filling of the Eurasia Basin with the Atlantic water.

In a broad sweep from the slope of the Kara and Laptev Seas, the Atlantic water continues across the Lomonosov Ridge and moves parallel to the slopes of the East Siberian and Chukchi Seas. From there it proceeds across the southern aspect of the Amerasia Basin to recross the Lomonosov Ridge and exit through the East Greenland passage.

The Arctic Bottom Water seems to originate in the Norwegian Sea and reaches a temperature of $-0{\cdot}8°$ C in the Eurasia Basin at 2500 m, and $-0{\cdot}4°$ C in the Amerasia Basin at 2000 m. The reason for this differentiation is that the colder and deeper water does not flow over the Lomonosov Ridge. The relations between the various water masses and the general circulation are shown in Fig. 1-2.

The Atlantic Ocean

As a unit, the Atlantic Ocean is sigmoid in form and extends from the threshold of the Arctic to the open seas of the Southern Ocean. It is more or less closed on the north by the Greenland–Iceland, Faroe, British Isles complex. It may be further characterized by its two mediterranean seas, the European and the American. The Arctic Ocean is often considered as a secondary mediterranean sea of the Atlantic also.

North Atlantic Ocean

The least distance across the Atlantic Ocean lies near a line drawn on the mercator projection from Natal to the Arquipelago dos Bijagos (off Portuguese Guinea). This line provides a convenient boundary between the South and North Atlantic Oceans. It has some bathymetric validity because the Sierra Leone Ridge is roughly parallel to it, and extends from the African continent to the Mid-Atlantic Ridge. Between the latter and the South American bulge there is an unnamed plateau with limited relief which is flanked to the north and south by the Guiana and Brazil Basins, respectively.

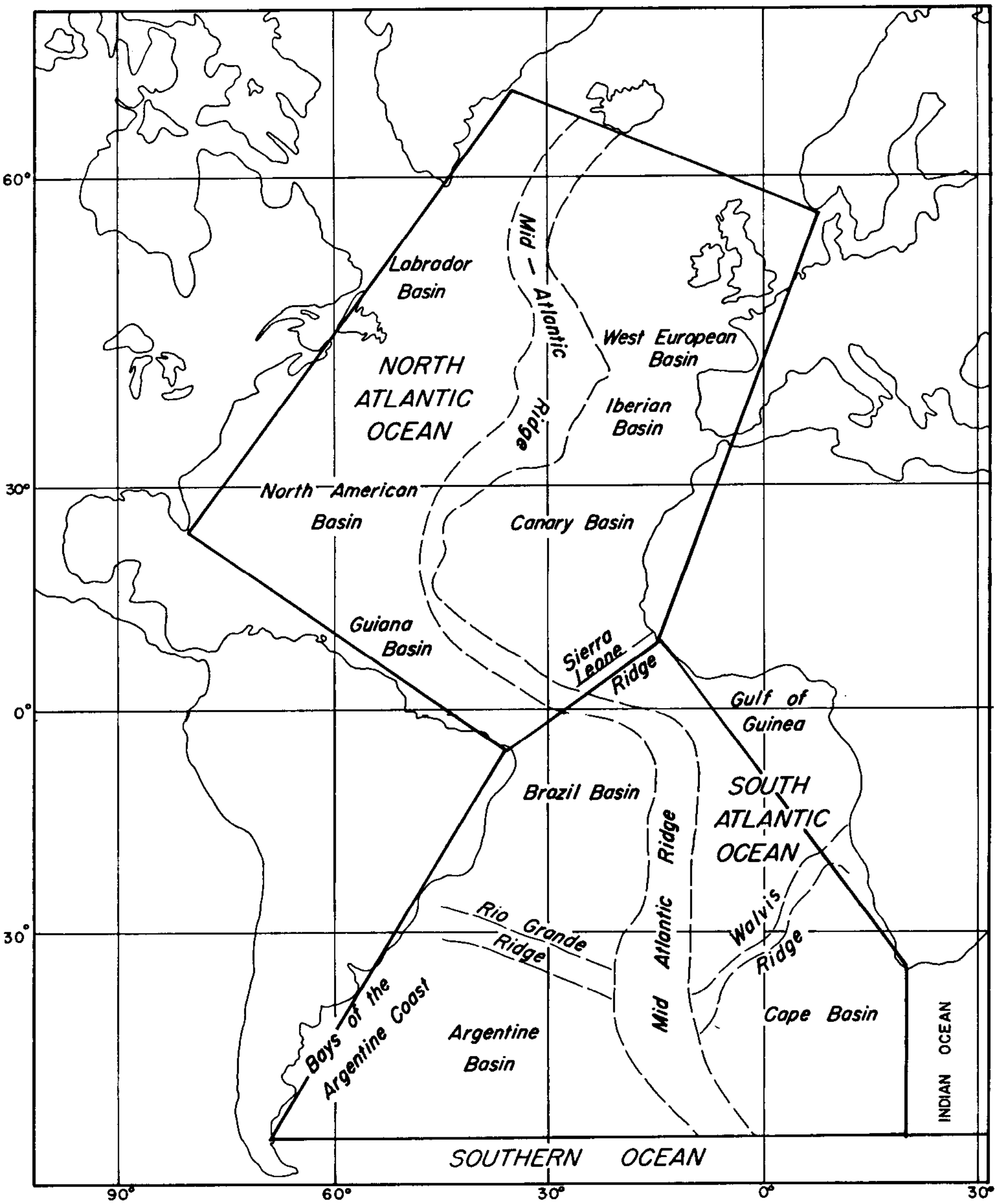

Fig. 1-3: A diagrammatic scheme to show the relations of the major basins and ridges of the North and South Atlantic. The boundary between the South Atlantic Ocean and the Southern Ocean is drawn at 52° S latitude. The South Atlantic Indian Ocean boundary is also by definition. (Adapted from US Naval Oceanographic Office Chart of the World No. H. O. 1262A, 10th Edition.)

A line drawn from the Arquipelago dos Bijagos to Kristiansand in Norway completes the east side of a rough rectangle which can be drawn to enclose the North Atlantic Ocean (Fig. 1-3). The principal bathymetric features of the North Atlantic can be most easily described by using the reference rectangle. It is seen that the Mid-Atlantic Ridge and associated structures divide the whole basin into almost symmetrical portions, each containing a series of basins. The east side of

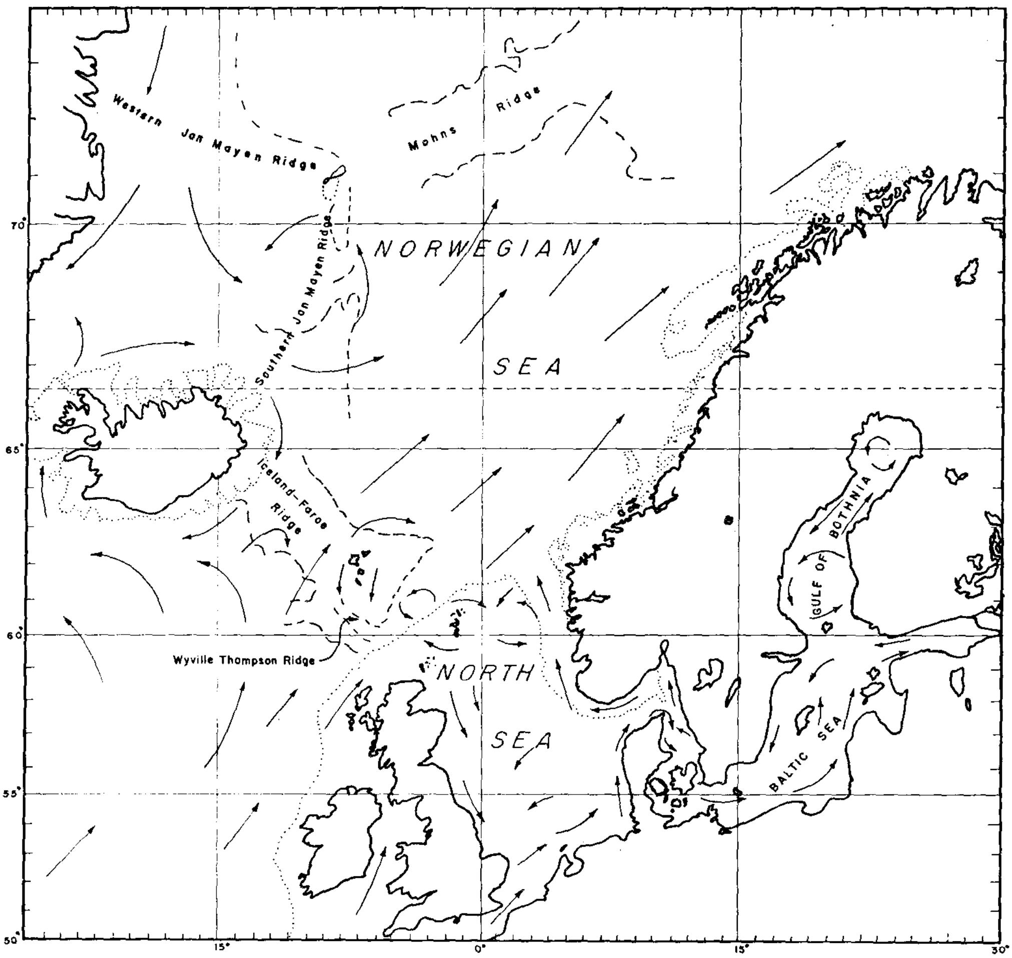

Fig. 1-4: The major geographic features in the region of the Norwegian Sea and the North Sea. The water circulation is shown. The dotted lines represent the 100 fathoms (183 m) contour. Ridges are indicated by dashes. (After various sources.)

the ridge is divided into the West European Basin, the Iberian Basin, the Canary Basin and the Cape Verde Basin. The region west of the Mid-Atlantic Ridge is divided into the Labrador Basin, the Newfoundland Basin, the very large North American Basin and the Guiana Basin.

The secondary seas of the North Atlantic are found on the periphery of the reference rectangle.

The Norwegian Sea and the Norwegian Basin lie in a semicircle formed around their southern perimeters by Norway, the British Isles, and Iceland. The Norwegian Basin is separated from its more northerly neighbour, the Greenland Basin, by Mohns Ridge (Fig. 1-4).

The North Sea is not a large geographic unit, but its location amidst one of the oldest population centres of the western world makes it one of the better known arms of the sea. The North Sea Basin is a segment of the Northwest European Shelf whose periphery extends from the coast of Norway to the coast of France in the Bay of Biscay (Figs. 1-4, 1-5).

The Celtic Sea (Fig. 1-5) is not a major arm of the sea and is not generally indicated on maps, but it is included here because of the frequent appearance of the name in oceanographic literature. COOPER and VAUX (1949) (see also COOPER, 1967) established the validity of the term and defined it as follows:

'(1) On the east by the shortest line between the western point of the Island of Ushant (Ile d'Ouessant) and Lands End (Cornwall) and by the shortest line between Lands End and Ramsey Island, off St. David's Head, Pembrokeshire. (2) On the north by the shortest line from Ramsey Island to Carnsore Point, Co. Wexford, by the south coast of Ireland from Carnsore Point to Dursey Head, Co. Kerry, and by the shortest line from Dursey Head to the 200 m. (or alternatively the 100 fm.) contour. (3) On the west and southwest by the 200 m. (or 100 fm.) contour. (4) On the south by the shortest line from the western point of Ushant to the 200 m. (or 100 fm.) line.'

As the Celtic Sea stands on the northern flank of the English Channel, so stands the Bay of Biscay (Fig. 1-5) on the southern. The Cantabrian Mountains plunge through Asturias into the ocean to form the steep southern wall of the bay, and the northwest terminus of the Pyrenees marks the northward turn of the coast. At this point the continental shelf broadens and becomes confluent with that of the Celtic Sea.

The European Mediterranean is a double sea, all but isolated from the world ocean (Fig. 1-6). The western basin is characterized by deeper water than is found in the eastern basin (maximum depth of 4600 m), the comparatively restricted continental shelf, and limited communication with the Atlantic Ocean. The floor of the Western Mediterranean is characterized by the Balearic Abyssal Plain (HEEZEN and MENARD, 1963). The Tyrrhenian Sea, embraced by southern Italy, Sicily, Sardinia, and Corsica, is a separate basin within its own right with its deeper waters having limited access to the outside. The Western Mediterranean basin is separated from the eastern basin by the comparatively shallow and narrow passage between Sicily and Tunisia. The eastern basin is a common receiver for the waters of the Adriatic, the Aegean, and through the latter, the Black Sea. However small the total area, it contains the most extensive shelf area of the entire Mediterranean in three places: off Tunisia and Tripolitania, the inner two-thirds of the Adriatic and the Aegean. One would expect the Nile to have contributed more to the bottom relief of this basin but according to HEEZEN and MENARD (1963), tectonic activity in the area is too recent for the Nile sediments to register an effect.

The Labrador Sea is continuous with Baffin Bay to the north. The axis of the Labrador Basin is formed by an extension of the mid-ocean canyon originating in

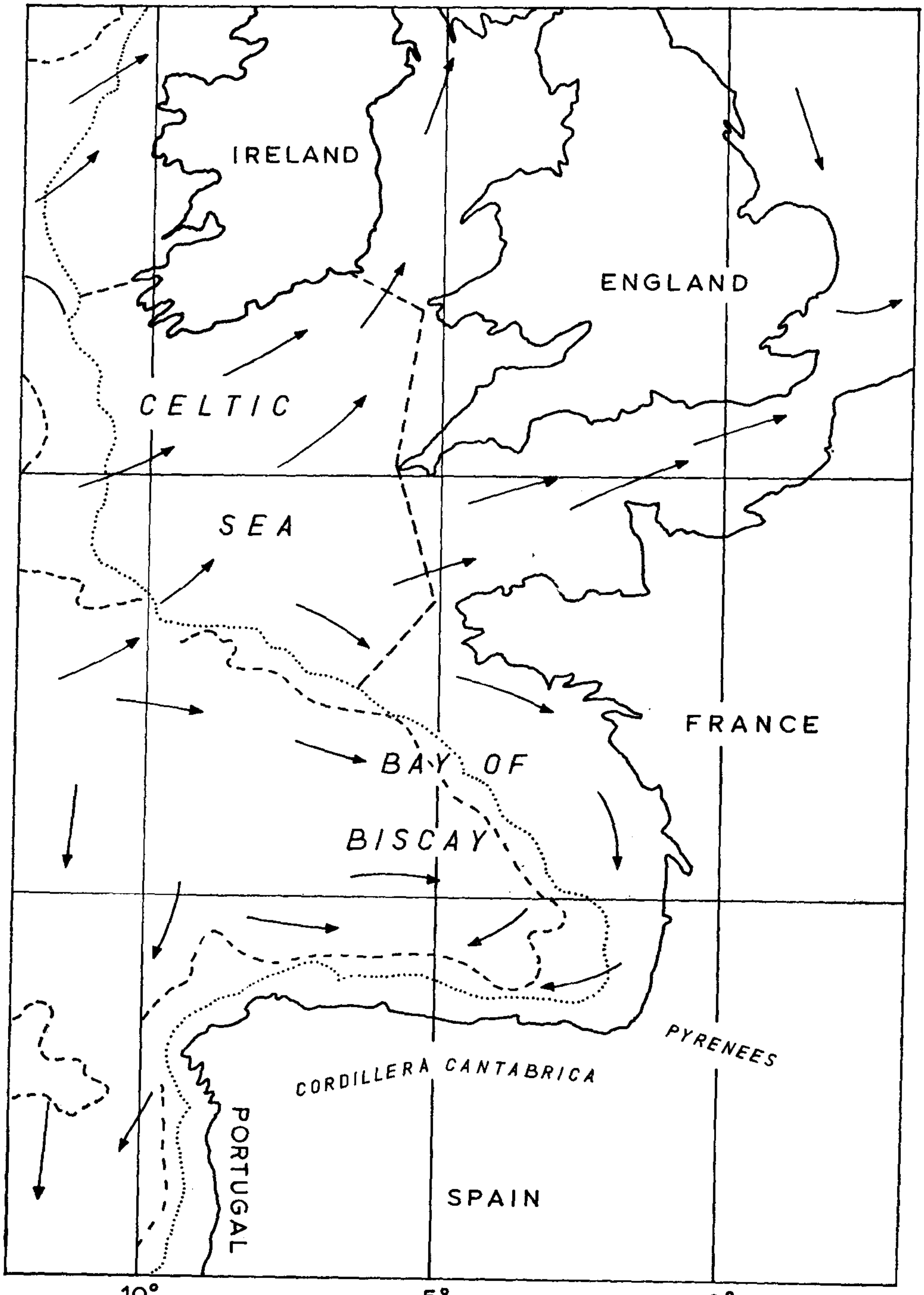

Fig. 1-5: The Celtic Sea and the Bay of Biscay. Dotted line: 100 fathom (183 m) contour. Arrows indicate surface currents. (From US Hydrographic Office Chart No. 5247, and GROSVENOR, 1963.)