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DET NORSKE VIDENSKAPS-AKADEMI I OSLO

HJALMAR BROCH

BENTHONIC PROBLEMS IN ANTARCTIC AND ARCTIC WATERS
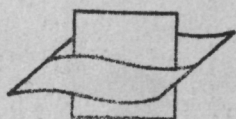
WITH 6 FIGURES IN THE TEXT

DET NORSKE VIDENSKAPS-AKADEMI I OSLO

SCIENTIFIC RESULTS
OF THE NORWEGIAN ANTARCTIC
EXPEDITIONS 1927—1928 ET SQQ.
INSTITUTED AND FINANCED
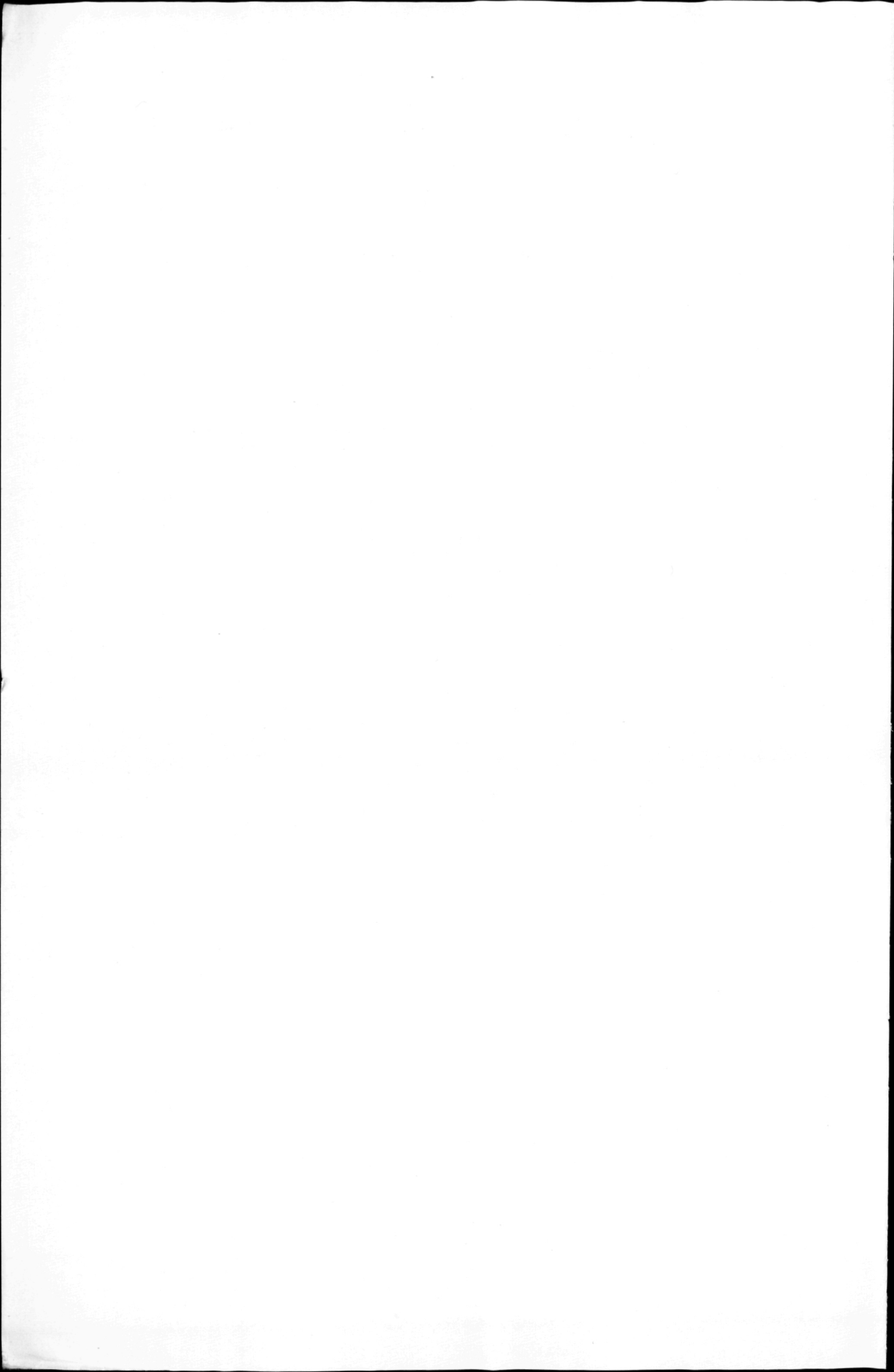### BY CONSUL LARS CHRISTENSEN

EDITED BY
OLAF HOLTEDAHL

VOLUME III

Contents of Volume III.

DET NORSKE VIDENSKAPS-AKADEMI I OSLO

HJALMAR BROCH

BENTHONIC PROBLEMS IN ANTARCTIC AND ARCTIC WATERS

WITH 6 FIGURES IN THE TEXT

Preface.

Most of the collections from the cruises of the "Norvegia" in Antarctic Seas have been worked up and their results published in the present series of scientific reports. Accordingly, this seems a suitable occasion on which to give a short review of some antarctic and arctic zoogeographical problems which have arisen during recent years. Since the last world war several discoveries have been made, especially in the North Polar Sea, which in many ways have clarified and widened our conceptions of the conditions of life in both Polar Oceans, and it has become urgent to compare the ecological conditions of the benthonic animal communities in these waters, which differ fundamentally in several ways. It has also become clearer that ecology forms the main basis for an understanding of zoogeography.

I am very much indebted to Dr. N. A. Mackintosh of the National Institute of Oceanography who again kindly allowed me to use the chart of the North Polar Seas prepared by his staff for my paper on the Discovery pennatularians (1958). Special thanks are due to Miss Helene E. Bargmann of the National Institute's staff who placed at my disposal a series of notes from the Discovery Reports and other literature together with the recent Australian charts of the Antarctic Seas, and who has also revised the text. – The staffs of the Marinbiologisk Institut, Oslo and of the Norsk Polarinstitut, Oslo have helped me in several ways, the latter by drawing the charts of the Southern and Northern Oceans.
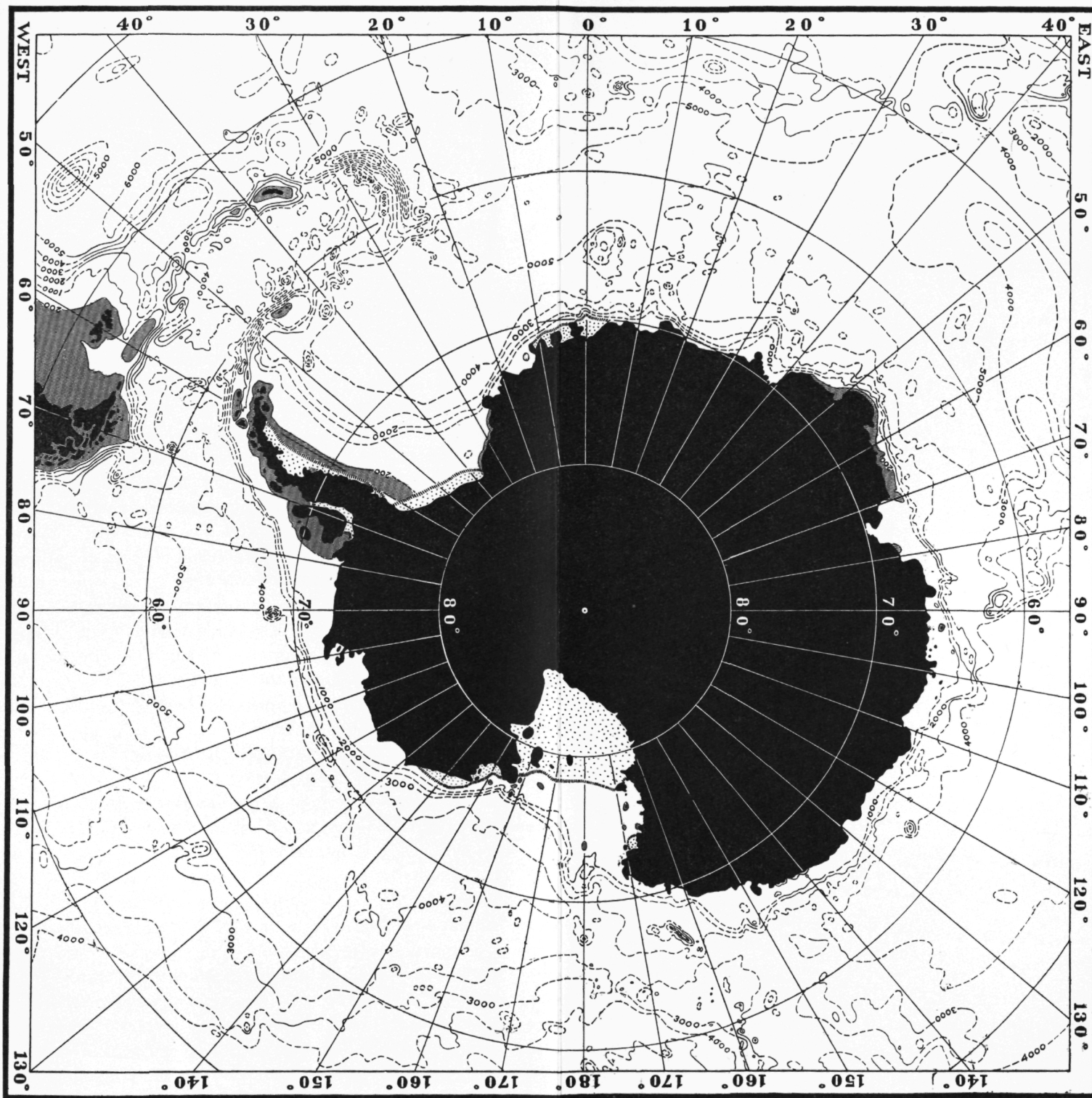
Oslo, May 1961

Hjalmar Broch

Fig. 1.
The Southern Ocean (After recent Australian Charts)

Basic Conditions of the Antarctic Benthos.

A glance at the geomorphological features of the two polar regions shows at once that in many respects the zoogeographical problems must be different, or even contrary in both places. Simplified, we may say that the central Arctic Sea constitutes a large and very deep basin or bowl, the brim or "shelf" of which in its broad features is rather shallow and constitutes a marked barrier to the temperate deepwaters of the adjacent oceans, whereas the Antarctic Continent is an upturned bowl, an enormous island on all sides of which the shores slope rather steeply down into the deepwaters without a marked continental "shelf"; it is moreover separated from the nearest antiboreal neritic regions by broad tracts of deepwater. The antarctic neritic region accordingly is generally considered as very small and distinctly limited. To quote Ekman (1953, p. 221): "In these regions where the limits of the Antarctic would be expected to run there is no shelf but instead a more or less extensive abyssal region. The zoogeographer runs here no risk of drawing an artificial boundary where nature has none but only a broad mixed region. Nature itself has drawn the boundaries here with all desirable clarity. The old saying of Linné "Natura non facit saltus" finds here an exception which is not unwelcome to regional zoogeography. No other large faunal region in the world can match the Antarctic in the sharpness of its boundaries."

It is evident from this that in Ekman's opinion a true antarctic neritic fauna either does not exist at all or, at most, is very reduced, because a "shelf" in his opinion is wanting. However, of course a real neritic zone does exist, although the bottom only deserves the designation of a (continental) shelf in small and mostly well separated localities. This is the case for example around the Balleny Is, around the South Shetland Is, in the Ross Sea, and in scattered places elsewhere along the coasts of the Antarctic Continent. On the other hand, it would be wrong to disregard the steep continental slopes of the mainland. Certainly the upper parts of them harbour a characteristic animal community with several typical neritic species, although even today, we must confess that the benthonic animal world of these shallower localities, and especially the fauna of the upper part of the slopes of the mainland have only been very scantily explored, if at all, the fringing packice presenting a great obstacle to the working of gear.

The northern hydrographical limit of the Antarctic Zone in the upper water layers lies along the Antarctic Convergence. This means that several scattered and isolated islands and groups of islands must be included within the region, the S. Orkney Is, S. Georgia, the S. Sandwich Is, Bouvet I., Heard I. for example among others, and in these localities more or less restricted neritic areas also occur. Although the animal life has also been rather unsatisfactorily explored in these places, every indication points in the direction that here the shallow-water fauna must be considered in most places to be low-antarctic as compared with high-antarctic coastal waters along the Continent.

The Antarctic Convergence in the surface layers also constitutes the northern boundary between the Antarctic Plankton and the antiboreal fauna. This however, is not the case in the benthonic world where the neritic zone everywhere borders on the deepwater. In the Antarctic, as elsewhere, the faunistic border between the shelf and the deep-sea ought to be drawn theoretically where the numbers of shelf species and deep-sea species are in the ratio 50 : 50. Judging from the reports of expeditions, the ratio must have somewhat variable proportions in different animal groups, and it would appear that even with a greater and more exact knowledge of the benthonic animal world, we would remain uncertain of these figures, because there is evidently no narrow boundary but a very broad faunistic connecting transition zone.

Bathymetrically the position of hydrographic isotherms, isohalines etc is nowhere absolutely stable. On the contrary, observations along the submarine ridges as well as arctic currents in the Northern Atlantic Ocean have indicated great waves for example in the lower marginal layers of the Atlantic Current. Through such waves the hydrographic boundary may be displaced considerably up or down for shorter or longer time in different places. Presumably along the Antarctic Continent similar oscillations also give rise to temporary displacements and "irregularities" in the course of the hydrographic curves.

Another factor which tends to obscure the boundary lines in the benthonic fauna is the greatly varying mobility of the animal groups or species. Fishes are generally rather agile and will accordingly move in accordance with the submarine waves. This has been established for a series of arctic Lycodinae, which always are met with along the submarine ridges between Scotland-Iceland and Iceland-Greenland on the negative side of the zero-isotherm but which, like most fishes characteristic of the icy cold bottom layers of the Norwegian Sea, never pass across it into Atlantic water of positive temperature. Though here from time to time the 0°-isotherm has changed its position in many places, the said Lycodinae are always present close by. – Most of the benthonic invertebrate animals are quite or almost quite stationary when they have passed their larval stages and settled on the sea bottom, and accordingly they cannot shift to

other localities in accordance with the waves. It is, therefore, their tolerance of the degree of eurythermy, euryhalinity etc., which determine the details of their distribution, whereas their degree of eurybathy broadly decides their vertical occurrence.

The dispersion and distribution of species throughout depends on the currents. "It is rational to deal first with the simpler conditions and gradually to enter upon the more complicated. This can be done by first discussing the Antarctic Ocean, where the latitude effect is easily explained, where the waters are in free communication with those of the major oceans, and where the system of prevailing currents is unusually clearcut." (Sverdrup, Johnson and Fleming, 1942, p. 605).

Ekman (1953, p. 211) gives a concise review of the currents in the surface layers from which we shall fix our attention on the following: "The whole of the temperate oceanic region in the southern hemisphere and the greatest part of the antarctic oceanic region is influenced by the *West Wind Drift*. No other ocean current can compare, either in its length or its width, with this circumpolar current. It washes all temperate oceanic islands in the Southern Ocean, the southern part of South America, the south coasts of Africa and Australia and branches off into currents flowing into a northerly direction near these continents. . . . . .

"The West Wind Drift does not reach quite down to the Antarctic Continent. Its coastal region and ice fringe are washed by the *East Wind Drift* which flows in an opposite direction and is also circumpolar."
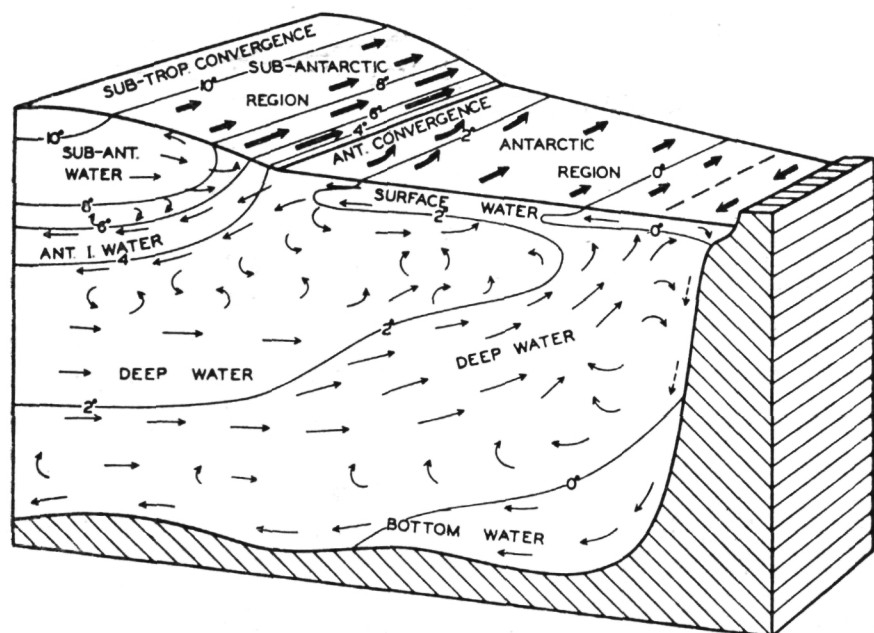

Fig. 2. Schematic representation of the currents and water masses of the Antarctic regions and of the distribution of temperature. (Sverdrup et al. 1942.)

Ekman also emphasizes that the *Antarctic Convergence* is situated within the region of the West Wind Drift.

It is of interest to compare this with the schematic representation of the currents and water masses of the antarctic regions (Fig. 2) after Sverdrup, Johnson and Fleming (1942, p. 620). It is evident here that the currents are the most important factors determining the living conditions and dispersion of the bottom animals both on the continental shelf and along the adjacent slopes towards the deepwater, i. e. both horizontal and vertical currents and convection movements have their effect. The remarkably small differences in temperature from the surface downwards into the deep-sea are doubtless of secondary importance in most species, and whereas obviously the zero-isotherm in arctic waters is an important limiting borderline, in antarctic waters it seems to be of subordinate significanse, if of any at all.

The method of spreading of benthonic animals from the high-antarctic neritic zone to low-antarctic localities or from one low-antarctic locality to another has been much discussed and is also touched upon in some reports of the "Norvegia" expeditions. Theoretically we may say that the currents (comp. fig. 2) do not present any obstacles but seem much more to favour a transport of vagal stages of bottom animals. This appears clearly from the following words of Sverdrup, Fleming and Johnson (1942, p. 620): "one cannot consider the Antarctic Circumpolar Water mass as a body of water which circulates around and around the Antarctic Continent without renewal. On the contrary one has to bear in mind that water from the antarctic region is carried towards the north and out of the region both near the surface and near the bottom, and that deep water from lower latitudes is drawn into the system in order to replace the lost portions."

Ekman (1953, pp. 239–240) has calculated the probability of echinoderm larvae traversing the oceanic gaps between the high-antarctic continental shelf and the low-antarctic, and between the anti-boreal neritic localities, basing his work on Th. Mortensen's studies and results concerning the development and duration of their pelagic period in the tropics. These interesting calculations in his opinion prove that "An effective drifting of a number of larvae every 1000th year means about 1000 such drifts during the time of excistence of the species." (How long does the time of existence last in different species or animal groups?) – Ekman thus admits the possibility of a larval transport by surface currents (West Wind Drift) which "may have played a part for a few species of echinoderms in the colonisation of oceanic islands of the Southern Ocean. For certain species of other animal groups, too, the same conclusion is valid."

It is hardly necessary to point out here that our knowledge of the ecology of antarctic benthonic animals is rather deficient to say the least of it. As to the larval stages, we may possibly compare them to a certain degree with arctic species of the same groups; at all events a few obser-

vations give hints of the same retardation of the larval development and the same pronounced tendency to care of the young in antarctic as in arctic waters.

Both in arctic and subarctic waters, several invertebrates produce resting stages of different kinds, and this is certainly the case in corresponding regions of the southern hemisphere also. Earland (1934, p. 20) emphasizes the zoogeographic importance of this in his paper on benthonic antarctic Foraminifera: "In the life history of those few species which have been worked out there are two forms, the megalosphere and microsphere, and the megalosphere form generally reproduces by the formation of mobile zoospores which conjugate and settle down as microspheric individuals. This is obviously a method of reproduction favourable to wider distribution than the asexual-reproduction of the microspheric individual. In this latter case the young organism is born in the proximity of the parent, forms a test, and is thereafter dependent solely upon own powers of movement. . . . But if, like a great many similar organisms, these zoospores have the power to pass into a resting-spore condition, they might well be transported for long distances, in a living state."

Extensive knowledge of ecology is clearly necessary. It seems natural to assume that the ecological demands of a species are very stable, and in reality both historical biogeography and paleobiology largely build on this view in their reconstructions.

We have of course to admit that studies of benthonic animals have hitherto played a lesser part in most antarctic expeditions. It is true to say that other problems have generally prevailed, and when time has been conceded to benthonic investigations, the work has necessarily had to be confined to faunistic collections. The Antarctic Region is so vast and so difficult of access, that the leaders of the expeditions do not generally like to devote the time necessary for such side-line investigations, the resukts of which cannot bring particular publicity. In these regions especially zoologists are in need of more or less stable biological laboratories or "floating biological stations" where they can themselves decide, when, where and how they shall work. The prominent results of the Discovery Investigations have sufficiently demonstrated this; ecological research mostly craves time, independency and gear.

Lack of such conditions are to a great extent the cause of the scantiness of our knowledge of ecology and must take its share also when we turn to the systematics of benthonic animals in the Antarctic Region. All species exhibit a more or less extensive faculty of variation, which in several cases is correlated by some means or other with ecological conditions. Some few specimens from a few widely scattered localities often present a pitfall to specialists. It is always necessary to study the individual variations, and it may be rather difficult to decide between an extreme variant and the representative of a wished for *nova species*. Such cases have also caused great

trouble to zoogeography. Here the richer collections of recent expeditions
have contributed much in creating a better foundation, but it is evident
that even today our knowledge still needs to be extended especially in the
field of antarctic ecology.

After his reflections concerning the inadequacy of currents and ecology
as factors in the distribution of benthonic animals in the Antarctic Ocean,
Ekman (1953, p. 240) writes: "What importance should be attributed to
this means of distribution when we have to decide what the marine zoogeo-
graphy of the Southern Ocean can tell us about former land connections
and non-abyssal under-water ridges?" A little further on he adds "also on
the phylogenetic course of evolution?"

Zoogeographers quite frequently have somewhat of a reputation as
"bridge-builders" among scientists. It is also an old saying that if all their
land-connections were true, there should be no water left in the oceans!
However, there is no doubt that from geological evidence certain connecting
ridges did exist in the past. In our time, when modern soundings have
taught us that the deep-sea bed is only plane in a few places, and is mostly
intersected by broader or narrower valleys between mountains and ridges,
nobody doubts that local risings and sinkings of the sea bottom have taken
place also in the Antarctic and that probably such epirogenetic movements
have played a part in the formation of the benthonic animal environment
of antarctic waters of today.

The words of Ekman show that he prefers the theories of ridges to
ecology, notwithstanding that many zoogeographers 1. construct their
ridges according to recent and often rather scattered evidence and 2. after-
wards again use their own hypothetical ridges as a proof that the habitat
of the species must be in conformity with the present records. Apparently,
some of them also fail to see that hydrographical conditions may be influ-
enced by innovations in the bottom relief.

Odhner (1944) pays great heed to the ridges, to the risings and sinkings
of parts of the sea bottom, and he is especially interested in the forces
which cause these movements. In his Constriction Hypothesis, Odhner
(1934) discusses these problems and again returns to them in the present
series. We may quote from his paper here (1944, p. 39): "The secular
movements in question were thought to be caused on one hand by the
changes of temperature in the earth's crust, and on the other hand by the
structure of the crust as a mosaic of undulations, positive and negative
vaults, or geanticlines and geosynclines. The earth's crust within these
vaults was assumed to yield to changes of temperatures from internal and
external sources in the same way as technical vaults or arch bridges, which,
as known, elevate their vertex in the warm season and depress it in the
cold one, according to their dilation by heating and their constriction by
cooling."

It is outside the scope of the present paper to discuss Odhner's Con-

striction Theory. But in connection with antarctic zoogeography one question obtrudes: when such changes of temperature are going on in the earth's crust (in this case, therefore, in the bottom layers of the Antarctic Ocean), would they not for some time at all events alter the ecological conditions to such a degree that most of the species which exist here under "normal circumstances" if at all, could barely exist in the locality during these revolutions? Or do we have to assume that nature during such upheavals suspends to a certain degree the ordinary ecological demands of species or individuals?

In his discussion of the geographical distribution of antarctic sea urchins, Mortensen (1910, p. 100) says that there must have existed "a former connection between South America and the Antarctic Continent; especially the occurrence of the viviparous genus *Abatus* in both these regions is conclusive evidence of such a connection", and in the same way he advocates a submarine ridge between Kerguelen and South America. Much weight evidently is given to the complete lack of free-swimming stages during development and to the absence of suckers on the ambulacral feet in the genus *Abatus*.

Here it is necessary to emphasize that yolk-rich eggs and the absence of free-swimming developmental stages are very characteristic of a great many antarctic as well as arctic bottom animals of the continental shelf. This has been stressed by Thorson (1934, 1936) also. This of course prevents their transport by currents and in the case of adult echinoids the absence of suckers precludes the possibility of their clinging to floating objects.

The *Abatus* problem is again reviewed by Ekman (1953, p. 241) from various points of view: "But it is particularly relevant to discuss this question [i. e. parallel or divergent phylogenetic development of species] in connection with the Zoogeography of the Southern Ocean. Of the eight species of the sea-urchin genus *Abatus* a few occur in two or more regions which are separated by abyssal depths, the rest occur only in one shelf region or in the various parts of the Antarctic Continent. . . . It has therefore been assumed that their occurrence in separated regions is a proof of fairly late land connections of under-water ridges between these regions. Here the possibility of parallel development should be taken into account. But another explanation is more probable. Several *Abatus* species are found at archibenthal depths. Their occurrence at these depths makes it not improbable that they also tolerate abyssal surroundings; the most southern abyssal regions are not so well investigated that this possibility can be rejected. Under these circumstances it would be precipitate to deny the possibility of a present-day communication between the different populations and to suppose that the distribution and ecology of these species proves the existence of a closer Quaternary or late Tertiary geographical connection between their present-day localities."

Dealing with the so-called "pairs of species" among Atlantic-Arctic

bryozoans, Nordgaard (1916, p. 95) had already made a suggestion which coincides with the last possibility mentioned by Ekman. Both authors are evidently most inclined to date one of the original species back to the Tertiary. It is of course very tempting to look for the ancestors of recent antarctic species in Tertiary stratifications, and we meet with the same tendency in Soot-Ryen's paper on antarctic pelecypods where he writes (1951, p. 38): "As far as I know, none of the recent species is recorded from the Tertiary beds, but the finds of Tertiary Pelecypods are hitherto very few." A little farther (l. c., p. 42) he also touches on the large numbers of the antarctic pelecypod fauna which are "able to live in great depths or closely or related to such species. . . . . These species, which generally are cold stenothermal and able to live in various depths, may always find conditions suitable for their existence and have a refugium in the deeper waters, when littoral conditions become too severe. . . . It is a striking fact that nearly all the more littoral species, here considered to be old inhabitants of the Antarctic region, are ovoviviparous and retain their young somewhere within the mantle cavity until they have developed a definite shell."

It is evident that an unmistakable relationship exists between the benthonic antarctic shelf fauna and that of the archibenthal region. This is doubtless due to a certain similarity in the ecological conditions, and this also gives us a hint as to why several deep-sea animals like *Umbellula lindahli* have been captured at depths near the S. Sandwich Is lesser than at any other locality, even if we include the arctic *encrinus*-group (see Broch 1958 and below on pp. 19–20).

Whereas in earlier days the *"Bathybius"*-theory was adhered to by a majority, it is generally accepted in our time that the cradle of animal life has been in the shallow waters of the sea where bottom animals are concerned. To a certain degree this has apparently paralysed or hypnotised the chain of reasoning in many investigators so effectively, that they always look for predecessors in the shallower waters. Nevertheless, many species among the shallow-water animals certainly are descendants of species which have lived, or even live today in the deeper regions of the oceans. This certainly holds good for a series of species of benthonic animals in the Antarctic Ocean, where no sudden break of temperature, salinity etc creates abrupt boundaries. It is accordingly not out of place to say that the antarctic fauna of the continental shelf has been derived without doubt from archibenthal as well as from shallow-water ancestors in neighbouring habitats.

Returning again to our example, viz. the genus *Abatus*, a simpler explanation than submarine ridges and the like seems more natural.

Students of genetics are well acquainted with the great number of common mutants which occur in their *Drosophila* cultures, wherever in the world they work – in Europe or America, Australia, Africa or Asia,

the same main stock of mutants always turns up in their laboratory cultures. Very probably most of the same mutants are found in the natural habitat of *Drosophila* also, but here they are most likely destroyed in the struggle for life, having some handicap or other as compared with the "normal", or wild type. However, advantageous mutants can probably also arise, and under favourable ecological conditions, by isolation or selection, furnish a basis for the development of a *nova species*.

It does not seem unlikely that the *Abatus* phenomenon has come into existence in this way, i. e. that some archibenthal *Abatus* species at one time or other has been (or is) briskly mutating and has also produced all over its habitat mutants which under ecologically favourable conditions on the shelf have developed into separate species. This may have occurred anywhere in the large domain of a "mother species", especially in periods of more intensive mutation, and the same mutants accordingly may have ascended into shallower waters in widely separated places, simultaneously or successively, and without having recourse to submarine ridges or pelagic stages in their development.

It may be a question, whether we are facing something of this kind today among the antarctic and antiboreal fishes. Nybelin (1947) has described a series of local subspecies of antarctic fishes some of which might well be recently isolated mutant groups.

In this connection we also ought to recall the marked tendency in deep-sea animals to extend their habitat into shallower waters in the Polar Seas. This is especially conspicuous in the Pan-antarctic region, and it seems probable that a great percentage of the shallower benthonic species of this region originate from archibenthal or even abyssal ancestors.

Basic Conditions of the Arctic Benthos.

Several actual questions concerning the benthonic animals, their conditions of life and their biogeography in Antarctic waters are thrown into sharper relief by comparison with the circumstances in the Arctic Ocean. It is accordingly convenient to recapitulate here some elementary features of the hydrographic and biological data in Arctic Seas which, however, are far more complex than those in the Antarctic.

We must above all keep in mind that the Arctic Region consists of three fairly effectively separated territories: 1. the central and deep Polar Sea, the deep-waters of which after having passed the Nansen ridge between Spitsbergen and Greenland continue in the deep basin of the Norwegian Sea southwards to the submarine ridges between Scotland-Iceland and Greenland. The deepest part of these ridges in the Faroe-channel is about 600 m below the surface. 2. Another isolated and rather small basin in Baffin Bay: this is fairly well isolated from the central Polar Sea by the

shallow sounds between the arctic islands from Greenland over Scoresby Land to Labrador, whereas a submarine ridge across the Davis Strait marks the border between the deep waters of Baffin Bay and the Atlantic Ocean. 3. The Ochotsk and Bering Seas also belong to the Arctic Region, and we may say that here conditions are most in harmony with the benthonic territories of the Antarctic Ocean, because here the continental shelf along a broad front gradually passes into the archibenthal and farther into the abyssal, and even into the hadal deeps of the northernmost Pacific Ocean.

The central Arctic Sea (Fig. 3) has a very extensive continental shalf, both between the European-Siberian coast and the adjacent islands down to some 200 m, and also in the sounds of the American Archipelago from Greenland westwards, where the depths only pass below 200 m in a few places. But the central deep basin is limited at the shelf by very steep slopes which descend from about 200 m to 2000–3000 m or more.

Basing his work on mathematical calculations of tidal observations from the "Maud" Expedition 1918–1925, Fjeldstad (1936, p. 55) wrote: "The soundings in the Beaufort Sea are few in number, but they indicate that the continental shelf does not extend far to the north. A possible explanation would be that north of the Beaufort Sea there might be a ridge with comparatively small depths. The almost syncronity of the tide along the coast of Alaska demands that this conjectured ridge or plateau extends unbrokenly from the Siberian Shelf to the Arctic Archipelago." - Recently, in his review of the American investigations into the hydrography of the upper layers in the Polar Sea, north of Alaska 1951–1952, Worthington (1953, p. 550) after discussing the distribution of the temperature writes as follows: "There are two possible explanations for this: (1) The deep water entering the basin from the Norwegian Sea has been warmer in recent years than it was in Nansen's time, and (2) there is a submarine ridge, running roughly from Ellesmere I to the New Siberian Islands, which separates the deepest water of the Beaufort Sea from the remainder of the basin."

The deductions of Fjeldstad and Worthington had already been corroborated in 1948 during a Russian expedition under the leadership of Professor Gakkel, who discovered and explored the Lomonosov Ridge. This submarine range has elevations rising to 2500–3000 m above the sea bottom and stretches from the New-Siberian Islands across the North Pole to Greenland and Ellesmere Island dividing the deep of the central Arctic Ocean into two large basins (comp. the chart, Fig. 3). "In some places its peaks rise to 954 m below the surface; its slopes are steep and saddles of a depth of 1500–1600 m and spurs are characteristic. Preliminary data indicate that the range was formed in Mesozoic or Tertiary times, and originally rose above the surface of the Arctic Ocean" (Webster, 1954).

On the other hand this long submarine mountain range is remarkably narrow with very steep slopes on both sides. On its Atlantic side a very

deep depression is situated between its foot, mostly about 4000 m deep, and the shelf north of Greenland and the Barentz, Kara and Laptev Seas. The greatest depth of this large depression exceeds 5200 m, and its deep-water communicates with that of the Norwegian Sea over the Nansen Ridge between Spitsbergen and Greenland. According to Russian survey-ings the ridge is traversed in the middle by a passage of some 3000 m depth.

On the Pacific side of the Lomonosov Ridge, the depth is not quite so great, although here also the foot of the range is about 4000 m in the middle. This somewhat smaller depression in the direction of the continental shelf bordering on the Canadian Archipelago, the Beaufort and the Chukotse Seas rises to a large plateau with a depth of some 2000–3000 m or a little more. A smaller depression in the southern part of the Beaufort Sea is about 4000 m deep.

The geomorphological features of the deep Polar Basin are furthermore complicated by an older folding system which cuts across more or less obliquely the main direction of the Lomonosov Range and which apparently is most obvious north of Greenland and the Canadian Archipelago. This older folding system, however, is apparently of subordinate importance in connection with the benthonic fauna of our time. The current system and the hydrography of the deep central Polar Basin on the other hand are in their broad features determined by the Lomonosov Ridge.

We may say that the Atlantic Current is the driving force in the entire arctic current system. At the northwestern point of Spitsbergen, the last main branch enters the Polar Basin proper, and from here it continues eastwards along the steep slope of the shelf. Because of cooling, the comparatively more saline Atlantic water gradually sinks deeper, and nearer the New Siberian Islands it is accordingly forced to turn to the left along the Lomonosov Ridge and to run in the direction of the northernmost part of Greenland. En route along the submarine mountain range, the Atlantic water is mixed with polar water and continues southwards over the Nansen Ridge along the eastern coast of Greenland as the Arctic East Greenland Current (Fig. 4).

A glance at fig. 4 at once shows us that only comparatively small quantities from the Eastern current system pass over the ridge and into the western basin. On the other hand, the current along the ridge towards Greenland brings about a clockwise circulation in the sea, north of the Canadian Archipelago and the Beaufort Sea. This means that there is only very little intercommunication between the Beaufort (western) basin and the eastern basin of the Polar Sea and especially also between their benthonic animal communities in the deeper parts.

In his pioneering zoogeographic studies of our norhern seas, Appellöf (1905, 1906, 1912) emphasizes that the Polar Sea houses two geographically distinct groups of benthonic animals, viz. an "eastern arctic" (by Ekman 1953, p. 180 renamed as "*Atlantic-arctic*") living in the Arctic Sea between

Fig. 4. Atlantic water circulation in the North Polar Basin (from Worthington 1953).

Labrador-Baffin Bay and the Laptev Sea, but never passing beyond the
New Siberian Islands towards east, and a "western arctic" group (Ekman
1. *c.* p. 182 more vagely mentions these species as "common to the North-
west Pacific arctic subregion and the Polar Sea"). These western arctic
species occur from Labrador-Baffin Bay westwards as far as Wrangell
Island, and also in the northernmost arctic parts of the Pacific Ocean. As
far as hitherto observed, these species seem to be of rather scarce occurrence
in the Beaufort Sea, probably because most of them have their abode on
the continental shelf which is of remarkably little extent here. Evidently
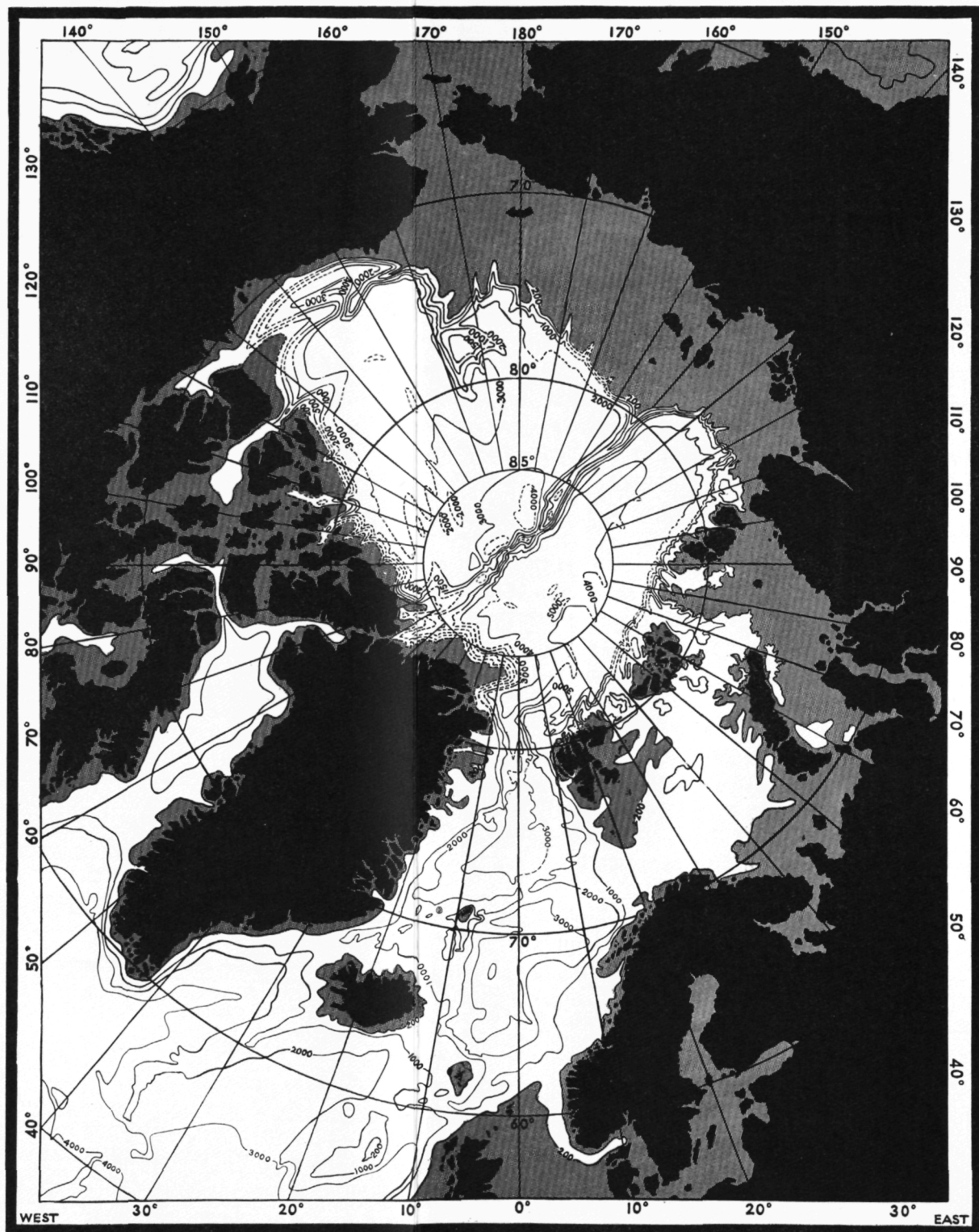
Fig. 3. The Northern Ocean (From Broch 1958, with some small corrections)

the western arctic species have entered into the central Polar Sea through
the shallow Bering Strait.

Appellöf (1912), von Hofsten (1915, 1916) and Broch (1924, 1937)
laid great stress on this phenomenon and tried to find the reason of these
faunistic differences between the eastern and western sides of the central
Polar Sea. The reason has now been revealed by the Russian discovery of
the Lomonosov Ridge and its influence on the current system of the central
Polar Basin (Webster, 1954).

Obviously the Atlantic Current has played and today also plays a great
part in the history of the population of the benthonic region of both the
continental shelf and the deep sea in the central Polar Basin. It is evident
that free-swimming or drifting larval and young stages of Atlantic species
are carried into the Norwegian Sea by the Atlantic Current. Some specimens
are able to bear foundering in the icy cold bottom layers beneath the current
(i. e. below some 600 m), and they may even grow up here, apparently as
normal individuals. However, as far as we can see, their propagation is
checked in some way or other. The occurrence and records of such stray
specimens are more or less scattered. But taken together the records give
us a fair illustration of the course of the Atlantic Current, from the Faroe
Channel through the Norwegian Sea and at all events to the northern coast
of Spitsbergen (see Broch 1912, 1918); the numbers of records of course
diminish with the growing distance from the Faroe Channel.

The depth of the Faroe Channel, through which the Atlantic Current
passes into the Norwegian Sea, is about 600 m, and the lower limit of the
current continues at this depth practically all through the Norwegian Sea,
and the border between the current and the arctic deep-water is distinctly
marked by the great jump in temperature within a very few meters. Whereas
the Atlantic water at the southern slope of the Wyville Thomson Ridge at
about 700 m depth is 4°–7° C, the temperature at the same depth on the
northern slope is zero or below (Fig. 5).

On the arctic continental shelf, von Hofsten (1915) and Lemche (1941)
draw the limit between the high-arctic and the lowarctic subregions at the
0°-isotherm, notwithstanding that some earlier authors had been inclined
to draw the limit a few degrees higher, because some high-arctic species
may occur in beach pools and endure temperatures sometimes rising to
some 4° C or a little more. – It was pointed out first by the Danish Ingolf
Expedition in 1896 and again by the "Michael Sars" investigations in 1902,
that the 0°-isotherm constitutes the absolute borderline where arctic and
Atlantic waters meet along the ridges from Scotland to Iceland and Green-
land for the fishes living in the deep waters.

This is not quite so conspicuous at first glance in the less vagal benthos.
However, we must here also pay heed to the incessant wave-motions of the
boundaries, which give rise to greater or lesser temporary displacements,
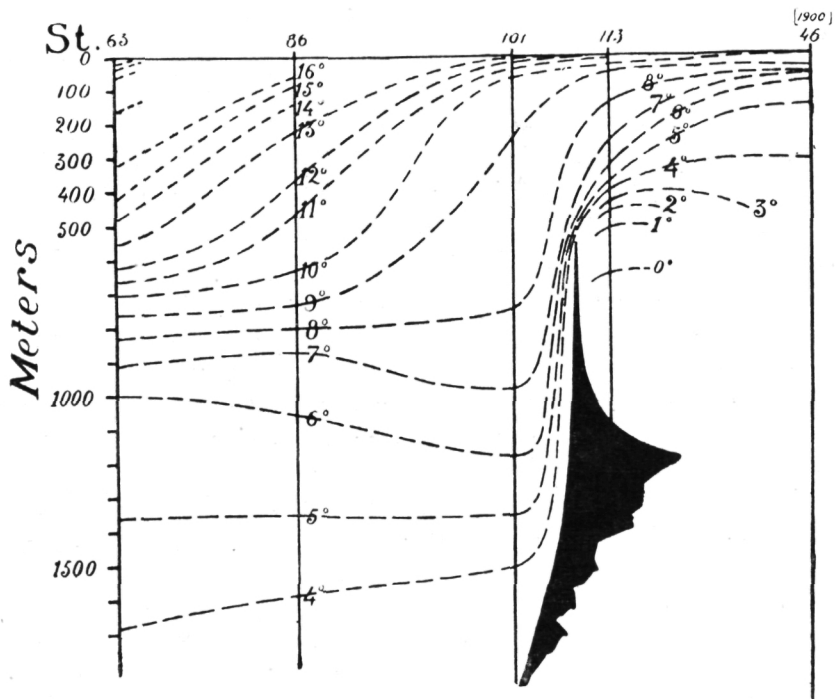both horizontally and vertically, in the position of the 0°-isotherm. Neverthe-

Fig 5. Distribution of Temperature from the Sargasso Sea (Station 63) to Lofoten
(Norwegian Sea).
Dept in metres; temperature Centigrade. (From Murray & Hjort 1912).

less, this isotherm is also indicated to be an important border-line in the
more or less sessil benthonic world.

The great jump in temperature at the lower limit of the Atlantic Cur-
rent in the Norwegian Sea is obviously of vital importance for the arctic
animal world, and immigrants from the warmer Atlantic Ocean, which can
stand the plunge into the arctic deep-water, certainly must either consist
of mutants able to survive remarkable temperature shocks, or they must
belong to specially eurythermal species. We must also keep in mind the
possibility that such a plunge occasionally may have the same effect as
temperature shocks in the laboratory which cause alterations in chromo-
some arrangement or other qualities.

Howsoever this may be, the benthonic deep-sea fauna of the central
Polar Basin shows undeniable affinities with that of the Atlantic Ocean.
It was certainly this which had arrested the attention of Appellöf (1912,
p. 547) when he wrote the following words: "A form in the Norwegian
Sea deep basin, *Colossendeis angusta*, is said to occur also in the Northern
Atlantic, but if we compare Atlantic and Norwegian Sea specimens we
immediately recognise considerable differences in their structure, the
latter being more robust and furnished with shorter legs and claws. Any

one seeing the two forms side by side would be able to tell the respective areas from which they come, though it may be difficult to find sufficient dissimilarities to designate them separate species." These words may be taken as an indication that Appellöf interpreted the two forms as ecologically (and consequently also geographically) determined groups of variants or as a "pair of species" in *statu nascendi*. Other examples of the same phenomenon which he pointed out in passing are:

Atlantic	Arctic
Pecten fragilis	– *P. frigidus* (now *Chlamys f.*)
Bathybiaster robustus	– *B. vexillifer*
Umbellula lindahli	– *U. encrinus*

It is not necessary to look for one of the species of these pairs back in the Tertiary, and it is not necessary for so and so many thousands or millions of years to have operated before the species could have stabilized their morphological features, if we may judge from results in the experimental laboratories of today.

Appellöf's last example, viz. *Umbellula lindahli - encrinus*, was recently referred to in a Discovery Report (Broch, 1958). It was suggested here that very likely we ought to follow Jungersen (1916, 1919) who considered the all but cosmopolitan *lindahli*-group as the mother-form, and the *encrinus*-group as a daughter-form which has arisen both in the deep of Baffin Bay and in the deep of the Norwegian Sea and the central Polar Basin. Although in the central Polar Basin, hitherto the *encrinus*-group had been regarded an eastern arctic "species", in this case an immigration from the Atlantic Ocean must certainly have taken place and also continues today, at all events into Baffin Bay. It is remarkable that *encrinus* has hitherto not been reported from the northernmost parts of the Pacific Ocean. The Bering Strait has evidently been too shallow also during the entire Quarternary to allow an immigration, even though small specimens have been found as shallow as 180 m in the Kara Sea (Broch, 1956).

Although it seems rather unlikely, we cannot absolutely deny the possibility that during a long period stray specimens of *U. encrinus* may have been transferred by the arctic East Greenland Current farther along the western coast of Greenland into Baffin Bay, yet it seems much more probable that now and again larvae of Atlantic specimens today pass the threshold between the Davis Strait and Baffin Bay. Typical slenderly built *lindahli* specimens have been recorded in the deep of Baffin Bay by Jungersen (1904, 1916, 1919) side by side with coarsely built specimens of the high-arctic "typical" *encrinus*. "A study of Jungersen's papers indicates that the morphological differences between *U. lindahli* and *U. encrinus* are more fluid in the Davis Strait, where no prominent submarine ridges accentuate the biophysical border lines as do the submarine ridges from Scotland past the Faroes and Iceland to East Greenland" (Broch, 1958, p. 276).

This close resemblance between *lindahli* and *encrinus* was clarified,

when the Norwegian assistant zoologist, Torger Øritsland, brought home
with him from antarctic waters three *Umbellula* specimens, which had been
caught on 30 November 1956 in a fish trawl 6 miles north of Coronation
Island (South Orkney Is) in 314–282 m depth, i. e. in the high-antarctic
subregion. Their total heights are 80, 90½, and 247 cm respectively. The
last specimen is the largest *Umbellula* "*lindahli*" hitherto reported, but is
only few centimeters higher than the largest specimen of *U. encrinus*, which
Jungersen (1904) described from the Norwegian Sea, a little south of
Jan Mayen from 697 m (÷ 0.4° C). Both specimens coincide in all dimen-
sions and proportions, the only difference being the lower number of auto-
zooids in the antarctic specimen (21 against 41 in Jungersen's arctic spec-
imen). The comparison of all these specimens proves "that *U. lindahli* is a
synonym of *Umbellula encrinus* (L. 1758), and that the arctic variants do
not distinguish themselves as an ecologically determined morphological
form" (Broch, 1961). With this new record we have accordingly to drop
Umbellula encrinus – lindahli from the "pairs of species". On the other hand
this accentuates another riddle which has been touched on earlier, viz. the
problem of eastern and western arctic species.

The Russians have found during their post-war explorations of the
arctic animal world that the fauna of the deeper parts of the Polar Sea
between the European-Siberian slope and the Lomonosov Ridge is much
richer and more varied, both in the pelagic and the benthonic habitats, than
hitherto assumed, and they announce that they have found a series of new
types "upsetting the theories of the scarcity of plankton in the Arctic Ocean
and of the relative uniformity of benthic fauna throughout the world"
(Webster, 1954, p. 75). But the picture evidently changes on the other side
of the Lomonosov Ridge: "the fauna is poor. In this region, the richest
collections were made at a depth of 100 m., where a current from the
Pacific has been identified" (Webster, 1. c., p. 75).

The hydrographical data given by Worthington (1953) and the Russians
in their preliminary publications (comp. figs. 4 and 6) show that the water-
exchange, especially in the deeper parts of the Beaufort Sea, cannot be
particularly extensive, the water-masses mostly seem to be circulating in
the deeper parts of the basin between the Lomonosov Ridge and Greenland –
North America, i. e. in the Beaufort Sea, and the influx of water through
the Bering Strait from the Pacific seems to be of quite subordinate dimen-
sions. This of course must influence the conditions of life, possibly bringing
about a depreciation of available oxygen for the benthonic animals as
compared with the deep-region on the other side of the Lomonosov Ridge.
With regard to the renewal and circulation of the water masses, the influence
of the Bering Strait cannot compare with that of the Scotland-Faroe
Channel.

A comparative study of the benthonic animal communities on both
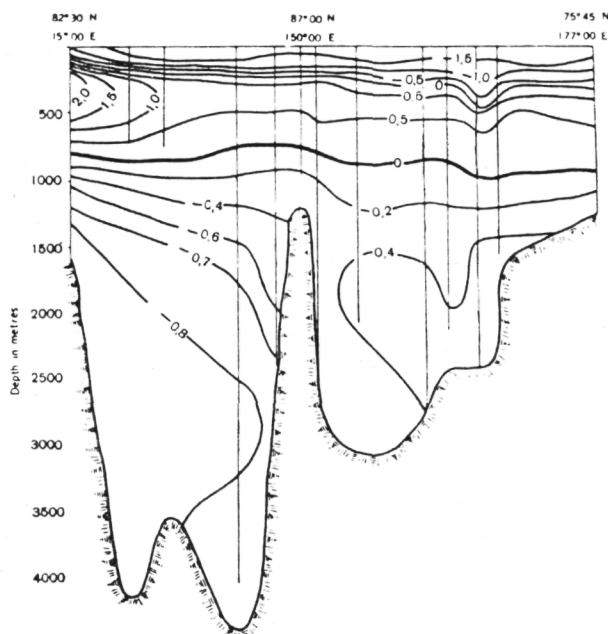sides of the Lomonosov Ridge and their living-conditions and ecology

Fig. 6.   Water temperatures (°C) on a section across the Lomonosov Ridge, from *Izvest. Akad. Nauk S.S.S.R., Ser. Geogr.* No. 5, 1954, p. 8.

should certainly furnish a basis for better understanding of many arctic and antarctic zoogeographical questions. Judging by the meagre available information, the conditions of the central Arctic deep-sea with its complex structure differ in so many ways from the comparatively schematic and uniform ecological conditions of the Antarctic that a detailed comparison in several cases might serve to disentangle the question of the deciding zoogeographical factors in respect of many species (or "cases").

It has already been briefly referred to that two more isolated peripheral territories of the Arctic Sea, viz. Baffin Bay and Davis Strait, and the Bering Sea are the only places where bottom relief and transition from the Arctic continental shelf to the more temperate Atlantic and Pacific deep-sea regions are comparable with the Antarctic continental slope. From the transverse ridge between Baffin Bay and the Davis Strait, the sea bottom slopes rather evenly down into the Atlantic deep-sea, and here the zoogeographical limits are fairly uncertain in the benthonic world, probably because both temperature and other features of ecological importance change very gradually with depth. We can for example allude to the sea-pen, *Umbellula thomsonii*, which seems "to avoid territories where arctic or antarctic waters influence the bottom conditions, although low temperatures may not necessarily be the main factor" (Broch, 1958, p. 273).

The continental shelf of the Okhotsk as well as the Bering Sea is deci-

dedly arctic, and the benthonic fauna of these territories is also arctic, although with a strong intermixture of Pacific species in the deeper parts. Today evidently an immigration of eurythermal Pacific-arctic neritic animals also goes on through the shallow Bering Strait, especially along the eastern side into northern Alaskan waters and the Beaufort Sea.

Through the years Russian investigators have intensively explored the sea of "The Far East", both the neritic and the deep-sea regions, and during the nineteen-fifties they have also extended their work to the hadal region (i. e. below some 6000 m). In 1953 under the leadership of the zoologist, Dr. L. A. Zenkewitch, their research ship "Vitiaz" thoroughly studied the 10382 m deep Kuril-Kamtchatka Trench. Both from here and from the other trenches investigated (Aleutian, Japan, Idzu-Bonin and New Britain Trenches), they brought home the sea slug, *Elpidia glacialis*, from depths greater than 6100 m (Zenkewitch, Birstein and Belaev, 1955), and the same species was caught by the Danish Galathea Expedition in the Kermadec, the New Britain and the Sunda Trenches at depths between 6620 and 8940 m (Wolff, 1960). These are most interesting records.

Ekman (1953, p. 298) writes: "But even more characteristic for the arctic deep-sea fauna [than four purely arctic abyssal sea slugs mentioned before] is *Elpidia glacialis* (about 20 localities), although it occasionally ascends in high-arctic regions to the lower shelf; most finds, however, come from abyssal depth down to 2900 m."

Its occurrence in the central Arctic Polar Sea today raises two questions: 1. Is *Elpidia glacialis* an eastern arctic species in its distribution, as our present data might seem to indicate, and 2. How far down does its habitat stretch in the central Polar Basin?

Elpidia has been mentioned here as an example of questions which have arisen since modern techniques have cleared the way for effective investigations in the abyssal and hadal benthonic world, and furnishes a case where a recent effective barrier between the central arctic abyss and the North Pacific hadal deep of the Kuril-Kamtchatka Trench affords a wide field for studies concerning epirogenetic movements and earlier deep-sea connections.

A general review of the long series of deep-sea trenches examined during the cruises of the Danish "Galathea" and the Russian "Vitiaz" along the Pacific coasts of Asia and in the Indo-Pacific area indicates that these trenches were possibly in communication *inter se* in times past and, therefore, cannot be considered as "effectively isolated". This may be one of the causes why their faunas are remarkably alike and uniform. In certain cases when one or other of the "common" species seems to be lacking in one trench, as for example *Elpidia glacialis* in the Philippine Trench (Wolff, 1960), this may be due to chance. The lack of a species in the catch may be due to several different factors (comp. Broch, 1960): e. g. the gear has not worked on the special bed preferred by the animal and thus missed it. The

investigations of the hadal region are at present insufficient to give us more than a preliminary outline of the benthonic fauna through positive records.

Whereas the central basin of the Arctic Sea is effectively separated from the trenches and does not pass beyond the limits of the hadal region, we have one trench within the Antarctic Sea which is well isolated from all other trenches, viz. the South Sandwich Trench with a depth of about 8300 m. This trench is all the more interesting, because it is situated witin the Antarctic Convergence and has therefore continuous connection with the upper high-antarctic water layers through the antarctic bottom water. However, hitherto no antarctic expedition has been equipped with the necessary gear, or had time to carry out an investigation of the benthonic world of this trench. A comparison of the South Sandwich Trench with the Indo-Pacific trenches would be of the greatest interest.

Some Faunistic Remarks on the Antarctic Benthonic Fauna.

In Antarctic Seas the benthonic animal community of the continental shelf is generally characterized as being remarkably rich in comparison with the Arctic. In several animal groups this seems to be corroborated by the Discovery Reports. However, we have to make a reservation with regard to the surface layers, viz. the tidal zone of the Antarctic Continent, where according to Dell (1952, p. 130) "No intertidal life can establish itself in the short period during which the Antarctic coast is not ice ensheathed. For a large part of the year the coastline is surrounded by a fringe of thick ice that keeps the immediate shoreline clean down to a depth of several fathoms. Below the limit which may extend as far down as 25 fms. a wealth of marine life exists, i. e. there is an abundant shelf-fauna below the reach of scouring." Obviously this applies to all the high-antarctic coasts. In low-antarctic islands there are probably, at all events in some straggling places, sheltered localities where species can endure the winter season in the tidal zone without being scoured. We cannot exclude the possibility that some antarctic species may endure being frozen-in, like arctic and boreal specimens of *Balanus balanoides* (comp. Aurivillius, 1895, and Feyling-Hanssen, 1953), the life of which is apparently completely suspended for a period, when the individuals are enclosed within the ice, at temperatures well below zero. However, it has not been possible to find any particulars concerning parallel cases in the accessible literature for antarctic or antiboreal localities.

It has commonly been maintained that the antarctic benthonic world is astonishingly much richer in species than that of the Arctic Seas. It is in reality impossible today to pass any authoritative judgement on this question. Even if we disregard from the Russian faunistic discoveries in the North Polar Seas, in the neritic region some difficulties immediately arise: obvi-

ously the antarctic neritic community is interwoven to a higher degree with the deep-sea species, some of which in high-antarctic waters have been caught at shallower depths than anywhere else. As an illustration we may again refer to the sea-pen, *Umbellula encrinus*, which has been mentioned above (p. 12).

The intermixture of cosmopolitan species evidently increases with depth, but at the same time the percentages seem to differ in different animal groups.

It is not surprising that our knowledge of benthonic Protozoa of the Antarctic Seas is rather meagre, and mostly confined to *Foraminifera*. These can be sorted out from preserved bottom samples, whereas the complicated work connected with preservation and sorting out of naked protozoans needs quiet laboratories and time, facilities which are rather scarce during most expeditions.

During the examination of hydroids from the "Norvegia" Expeditions, I was struck by the cleanness both of the colonies and of the polyp-stems, which in boreal and arctic waters often are beset with foraminifers. This fact is in agreement with the remark of Earland (1934) that the antarctic Foraminifera consist mainly of arenaceous species. Several species from the Discovery collections are cosmopolitan cold-water forms living in all oceans. On the other hand the collections also contain (1. c., p. 22) "a few species which appear to have a complete circumpolar distribution; they have been recorded from widely separated areas, but nevertheless are unknown outside the Antarctic."

The antarctic fauna of *Sponges* is according to Burton (1932) very abundant, and the specimens grow to a large size. Like the arctic the antarctic sponges also are almost exclusively siliceous, not keratose or pseudo-keratose like many of the warm water sponges. Burton (1. c., p. 378) combats the old contention of geologists that the growth of sponges is most prolific in warm seas. Quite on the contrary, by reason of "the abundance of sponges in the Antarctic, as shown by the present collections and by the verbal accounts of collectors, there is every reason to believe that sponges are at least as abundant in the Antarctic as in, say, the West Indies, Australian or the Indian Ocean. And the probability is that they are considerably more abundant."

According to Burton the sponge-fauna of the high-antarctic continental shelf including Graham Land and the South Shetlands consists dominantly of endemic antarctic forms, whereas low-antarctic localities like South Georgia have several species in common with the anti-boreal Falkland Islands and South America. Burton is of the opinion that this is due to the West Wind Drift, and he attributes a major rôle to the currents in his discussions of the distribution of sponges. This is the more interesting when we consider that generally it is maintained that marine sponges have no pelagic, or better, vagal stages which might be of importance for their

dispersion. This enigmatic group of animals still presents ecological problems which are of importance zoogeographically.

The obviously prolific development of the antarctic sponge fauna seems to be greatly at variance with the strictly antarctic *Hydroid* fauna which, as far as we are able to see today, cannot be characterized as especially rich. "The number of high-arctic species is also not very great as compared with more temperate seas. In so far the two coastal regions seem much alike. It is, on the other hand, in arctic waters obvious, and especially then nearer the borders against subarctic, or boreal territories, that the species mostly show an extraordinary abundance of individuals (and colonies) where they are present. A similar appearance does not seem to be common in the Antarctic, if we may judge from the data from the expeditions so far" (Broch, 1948, p. 4).

Judging from the scattered information from different expeditions, the antarctic regions seem to house only comparatively very few cosmopolitan hydroids; the bulk evidently consists of endemic species (see Broch, 1948). On the other hand antiboreal localities like the Burdwood Bank, south of the Falklands Islands, house a rich and varied population of hydroids, but as far as we have hitherto found the intermixture with antarctic species is very moderate.

Whereas *Madreporaria*, both in antarctic and arctic waters, are represented by only very few species, generally caught in scattered specimens, *Octocorals* seem to be comparatively numerous, and several of the gorgonarians evidently flourish like thick brushwood in particularly suitable antarctic localities. This is after all mainly contingent upon the fact that, on the one hand there are no clearly accentuated hydrographical borders between neritic, archibenthal and abyssal regions in antarctic waters, and that on the other hand the steep slopes of the Antarctic Continent as well as those of the low-antarctic and antiboreal islands are rocky to a very great extent. Both in antarctic and in antiboreal regions, colonies of Primnoidae may be caught in incredible numbers, e. g. the "lamp-brushes" of the whalers (*Thouarella* spp.) on the Burdwood Bank.

It is interesting to note the difference in the central Arctic Basin where, as far as known hitherto, gorgonarians are very scarce, whereas some few species of alcyonarians have been collected everywhere in great numbers, both in the neritic and in the deep-region. These species, however, are not panarctic in character, but have a very wide distribution in other oceans also.

A comparison with the *Echinoderms* is natural. These animals must be regarded as sessil benthos, because their locomotive faculty is quite minimal. On the other hand they are generally not rooted on the bottom or fixed to rocks like most of the coelenterates. They are, therefore, richly represented in the collections of most expeditions, and Ekman (1953) has chosen them as one of the main and best accessible pillars in his picture of the antarctic circumstances and for a comparison with the arctic bottom world.

Ekman gives the interesting information that according to the data available in 1953, the Antarctic houses 256 echinoderm species as against only 52 in the Polar Arctic Sea, and of these numbers the endemic antarctic and arctic species constitute 73 % and 29 % respectively, and he furthermore emphasizes that the arctic neritic zone "does not possess a single seaurchin".

However, when considering these figures, we have to bear in mind that those from the northern waters apply only to the central Polar Sea. Ekman (l. c., p. 227) especially emphasizes that in this connection he has left out the Okhotsk and the Bering Seas, i. e. just those parts of the Arctic, in which the ecological conditions of bottom relief and hydrography are most akin to the Antarctic. Nevertheless his figures are all very interesting.

The imposing numbers of southern species are apt to give an impression that the echinoderm fauna must be especially well worked out. However, the opinions of the specialists evidently diverge in this respect. Mortensen (1909, 1910), Koehler (1912), and Ekman (1925) have given reviews and zoogeographical analyses of the *status quo* of the knowledge in those years, and in his later paper on the Discovery collections, Mortensen (1936) refrains from a new zoogeographical analysis and terminates with the following remark (l. c., p. 203): "Exclusive researches in the vast, almost unknown area of the Antarctic to the south of the Pacific Ocean would make a renewed discussion of the zoogeographic problems of the Antarctic region profitable – but such researches are still only a desideratum, as are also more extensive investigations of the bottom fauna of the Antarctic deepsea." His view is shared by Fisher (1940, p. 72): "The new species in the Discovery collection, some from regions already partly explored, indicate that we are yet a long way from having a complete picture of the Antarctic fauna." – – A couple of years after the publication of Ekman's "Zoogeography", Madsen (1955, p. 3) writes: "The Antarctic fauna of echinoderms is, however, now so well known, especially through the papers of *Koehler* and the Discovery Reports that in the following enumeration of the species I have mainly confined myself to refer to those papers."

The excessively rich development of echinoderms in antarctic and antiboreal waters as compared with the central Arctic Polar Sea certainly must be due to the uninterrupted intercommunication between the neritic and deep-sea regions through the archibenthal region, literally, all round the Antarctic Continent and its scattered and isolated islands. No hindrances like the Bering Strait or the North-Atlantic Ridges bar the open communication in this or that direction. And in all probability such circumstances have been rather stable in the Southern Ocean for such long periods, that mutations and selective forces have been enabled to mould a series of new species betwixt the old intruders or the remains from yet older populations.

Whereas the echinoderms have occupied a large place in analyses of

the antarctic benthonic animal community, the *Mollusca* have attracted less attention. The great paper of Powell (1951) shows us that the antarctic and antiboreal waters house a large series of Gastropoda and Lamellibranchia. Unfortunately, however, Powell pays no heed to natural biogeographical regions, nor to the importance of the Antarctic and Subtropical Convergences, and it is accordingly hardly possible to trace the endemic antarctic species in his tables. On the other hand, he discusses the importance of a connexion between the southern and northern regions along the western American coastline which, continued by the Scotia Arc, "shows that it is reasonable to suppose that the bulk of the southern high-latitude molluscan fauna could have been derived from the Americas, particularly the western coastlines" (l. c., p. 72).

Simultaneously with Powell's treatise, a paper on antarctic pelecypods was published by Soot-Ryen (1951). Based on the collections of the "Norvegia" expeditions and all available literature, Soot-Ryen has summed up the lamellibranchiate species observed south of the Antarctic Convergence up to that time. The result was 92 species of pelecypods, i. e. all but the same number as we know from Arctic Seas (the northernmost Pacific-arctic territories not included), – 66 (about 72 %) of the antarctic species being endemic. The lamellibranchiate populations of antarctic and arctic waters seem to be rather consistent, but their taxonomic composition is quite different. On the authority of Thiele (1913), Ekman (1953, p. 225) gives 79 antarctic neritic species of lamellibranchs, 79 % of which have been signified as endemic.

One of the most striking features of the antarctic benthonic animal world is the obvious scarcity of Decapod *Crustacea*. We must of course be very cautious as to negative features on the whole. But everybody who has worked in Antarctic Waters has been struck by the peculiar absence of crabs, lobsters, shrimps and prawns etc. in shallow waters. It was, therefore, a great surprise to find in «Sea Frontiers» for Nov. 1960 (Vol. 6, No. 4), a photograph of animals taken with a trawl in the Weddell Sea at 164 fathoms by the U. S. S. "Staten Island", where among other animals were two small shrimps, the largest one hardly 5 cm long. It is thus certain that at all events shrimps occur a little below the limit of the antarctic neritic zone. However, it does not seem likely that they are numerous enough to build up an industry on.

The scarceness of decapod crustaceans seems to a certain degree to be eked out by a rather excessive development of amphipods and isopods. Ekman (1953, p. 224) writes that "There are approximately 310 species of amphipods, of which 75 % are endemic." It is not possible at the moment to compare these figures with corresponding ones from arctic waters, but we know that here the benthonic fauna is also very abundant in species of amphipods and isopods. There is, however, another matter in antarctic seas, which has attracted some attention, viz. the abundance of large-sized

species, especially of isopods, both in shallow-water and in the deeper parts of the neritic zone. It suffices here to point to the broad and flat, up to about 3 cm long, *Serolis* species which are very characteristic of southern waters, and the up to some 12 cm long giant *Glyptonotus antarcticus*, an endemic antarctic species which has near, but comparatively rather small, relatives in northern waters. – It is at present not possible to establish the reason why amphipods and isopods have developed so copiously in antarctic and antiboreal regions. But involuntarily the question comes to mind, whether the scarcity of decapod crustaceans may be connected in some way with this phenomenon.

The singular isoped genus *Serolis* constitutes a rather isolated family of its own, Serolidæ, which seems to have originated in antarctic waters. Obviously the genus is eurybathic, it has been found at depths from 15 down to 3500 m. It seems accordingly most natural to assume with Ekman (1953, p. 234) that "the migration to the most northerly regions took place through the abyssal regions." Sheppard seems most given to consider the neritic species as more tied to localities than to ecological conditions, and in her zoogeographical remarks concerning the *Serolis* species of the shelf she finds it "significant that the existing species are found off the coast of South-east Australia in a region which was the last to lose its connexion with the southern continent" (1933, p. 264).

According to the papers of Barnard (1932), Sheppard (1933), and Stephensen (1947), the faunistic differences between antarctic and anti-boreal regions have become ever more accentuated in the literature on amphipods and isopods, and the groups have given valuable evidences of faunistic differences between a high-antarctic and a low-antarctic subregion, the existence of which must evidently be sought for in ecological peculiarities. The Antarctic Convergence is of course the reason why the limit between the pan-antarctic and the antiboreal regions is more obvious.

It would lead us too far to discuss here the antarctic benthonic fauna in all respects, our knowledge of them is in addition in most cases too scrappy. However, on several occasions the papers dealing with the antarctic and antiboreal bottom animals touch upon the question of *bipolarity*.

Ekman (1953) has discussed this phenomenon at length and by his exact formulations has contributed to the disentanglement of the confusion which characterized many discussions on the subject. – Among the benthos the *Gephyrea* constitute the classic examples, and in his paper Stephen (1941) lists about half of the 23 antarctic species as bipolar in the wider sense of the word. According to his data, most of these species are confined to the South American quadrant of the antarctic territories, and his deductions are most interesting in comparison with Powell (1951), who seems most inclined to derive the antarctic mollusc fauna on the whole from the Pacific *via* the Scotia Arc. In the same way Ekman (1953) also attaches

great importance to the thoroughfare in his discussions of longitudinal distribution and bipolarity. But on the other hand his taxonomic conceptions as to the gephyreans seem to diverge a little from those of Stephen.

We shall not here go more fully into the bipolarity problem which holds an important place in Ekman's marine Zoogeography. –

In the plankton world, the disentanglement of ecological questions may seem more simple than in the benthonic communities. The circumstances of the plankton organisms are in so far simpler that these are dependent on hydrographic conditions alone. Moreover, several of the planktonic animals so obviously play a great part as food for animals of economic value, like whales and fishes, that they catch the main interest of practical leaders as well as biologists during expeditions.

The role of benthonic animals in the mechanism of oceanic biology is far less obvious, affording students and practical zoologists a cursory view, which is nevertheless equally important. At the same time a study of the benthos is more complex: here we have also to pay heed to details of the nature of the sea bottom, the different facies of which are of vital importance in the biology and ecology of benthonic species. Moreover the technique of collecting, when wanted, needs more gear and time than plankton collecting. Altogether, it is not to be wondered that especially in the polar seas the basis of benthonic marine zoogeography is rather deficient, and that our informations as to specific ecology of antarctic and arctic animals suffers from want of knowledge. "But such researches are still only a desideratum, as are also more extensive investigations of the bottom fauna of the Antarctic deep-sea" – these words of Dr. Th. Mortensen written in 1936 also hold good today.

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