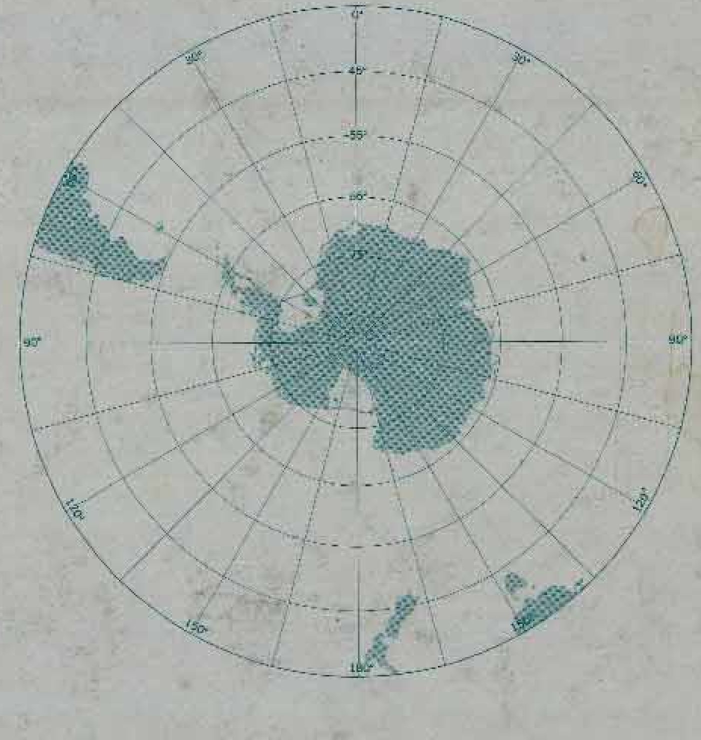
Antarctic Map Folio Series

FOLIO 11

Distribution of Selected Groups of Marine Invertebrates in Waters South of 35°S Latitude

A. W. H. Bé; H. Boschma and T. P. Lowe;
J. S. Bullivant; E. W. Dawson;
J. H. Dearborn and J. A. Rommel; R. K. Dell;
S. J. Edmonds; H. B. Fell and S. Dawsey;
H. B. Fell, T. Holzinger, and M. Sherraden;
M. W. Foster; S. R. Geiger and C. Brahm;
J. W. Hedgpeth; N. S. Hillman; D. E. Hurley;
V. M. Koltun; P. Kott; D. L. Pawson;
A. Ross and W. A. Newman; D. F. Squires



AMERICAN
GEOGRAPHICAL SOCIETY

1969

Antarctic Map Folio Series

VIVIAN C. BUSHNELL, Editor
JOEL W. HEDGPETH, Coeditor of Folio 11

The objective of the Antarctic Map Folio Series is to summarize in a succinct manner the present knowledge of the Antarctic; the Series will consist of some twenty folios, each devoted to one subject or scientific discipline. The areal extent of the coverage will vary from one folio to another. For example, folios dealing with atmospheric and oceanographic parameters will present data north of what is usually considered the Antarctic in order to furnish a meaningful picture, whereas studies of the ice sheet will necessarily be limited to Antarctica.

In planning the content of the Antarctic Map Folio Series, the advice of numerous scientists with many fields of interest has been sought with a most gratifying response. Much helpful guidance has also been furnished by the scientists on the staff of the Office of Antarctic Programs at the National Science Foundation.

Plates in Folio 11

Editor's note:
The Antarctic Convergence line shown on the plates is taken chiefly from Mackintosh. However, between 10°W and 270°W Gordon's mean value, which incorporates new data, is used (A. Gordon, 1967, Folio 6, Antarctic Map Folio Series); between 60°E and 90°E the position is approximated according to information from R. Delépine (personal communication) that the Convergence is found between the Kerguelen Islands and Heard Island.

Published under a contract with the
NATIONAL SCIENCE FOUNDATION

by the

AMERICAN GEOGRAPHICAL SOCIETY
Broadway at 156th Street
New York, New York 10032

Library of Congress Catalog Card No. Map 64-29

Published Folios

1964

Folio 1. Aeronomical Maps for the Antarctic, by R. Penndorf, T. M. Noel, G. F. Rourke, and M. A. Shea

Folio 2. Physical Characteristics of the Antarctic Ice Sheet, by C. R. Bentley, R. L. Cameron, C. Bull, K. Kojima, and A. J. Gow

1965

Folio 3. Antarctic Maps and Surveys 1900–1964. Plates Compiled by the American Geographical Society with the Cooperation of the United States Geological Survey. Text by George D. Whitmore.

1966

Folio 4. The Antarctic Atmosphere: Climatology of the Troposphere and Lower Stratosphere. Plates compiled by the National Weather Records Center. Text by W. S. Weyant.

1967

Folio 5. Terrestrial Life of Antarctica, by S. W. Greene, J. L. Gressitt, D. Koob, G. A. Llano, E. D. Rudolph, R. Singer, W. C. Steere, and F. C. Ugolini

Folio 6. Structure of Antarctic Waters Between 20°W and 170°W, by Arnold L. Gordon

Folio 7. Glaciers of the Antarctic, by John Mercer

Folio 8. The Antarctic Atmosphere: Climatology of the Surface Environment. Plates compiled by National Weather Records Center and W. S. Weyant. Text by W. S. Weyant.

1968

Folio 9. Magnetic and Gravity Maps of the Antarctic, by John C. Behrendt and Charles R. Bentley

Folio 10. Primary Productivity and Benthic Marine Algae of the Antarctic and Subantarctic, by E. Balech, S. Z. El-Sayed, G. Hasle, M. Neushul, and J. S. Zaneveld

1969

Folio 11. Distribution of Selected Groups of Marine Invertebrates in Waters South of 35°S Latitude, by A. W. H. Bé and others, coedited by J. W. Hedgpeth

Distribution of Selected Groups of Marine Invertebrates in Waters South of 35°S Latitude

Introduction to Antarctic Zoogeography

J. W. Hedgpeth[1]

THE OCEANOGRAPHIC SETTING

From the viewpoint of the distribution of marine organisms, the Antarctic Ocean is a system of concentric rings of water, moving slowly westward and downward near the roughly circular landmass of Antarctica, and eastward at the surface between the region of divergence at about 65°S (known as the Antarctic Divergence) and the great natural boundary of the Antarctic Convergence to the north (Deacon, 1937; Mackintosh, 1946). The region of divergence is roughly the limit of pack ice under present climatic conditions; during glacial periods the relationship between these two phenomena may have been different. This circulation pattern (Figure 1) corresponds roughly to latitude, and the water masses associated with it are more uniform in their temperature and salinity characteristics than around any other continent. The Antarctic Convergence, which lies at about 50°S in the Atlantic sector and 60°S in the

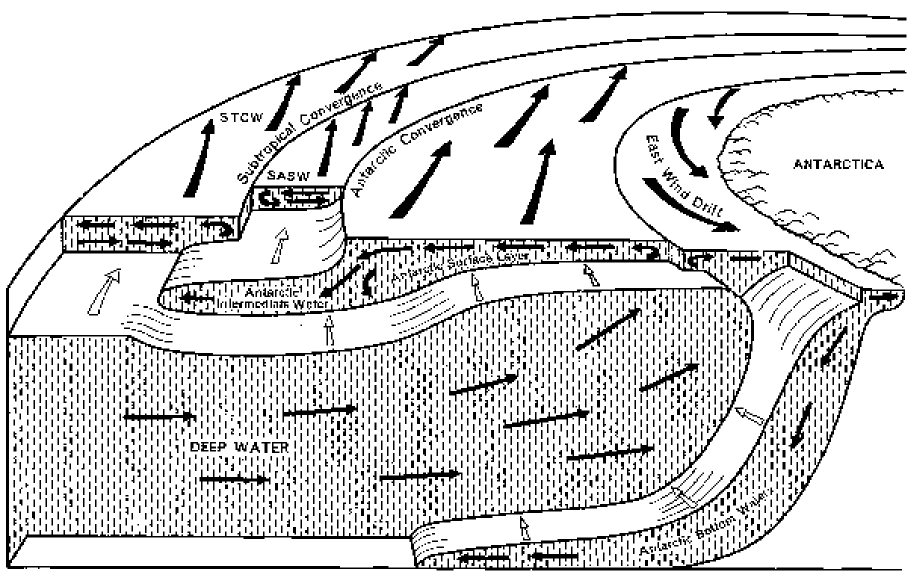


Fig. 1. The structure of Antarctic water masses (adapted from a diagram by R. I. Currie *in* David, 1965).

Pacific sector, is an almost stationary, permanent boundary. In Folio 6 of this series this is termed the Polar Front (Gordon, 1967). Surface waters to the south have temperatures below 1°C in winter and 3.5°C in summer and salinities less than 34‰, while the Subantarctic Surface Water just north of the Convergence is around 2.0°C in winter and of higher salinity. Surface temperatures increase gradually and more or less regularly with latitude northwards to the Subtropical Convergence about 10° north of the Antarctic Convergence, where the temperature changes from about 10°C to 14°C in winter, and 14°C to 18°C in summer (Deacon, 1963). There is also a sharp increase in salinity in this region. The Subtropical Convergence is more variable in position than the Antarctic Convergence, and extends northward to North Island of New Zealand and towards 40°S along both sides of South America. Strictly speaking, the term 'Antarctic Ocean' should probably be confined to the waters south of the Antarctic Convergence. British and New Zealand workers prefer the less precisely defined concept of the 'Southern Ocean' (for example, Knox, 1960; Deacon, 1963; Brodie, 1965). It is usually understood as lying south of the Convergence, but may include parts of the Subantarctic, that broad region between the Antarctic and Subtropical Convergences.

The surface waters of the 'Antarctic Ocean' form a layer about 200 m deep; at the Convergence this layer sinks below the warmer, lighter Subantarctic water. Near the continental shore the water is very cold and is more highly saline because of the ice cover. This cold, dense water, with temperatures below 0°C and salinities greater than 34.5‰, sinks northward from the shallow shelf regions as the Antarctic Bottom Water. Much of this water mass is formed in the Weddell Sea. The Antarctic Bottom Water moves northward and becomes mixed with the deep water of the Atlantic and Pacific Oceans, apparently without a gradient zone such as the surface convergences. Between the Bottom Water and the surface layers is the great intrusive mass of the warm Deep Water, originating in the Atlantic, Indian, and Pacific Oceans. Much of this water is derived from the Atlantic, and some of it by mixing with Antarctic Bottom Water.

Most of our information concerning the distribution of marine life is based on studies of the plankton of the upper layers and of the benthos; considerably less is known concerning the state of affairs in the deep waters of the bathypelagic regions.

Ekman's proposal (1953) to use the term 'Antiboreal' instead of 'Subantarctic' has not met with general acceptance, especially among oceanographers, who have declined to adopt the suggested change from Subtropical to Antiboreal Convergence. Some Soviet workers, for example, Vinogradova (1962), Andriashev (1962, but not 1965), and Lomakina (1964) have used the term 'notal' as the equivalent of Subantarctic (between the Convergences). In English, at least according to Webster III, this means 'pertaining to the back or dorsum,' and the word 'notalian' (which I have not encountered anywhere outside the dictionary), is defined by this august authority as the 'south temperate marine biogeographic realm that is bounded by the southern isocrymes of 68° and 44°F.' Fleming (1963) suggests that the terms 'Neoaustral' and 'Paleoaustral,' which he considers derived by false analogy to Nearctic and Palearctic, be replaced by the terms 'Neonotian' and 'Paleonotian' in paleontological usage. While one may be tempted by such a term as 'Paleonotian' for many discussions in this field, these and similar terms are subject to Fleming's criticism of false analogy, since they imply that the Southern Hemisphere is the back or dorsum of the globe. Most workers in this field have obviously found no objection to the use of the terms 'Antarctic' and 'Subantarctic' for the general biogeographic realms of what journalists often refer to as 'The Bottom of the World.'

PLANKTON DISTRIBUTIONS

The surface waters of the Antarctic comprise a relatively uniform biogeographic region, characterized by very high primary productivity which in turn is associated with a rich zooplankton population. El-Sayed (1968) estimates that the waters south of the Antarctic Convergence, which constitute about 5% of the world oceans, support a gross production in the order of 20% of the world oceans. On the basis of unit area, this means that the Antarctic is 400% more productive than the rest of the oceans. The dominant animal of the Antarctic is the krill *Euphausia superba* (Figure 2), which in the past supported the stocks of whales, and upon

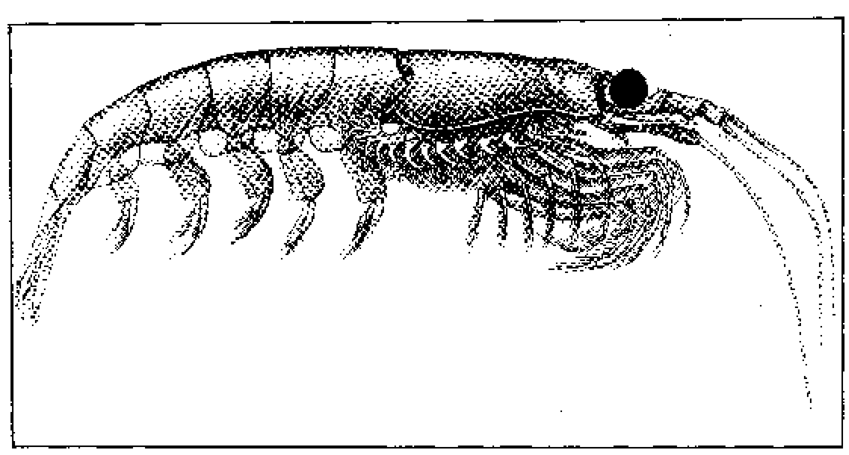


Fig. 2. *Euphausia superba* Dana (from Sars, 1885); magnified about 2.4 times.

[1]Marine Science Laboratory, Newport, Oregon

which several species of penguins, other sea birds, and many fishes depend (Marr, 1962). *Euphausia superba* is an Antarctic endemic, occurring, for the most part, south of the Antarctic Convergence (Figures 3, 4). Recent estimates of the total population of this single species vary rather widely, but suggest that the potential fishery for *Euphausia superba* might exceed that of all the other fisheries of the world combined. However, such a fishery would involve difficult processing problems.

This great productivity and the overwhelming abundance of this endemic species (along with other endemic zooplankton species of copepods, chaetognaths, and others) clearly set upper layers of the Antarctic Ocean apart as a separate and distinct region. Yet the regional abundance of this species indicates differences within the Antarctic Ocean itself. These differences are associated with the geographic conformation of the Antarctic continent. Most if not all zooplankton species are circumpolar in distribution, but they are not uniformly so, with the result that there are both qualitative and quantitative differences in the complex region of the South Atlantic, as well as the latitudinal differences south and north of the Antarctic Divergence. In the opinion of some workers, these differences merit recognition of sub-districts, such as 'high' and 'low' Antarctic zones (for example, Lomakina, 1964).

The Subantarctic waters do not comprise as discrete a zone for plankton as the waters south of the Antarctic Convergence. There are fewer endemic species, and most of the pelagic organisms are obviously derived from farther north, either as widely ranging species or closely related to warmer water species. David (1965) suggests that this colonization from the north is 'relatively recent' for chaetognaths; he believes that the fauna of the Antarctic waters are composed of 7 species, 3 of which are endemic, and that their basic distribution is circumpolar, the Antarctic and Subtropical Convergences acting 'to a greater or lesser extent as boundary regions for the fauna.' The occurrence of 4 species common to other regions suggests that, as far as oceanic distributions are concerned, the value of chaetognaths as 'indicator species' for specific water masses is moot. In any event, there is a tendency for zooplankton organisms to occur in latitudinal bands according to abundance.

The problem of latitudinal gradients has been discussed by a number of authors (see the review by Fischer, 1960), but perhaps without adequate emphasis on the population aspects. While it may appear, for example, that the total number of species in higher latitudes may be less than in the temperate or tropical regions, this diversity is apparently not as sharply marked with respect to populations. Such a diagram as Figure 5 shows the abundance, not of each species involved, but of all of them combined, and it does indicate that total numbers are greater in the Bering Sea than in the tropics. Several overlapping species of *Euphausia* occur in the Subantarctic seas (Figure 6), but this may be a misleading picture since it does not show relative abundances. According to Baker (1965), a single species tends to make up at least 50% of the total of all euphausiids in each ten degrees of latitude in the Indian Ocean, from the equator to from 60°S to 70°S. A further aspect of this problem is that of varying seasonal abundances of different species of the same genus.

According to Voronina (in press), for example, the three abundant mesoplankton copepods of the Antarctic have different cycles of development so that their maxima are spatially isolated. From these various considerations it is probably safe to assume that the overlapping distributions of planktonic organisms is more a reflection of the kinds of data at present available than of the actual situation in nature. When it is remembered that such distributions associated with different reproductive periods and rates may occur in an environment that is possibly as uniform as tropical waters are supposed to be, it is not difficult to suspect that as far as the plankton is concerned, the idea of latitudinal diversity, at least as simultaneous occurrence of more or less equally abundant species, may be overemphasized in the literature.

In any event, the broad picture drawn by Ekman (1953) of the pelagic zones of the southern regions is substantially correct, except that our knowledge of comparative abundances has increased greatly since his time, and the circumpolar distributions of many plankton species should be viewed as eccentric, represented by larger populations in the Atlantic sector (Scotia Sea and Weddell Sea) and thinner bands around the remainder of the Antarctic.

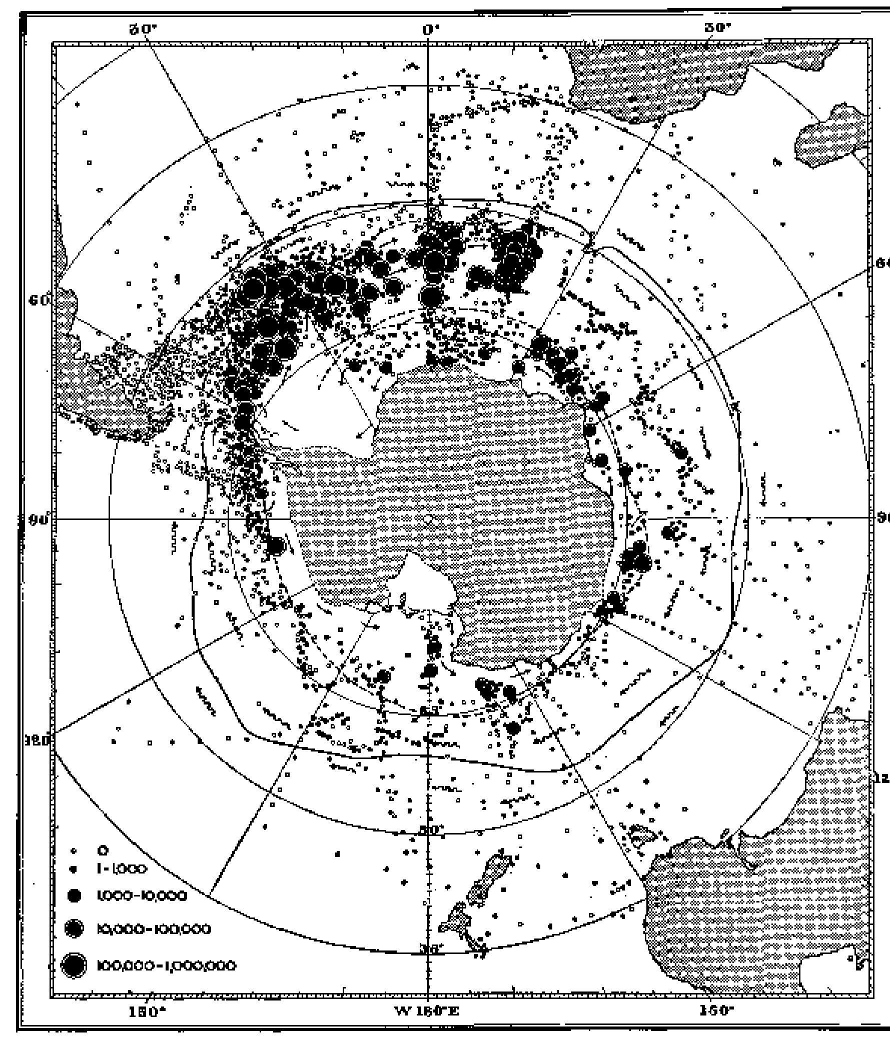


Fig. 3. Gross distribution of total euphausiid population (from Marr, 1962).

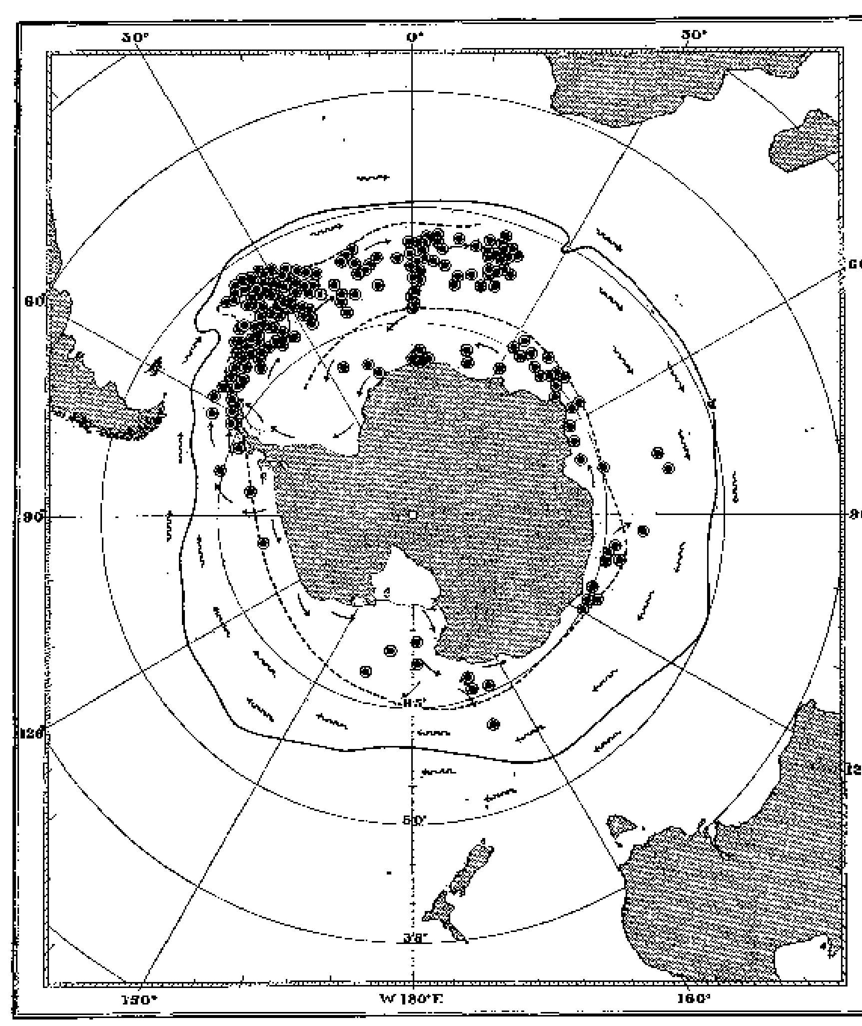


Fig. 4. Principal concentrations of *Euphausia superba* (from Marr, 1962).

THE BENTHOS

SUBLITTORAL ENVIRONMENTS. The near shore bottom of the Antarctic Ocean is a narrow region directly influenced by winter ice to a depth of 15 m to 30 m or more. This 'anchor ice' forms on the bottom as large crystals and in spring and summer is dislodged, rising to the undersurface of the annual ice, carrying entrapped organisms with it. As a result there is a bare region to a depth of 15 or 20 m occupied during the Antarctic summer by such vagile, foraging invertebrates as sea stars, echinoids, nemerteans, the isopod *Glyptonotus* and some pycnogonids (Dayton and Robilliard, in press). Below this is a zone consisting predominantly of sessile coelenterates, extending to 30 or 40 m, where it is replaced by a zone of sponges, bryozoans, ascidians, and numerous associated organisms. This zonal arrangement has been observed by divers in both McMurdo Sound and the Davis Sea (for example, Gruzov, Propp, and Pushkin, 1967); there appear to be some local differences due to slope or sediment types or ice action, but there are no significant differences in these widely separated areas, and the same pattern of zonal arrangement is probably circumpolar, at least in the near shore continental regions of the Antarctic.

Intertidal algae are absent from regions where the shore is ice bound for extended periods, but there is a well developed algal belt or region below extreme low tide, extending to about 37 m (Zaneveld, 1966). According to Zaneveld, this region can be subdivided into an upper belt or sublittoral fringe from low tide to 10 m, and a lower sublittoral belt down to 37 m. Below this is the elittoral or circalittoral region, extending from the sublittoral belt to the limit of macroscopic algae, which may be at a depth of several hundred meters in the Ross Sea. It is interesting to note that the

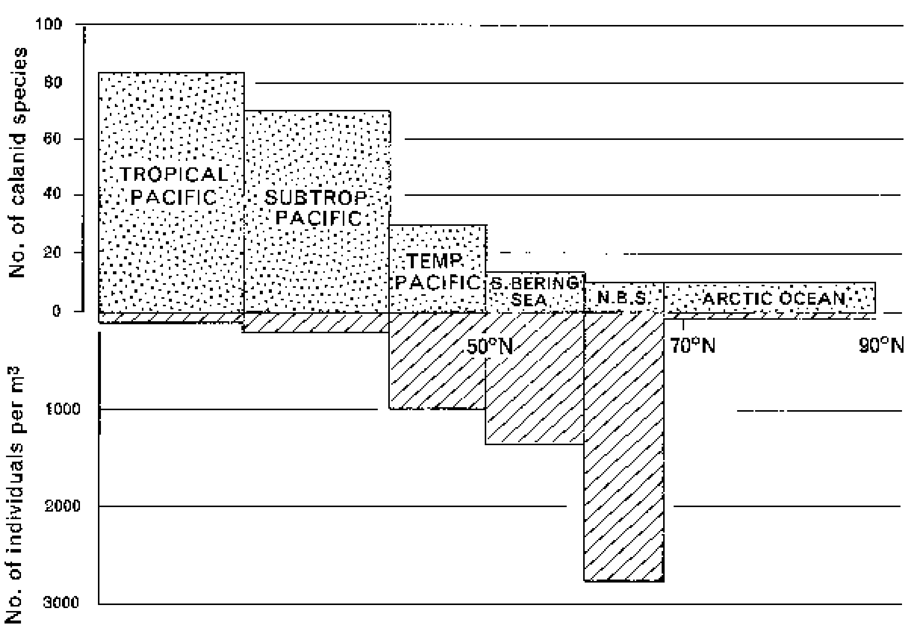


Fig. 5. Diversity gradient in pelagic calanoid copepods in the upper 50 m (adapted from a diagram by Brodsky *in* Fisher, 1960).

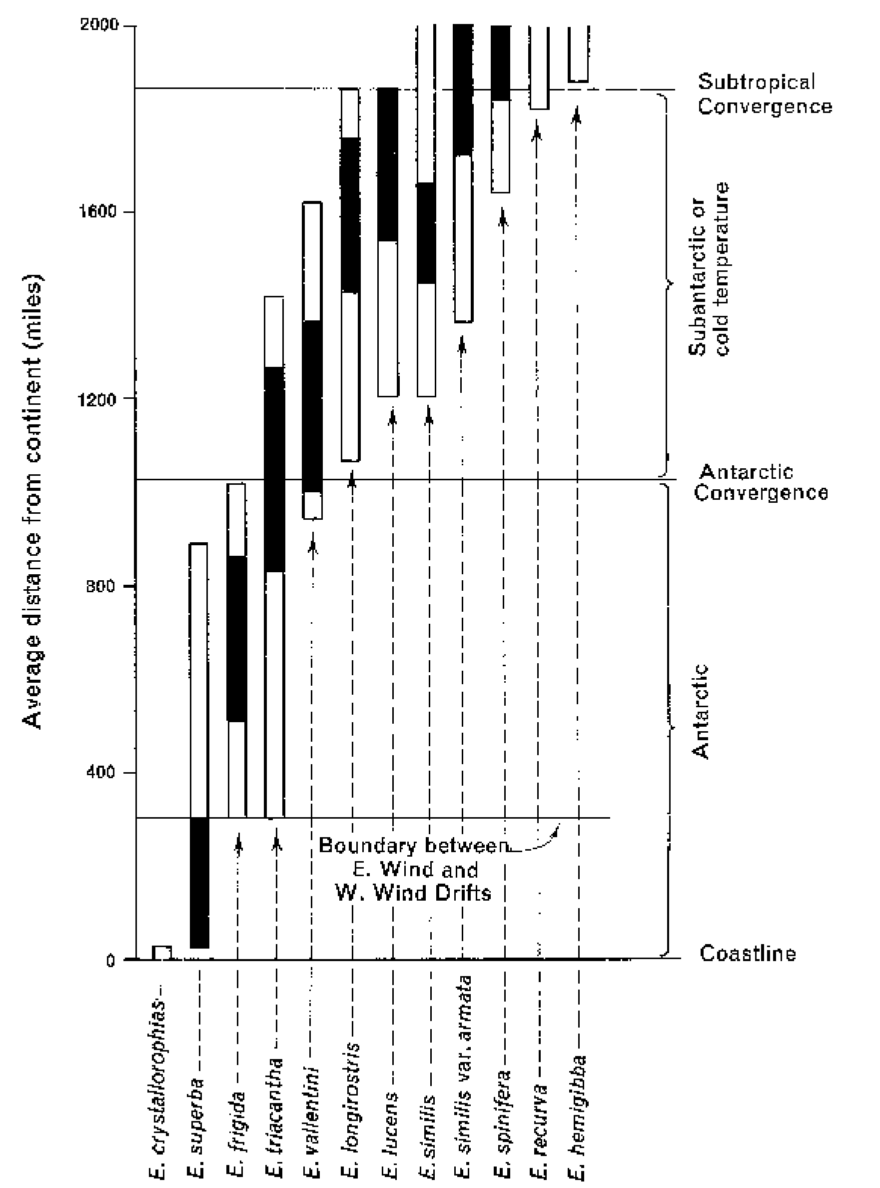


Fig. 6. Zonal distribution of species of *Euphausia;* the black parts indicate greatest concentrations (adapted from Mackintosh, 1960).

division at 10 m corresponds roughly to the region of unattached benthos observed by divers.

To the north, where the shore is free of ice for longer periods, algal growth increases, and on many of the Subantarctic islands there are abundant growths of macroscopic algae, especially *Durvillea*. This genus is not represented south of the Antarctic Convergence. However, two sublittoral brown algae are restricted to the south of the Convergence; these are *Phyllogigas grandifolias* from the South Shetlands to Cape Adare (or 73°S) and *Ascoseira mirabilis* on islands of the Scotia Ridge to the South Shetlands. *Macrocystis pyrifera* reaches its southern limits around South Georgia and the islands near the Antarctic Convergence from Prince Edward to Macquarie. For further information on the distribution of Antarctic macroscopic algae, see Neushul (1968) and Zaneveld (1968) in Folio 10 of this series.

THE ROSS SEA BENTHOS. The deeper parts of the Ross Sea, from 200 m to 400 m, are rich in assemblages of invertebrates; Bullivant (1967) recognizes three major assemblages of larger invertebrates associated with different types of bottom on the basis of qualitative samples and photographs. The first of these he calls the Deep Shelf Mixed Assemblage, associated with a fine sediment with erratic boulders, consisting for the most part of tubiculous polychaetes, rooted bryozoa, various echinoderms, and mollusks. The second type is the Deep Shelf Mud Bottom Assemblage, occurring on mud or sandy mud bottom with erratic boulders; tubiculous polychaetes are abundant here, along with sipunculids, a foraminifer and ophiuroids. The third assemblage is that associated with a bottom of cobbles embedded in muddy sand, consisting for the most part of hard bottom animals such as bryozoa, gorgonaceans, stylasterine corals and tunicates, several species of ophiuroids and pycnogonids. A number of minor assemblages were noted, including the McMurdo Sound glass sponge assemblage in depths of 69 m to 180 m, on a bottom of 'unsorted rock debris.' Some of these assemblages are not well defined quantitatively.

Taken as a whole the Ross Sea benthos consists primarily of sessile, filter-feeding, or fine particle-feeding invertebrates attached to numerous rocks, and cannot be compared with the shallow, soft, or level bottom communities of European waters. The nearest analogue seems to be the assemblage associated with cobble bottoms off Point Barrow. In deeper water where sediments are finer, sessile organisms are less abundant, and polychaetes, crustaceans, echinoderms, and mollusks are relatively more numerous.

It seems probable that similar assemblages occur all around the Antarctic, but comparable quantitative data of the sort that has been obtained for the infaunal bottom communities of northern latitudes will be very difficult to obtain for these essentially epifaunal assemblages. As Bullivant remarks, many of the common organisms making up these assemblages are circumpolar in distribution.

SEDIMENTS. Antarctic bottom sediments consist for the most part of glacial or 'iceberg' sediments brought from the continent by ice action. These are not deposited immediately near the shore but are carried out to the outer shelf and slope; they consist of muds, fine and coarse sand, and boulders; the finer sediments are greenish gray in color (Brodie, 1965). The region of glacial sediments corresponds roughly with the limit of pack ice; north of this region the predominant sediment is creamy yellow diatom ooze with patches of recent volcanics and foraminifera. These sediments are replaced farther north by foraminiferal ooze and large areas of red clay in deeper parts of the Pacific sector. Near shore the abundant filter-feeding animals of the bottom assemblages suggest low rates of sedimentation. It is possible that sedimentation may be comparatively light under the present climatic regime.

PATTERNS OF DISTRIBUTION. Ekman (1953) divided the benthic faunas of the shelf and near island bottoms into Antarctic and Antiboreal regions. For the Antarctic he recognized a high Antarctic subregion, in turn divided into the West Antarctic, including the Weddell Sea and Antarctic Peninsula, and the East Antarctic, including the Ross Sea. He considered the low Antarctic region to include South Georgia. He divided the Antiboreal region into a South American subregion with a strong Antarctic component, a region of oceanic islands, and a Kerguelen region. These generalizations were based, for the most part, on information from the first intensive era of Antarctic exploration and collecting before 1914; since then systematic work with many groups has been reappraised, and new information has become available. It should be noted that Ekman (or his translator) is not precise about such terms as 'region' and 'province' and indeed uses them interchangeably.

While many recent workers, including most of the contributors to this folio, do not find clear evidence of distinct East and West subregions, Koltun, in this folio, notes differences in the sponge genera of East Antarctica, including McMurdo Sound, and West Antarctica and believes that this cannot be explained on the usual grounds of inadequate collections. Kussakin (1967) designates as the East Antarctic province for isopods the region from somewhere in the Weddell Sea around the entire continent to 90°W in the Bellingshausen Sea, this is almost circumpolar (270°) and leaves the Antarctic Peninsula and nearby islands, with the exception of South Georgia, as his West Antarctic province. South Georgia is considered a separate province in this scheme. On the basis of fishes, Andriashev recognizes a Continental Province with East Antarctic and West Antarctic districts.

Except for the different uses of 'subregion' and 'province,' the divisions proposed by Andriashev and Kussakin are essentially the same. The East Antarctic of these distribution schemes is the continental near shore, or 'high' Antarctic, of Ekman and many authors following him, but Ekman's 'low' Antarctic included South Georgia, which, according to some systematists, merits recognition as a separate region or province. The South Georgian Province proposed for ascidians by Kott in this folio includes the islands of the Scotia Ridge and the Antarctic Peninsula, however. A number of the contributors to this folio suggest that the fauna of the Antarctic Peninsula and island arc is somewhat different in composition from the 'high' Antarctic region, and especially that it shows strong affinities with that of South America. The groups involved in such a distribution pattern include the Bryozoa, Brachiopoda, Mollusca and many echinoderms. Groups represented mainly by deeper water species, including the various types of corals, sipunculids, and echiurids do not show such a regionalization, and are more closely related to the Convergences than to continental and island configurations.