With the Author's compliments

EXTRAIT

RAPPORTS ET PROCÈS-VERBAUX DES RÉUNIONS DU CONSEIL PERMANENT INTERNATIONAL POUR L'EXPLORATION DE LA MER

VOL. XCV, 1935

A REVIEW OF SOME ASPECTS OF ZOOPLANKTON RESEARCH.

BY

F. S. RUSSELL,
Naturalist at the Plymouth Laboratory of the
Marine Biological Association of
the United Kingdom.

IT is now nearly one hundred years since the tow-net was first introduced by Johannes Müller (1846). Zoology was still in its early descriptive stage and a rich ground for the investigation of new species was thus opened up. About that time also the theory of evolution was assuming concrete form, to be firmly established by the publication of Darwin's "Origin of Species" in 1859. The evolutionary theory was the main directing force for the study of embryology, and in the development of this branch of zoology, research on plankton animals has played a greater part than that on any other population of the animal kingdom. We owe to the labours of the zoologists of the latter half of last century most of our present knowledge on the affinities and natural classification of the major groups of invertebrate animals. With the exception of insects, the invertebrates are essentially inhabitants of the sea, and almost all spend the earlier stages of their lives drifting in the water layers in the plankton community.

Among the first workers in this line of research was T. H. Huxley who sailed in 1846 in the "Rattlesnake" to Australian waters. In these days of elaborate and costly apparatus it is well to bear in mind what far reaching results can be obtained by the simplest means. Huxley used as his townet a bag of the bunting of which flags are made. With this simple net he sieved the sea at every available opportunity. As a result he demonstrated the true position of the medusae and siphonophores in the coelenterate kingdom, and also traced the affinities of the pelagic tunicates to the sessile ascidians of our sea shores. Of even more far reaching importance was the result of his examination of the medusae whereby he indicated the existence and importance of the germ-layers in the development of metazoa.

But to-day I do not wish to take as my theme the examination of plankton animals with the ulterior aim of elucidating problems purely morphological or embryological in nature. I wish rather to review those aspects of zooplankton research whose concern has been the study of plankton animals as members of a community, and for the part they play by their habits and abundance in the balance of life in the sea. The review will be concerned only with metazoa.

In reviewing the present position I shall try to embrace all the aspects of the situation. It is necessary to take the wide view without unduly stressing any particular problem, because we have suffered in the past from a tendency to pursue certain directions of enquiry to a disproportionate extent. As a result plankton research has become somewhat uncoordinated, and advance has been held up by a lack of consideration as to which are the problems that require special attention in order to bring our various fields of knowledge into line.

With such a wealth of data scattered amongst the biological literature of the world the task of review becomes impossible unless we first fix upon certain outstanding events around which the main sequence of the review can be evolved.

I have adopted the following landmarks as representative of the sequence of events after the introduction of the quantitative method by Hensen, leading to the publication of his Methodik (1895)

1. The Plankton Expedition in the "National" under the leadership of Hensen in 1889.
2. The comprehensive scheme for the collection of plankton throughout the North Sea and adjacent waters of the Atlantic, Channel and Baltic, during the years 1902 to 1908 by the International Council.
3. The completion by Lohmann in 1906 of a year's detailed survey of the total plankton production at Laboe in Kiel Bay.

During these two latter periods plankton study received a constant leavening element in the intensely biological outlook of Professor Gran.

4. The post-war period.

Three publications previous to the last period should also be mentioned as having left their mark in the history of plankton research and stimulated many workers, these were Adolf Steuer's "Planktonkunde" published in 1910; "Conditions of Life in the Sea" by James Johnstone, in 1908 and the "Depths of the Ocean" by Murray and Hjort in 1912.

I have taken these four periods because they illustrate the main problems that confront those concerned with zooplankton research. The first is the necessity of knowing the distribution and abundance of the plankton in the open ocean.

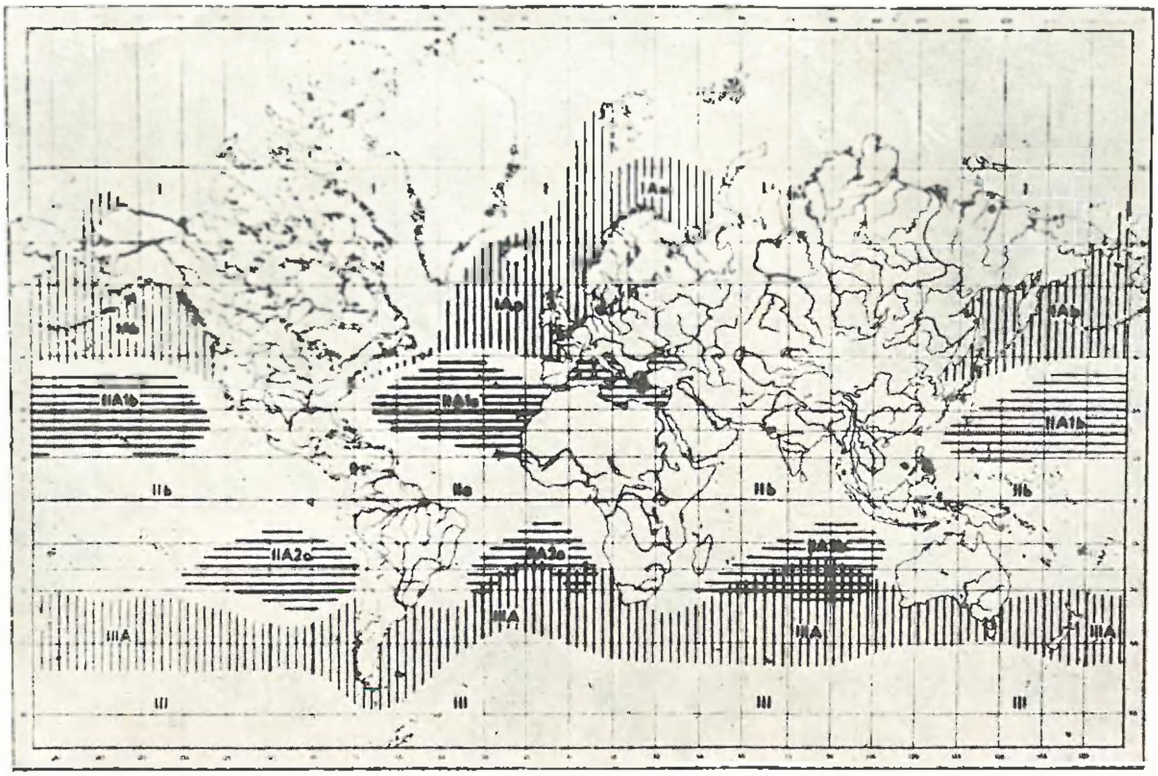

Fig. 1.

Distribution regions of oceanic plankton organisms (after Steuer, 1933, p. 292, Fig. 8, for Copepods). For explanation see Text.

Secondly comes the desire for a similar knowledge of the conditions in the coastal waters whose origin and movements are so largely governed by the oceanic circulation. In intimate connexion with this is the use of our knowledge of the plankton distribution as an aid to the interpretation of hydrographical data. Thirdly, knowing something of the animals' distribution we need to know about their relations with their animate and inanimate environment, and the causes of their fluctuations in abundance. This is a work that has so far only been attempted in coastal waters where the necessary observations can be made at frequent intervals throughout the year with the facilities of a laboratory close at hand. And finally the research has shown the need for even more detailed observations, for a close study of life-histories and habits, and for the examination of the more specialised problems that have arisen such as the relations between the plankton and the fish that are used as food by man.

Before any work on the biology of animals can be attempted the animals that we wish to study must be described and classified. This is a task that has gone on from the earliest days of marine biology and as regards the zooplankton much of our present knowledge has been built up from the results of the collections of the great oceanographical expeditions. Many years must elapse before the description of all the species of plankton animals is brought to completion. We can however say with gratitude to the workers in the past that in many groups today the necessary knowledge is reaching its final stages. Coincident with the descriptive work our knowledge of geographical distribution has grown and as the groups have been better known the distribution of the species among their faunistic regions has become more detailed.

It is probable that in ocean waters one of the main barriers to distribution is that of the temperature conditions. Animals adapted for successful reproduction in any given temperature range will be carried in the water masses and ocean current systems so far as the necessary temperature conditions are maintained.

When the temperature conditions have been taken into consideration the chief clues to the geographical distribution of the species are to be found in the systems of oceanic circulation. The

IT is now nearly one hundred years since the tow-net was first introduced by Johannes Müller (1846). Zoology was still in its early descriptive stage and a rich ground for the investigation of new species was thus opened up. About that time also the theory of evolution was assuming concrete form, to be firmly established by the publication of Darwin's "Origin of Species" in 1859. The evolutionary theory was the main directing force for the study of embryology, and in the development of this branch of zoology, research on plankton animals has played a greater part than that on any other population of the animal kingdom. We owe to the labours of the zoologists of the latter half of last century most of our present knowledge on the affinities and natural classification of the major groups of invertebrate animals. With the exception of insects, the invertebrates are essentially inhabitants of the sea, and almost all spend the earlier stages of their lives drifting in the water layers in the plankton community.

Among the first workers in this line of research was T. H. Huxley who sailed in 1846 in the "Rattlesnake" to Australian waters. In these days of elaborate and costly apparatus it is well to bear in mind what far reaching results can be obtained by the simplest means. Huxley used as his townet a bag of the bunting of which flags are made. With this simple net he sieved the sea at every available opportunity. As a result he demonstrated the true position of the medusae and siphonophores in the coelenterate kingdom, and also traced the affinities of the pelagic tunicates to the sessile ascidians of our sea shores. Of even more far reaching importance was the result of his examination of the medusae whereby he indicated the existence and importance of the germ-layers in the development of metazoa.

But to-day I do not wish to take as my theme the examination of plankton animals with the ulterior aim of elucidating problems purely morphological or embryological in nature. I wish rather to review those aspects of zooplankton research whose concern has been the study of plankton animals as members of a community, and for the part they play by their habits and abundance in the balance of life in the sea. The review will be concerned only with metazoa.

In reviewing the present position I shall try to embrace all the aspects of the situation. It is necessary to take the wide view without unduly stressing any particular problem, because we have suffered in the past from a tendency to pursue certain directions of enquiry to a disproportionate extent. As a result plankton research has become somewhat uncoordinated, and advance has been held up by a lack of consideration as to which are the problems that require special attention in order to bring our various fields of knowledge into line.

With such a wealth of data scattered amongst the biological literature of the world the task of review becomes impossible unless we first fix upon certain outstanding events around which the main sequence of the review can be evolved.

I have adopted the following landmarks as representative of the sequence of events after the introduction of the quantitative method by Hensen, leading to the publication of his Methodik (1895)

1. The Plankton Expedition in the "National" under the leadership of Hensen in 1889.
2. The comprehensive scheme for the collection of plankton throughout the North Sea and adjacent waters of the Atlantic, Channel and Baltic, during the years 1902 to 1908 by the International Council.
3. The completion by Lohmann in 1906 of a year's detailed survey of the total plankton production at Laboe in Kiel Bay.

During these two latter periods plankton study received a constant leavening element in the intensely biological outlook of Professor Gran.

4. The post-war period.

Three publications previous to the last period should also be mentioned as having left their mark in the history of plankton research and stimulated many workers, these were Adolf Steuer's "Planktonkunde" published in 1910; "Conditions of Life in the Sea" by James Johnstone, in 1908 and the "Depths of the Ocean" by Murray and Hjort in 1912.

I have taken these four periods because they illustrate the main problems that confront those concerned with zooplankton research. The first is the necessity of knowing the distribution and abundance of the plankton in the open ocean.

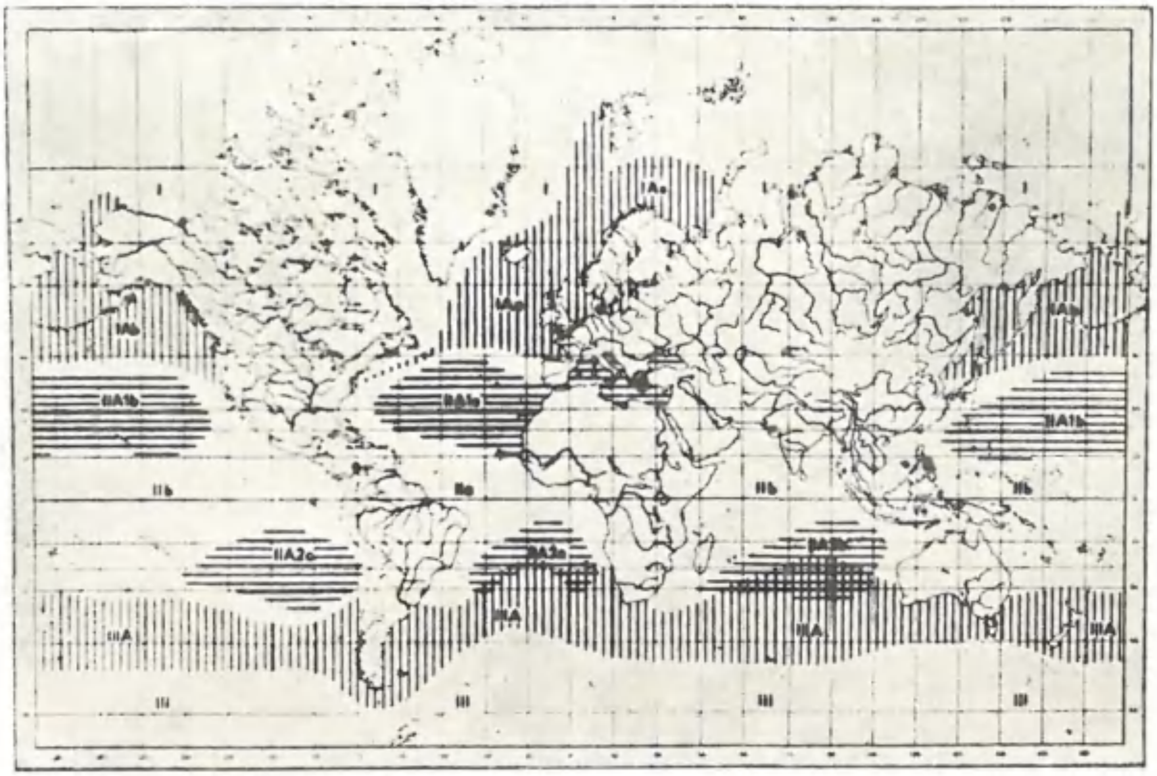

Fig. 1.

Distribution regions of oceanic plankton organisms (after Steuer, 1933, p. 292, Fig. 8, for Copepods). For explanation see Text.

Secondly comes the desire for a similar knowledge of the conditions in the coastal waters whose origin and movements are so largely governed by the oceanic circulation. In intimate connexion with this is the use of our knowledge of the plankton distribution as an aid to the interpretation of hydrographical data. Thirdly, knowing something of the animals' distribution we need to know about their relations with their animate and inanimate environment, and the causes of their fluctuations in abundance. This is a work that has so far only been attempted in coastal waters where the necessary observations can be made at frequent intervals throughout the year with the facilities of a laboratory close at hand. And finally the research has shown the need for even more detailed observations, for a close study of life-histories and habits, and for the examination of the more specialised problems that have arisen such as the relations between the plankton and the fish that are used as food by man.

Before any work on the biology of animals can be attempted the animals that we wish to study must be described and classified. This is a task that has gone on from the earliest days of marine biology and as regards the zooplankton much of our present knowledge has been built up from the results of the collections of the great oceanographical expeditions. Many years must elapse before the description of all the species of plankton animals is brought to completion. We can however say with gratitude to the workers in the past that in many groups today the necessary knowledge is reaching its final stages. Coincident with the descriptive work our knowledge of geographical distribution has grown and as the groups have been better known the distribution of the species among their faunistic regions has become more detailed.

It is probable that in ocean waters one of the main barriers to distribution is that of the temperature conditions. Animals adapted for successful reproduction in any given temperature range will be carried in the water masses and ocean current systems so far as the necessary temperature conditions are maintained.

When the temperature conditions have been taken into consideration the chief clues to the geographical distribution of the species are to be found in the systems of oceanic circulation. The oceans can now be divided into definite masses of water with different characteristics. These different masses are constantly moving and are separated from one another by regions of mixed water which may be wide or narrow according to the locality. Such regions are the antarctic, the subtropical and the tropical convergences in the south, and the transition regions in the north which vary from narrow zones with well defined boundaries between warm and cold waters in the west to the widespread mixing regions in the east. Each body of water has its own somewhat characteristic plankton fauna at different levels. These faunas tend to mix at the boundaries, some species of the colder water surviving under favourable conditions found at deeper levels. Thus the distribution of the arctic planktonic fauna dips beneath the surface layers towards the south.

In a recent work on the geographical distribution of copepods Steuer (1933, p. 291) has adopted the following scheme, (Fig. 1).

I. Circum-polar Arctic.
    A. Sub-arctic (temperate, northern transitional, or boreal)
        a. Atlantic.
        b. Pacific.
II. Circum-equatorial tropical.
        a. Atlantic.
        b. Indo-pacific.
    A. Sub-tropical
        1. Northern sub-tropical.
            a. Atlantic (and Mediterranean — Black Sea)
            b. Pacific.
        2. Southern Sub-tropical.
            a. Atlantic.
            b. Indian.
            c. Pacific.
III. Circum-polar Antarctic.
    A. Circum-polar Sub-antarctic (southern transitional).

It is never possible to confine living organisms within the limits of precise schemes, and while such a classification is convenient the boundaries do not hold for all species. The most important limiting factor is probably temperature and each species may have its own limits. There is thus some overlap in the limits of distribution of species in the transition zones; this has been made clear by the work of the Discovery Expedition in the southern Atlantic (Mackintosh, 1934). Yet in regions where the transition in temperature is abrupt, and amounts to several degrees, many species find their limits, and the faunas of the neighbouring water masses become clearly demarcated.

Since in many groups the majority of species are now fully described it should be the aim of future expeditions to make our knowledge of geographical distribution more complete. The data thus obtained will act as bench-marks for the study in years to come of the secular changes in the water movements of the ocean. With this idea in mind I have produced a preliminary table (Table I) giving the number of known species in the more important plankton groups and their subdivision into broad geographical areas. It has only been possible to produce such a table with the cooperation of many specialists in plankton animal groups. I owe a debt of gratitude to the following workers for their very willing and painstaking assistance.

Dr. S. T. Burfield (Chaetognatha); Mr. G. P. Farran (Copepoda); Professor P. Fauvel (Tomopteridae); Miss A. B. Hastings (Tunicata); Dr. P. L. Kramp (Medusae); Professor Th. Mortensen (Ctenophora); Dr. K. Stephensen (Amphipoda); Professor W. M. Tattersall (Euphausiacea); Mr. A. K. Totton (Siphonophora).

The production of this table brings out some points of interest.

1. The greater number of cold water species in the south as opposed to the north.
2. The phenomenon of epiplanktonic[1]) bipolarity.
3. The small number of purely sub-antarctic species of copepods and perhaps other groups.
4. Differences between the faunas of the different oceans.
5. The inequality in the state of our knowledge on different groups.

In all groups (except the meroplanktonic medusae and the essentially bottom living Gammarid Amphipods) the preponderance of southern over northern cold water species is evident. This fact has been remarked on by Meisenheimer, (1905, p. 90) for the pteropods. He suggests an obvious cause in pointing to the much greater area of confluence between warm and cold waters in the south than in the north as conducive to the opportunity for increased evolution of species from the warm species-producing centre. But there is an added factor that our increased knowledge of oceanic circulation brings to light both on this problem and that of bipolarity. Before proceeding it should be pointed out that Steuer (1933, p. 284) has suggested that there are no truly arctic Gymnoplean Copepods, but that the arctic and sub-arctic regions should be taken together. He gives as an example *Calanus hyperboreus*, a species that has been

---

[1]) In my original manuscript I had used the word "bipolar"; it was however pointed out to me by Dr. H. B. Bigelow that the original meaning of this word implied discontinuous bipolarity (see also Stiasny, 1934); it is necessary to find some other term and I have used "bipolar-epiplanktonic" as denoting that these species occur in the surface waters in north and south, though when present in warm latitudes they are mesoplanktonic.

(Continued on page 12).

Table I.

Numbers of species of holoplanktonic animals, and meroplanktonic coelenterates.

	Arctic	Arctic-Boreal and Boreal	Antarctic	Sub-antarctic	Bipolar-epiplanktonic	Cosmopolitan	Warm	Deep Sea	TOTAL
COELENTERATA									
Antho-, Lepto-, and Scyphomedusae[1]	20	100	10	15	—	—	370	20	535
Trachy- and Narco-medusae[1]	4	10	3	6	—	—	90	21	134
Siphonophora									
Calycophorae	—	—	2		1	—	64	5	72
Physophorae	—	?1	2		—	—	29	2	34
Ctenophora	1	2	2	1	—	2	69?	3	80?
NEMERTEA	—	—	—	—	—	—	—	34	34
POLYCHAETA									
Tomopteridae	—	?1	?4		1	—	38	?	44
CHAETOGNATHA	—	2	2		2	—	18	6[2]	30
CRUSTACEA									
Cladocera	—	1	—	—	(3)	—	3	—	7
Copepoda	7	10	32	5	1(5)	10	489	195[3]	754
Amphipoda									
Hyperiidea	2	—	10	—	—	2	250	28[4]	292
Gammaridea	7	—	—	—	—	—	20	17[4]	44
Euphausiacea	—	6	2	7	(1)	—	46	23	85
MOLLUSCA									
Pteropoda									
Thecosomata	—	—	2		1(1)?	—	44	3	51
Gymnosomata	—	1	2		(1)?	—	37	?	41
Heteropoda	—	—	—	—	—	—	90	—	90
TUNICATA									
Appendicularia	2	1	6		—	1	48	3	61
Thaliacea									
Doliolidae	—	—	1?		—	—	11	—	12
Salpidae	—	—	1		—	—	24	—	25
Pyrosomidae	—	—	—	—	—	—	8	—	8
TOTAL	178		115		17	15	1754	360	2433
(Excluding meroplanktonic Medusae	58		90		17	15	1378	340	1898)

Distribution of warm water species.

	In 3 oceans	Atlantic and Indian	Atlantic and Pacific	Indian and Pacific 1)	Atlantic only 2)	Indian only	Pacific only	Mediterranean only	TOTAL
COELENTERATA									
Antho-, Lepto-, and Scyphomedusae	11	4	21	32	160	60[3]	100	?	
Trachy- and Narco-medusae	15	3	5	4	45	9[2]	17	?	
Siphonophora									
Calycophorae	24	—	8	15	9	1	4	—	61
Physophorae	10	1	2	9	4	—	3	—	29
Ctenophora	2	—	—	10	24	4	16	9	65
NEMERTEA									
POLYCHAETA									
Tomopteridae	3	1	3	3	6	7[4]	8	7	37
CHAETOGNATHA	9	1	—	4	3	—	1	—	18
CRUSTACEA									
Cladocera	3	—	—	—	—	—	—	—	3
Copepoda	146	30	58	57	106	27	65[6]	?	489
Amphipoda[7]									
Hyperiidea	54	30	23	1	83	26	26	7	250
Gammaridea	3	1	2	—	10	3	1	—	20
Euphausiacea	14	1	4	4	11	2	16	?2	52
MOLLUSCA									
Pteropoda									
Thecosomata	24	2	3	2	7	1	3	2	44
Gymnosomata	5	2	1[5]	6	12	2	5	4	37
Heteropoda	8	4	6	16	27	3	9	17	90
TUNICATA									
Appendicularia	9	7	—	2	20	1	3	5	47
Thaliacea									
Doliolidae	6	3	—	—	1	1	1	—	12
Salpidae	15	3	—	1	2	2	1	—	24
Pyrosomidae	3	2	—	—	—	3	—	—	8

1st column.

( ) = Bipolar sub-arctic and sub-antarctic.

[1] Approximate Numbers.

[2] Mesoplankton — below 100 fathoms and mostly deeper.

[3] Below 200 fathoms, mostly not found in epiplankton at night.

[4] At least 300—500 m. wire out.

2nd column.

[1] Including Indo-Pacific Region (Siboga).

[2] Including Atlantic-Mediterranean.

[3] Including Siboga results.

[4] Six in Red Sea only.

[5] Pacific and Mediterranean.

[6] Including Indo-Pacific (Siboga).

[7] Siboga results divided between Indian and Pacific according to localities.

NOTES TO TABLE I.

The following definitions have been used:—

Bipolar-epiplanktonic. Those species which are found in surface layers in northern and southern cold waters but when present are found only in deep layers in warm latitudes.

Cosmopolitan. Those species which are found alike in surface warm and cold waters.

Deep Sea. Those species living below a depth of about 200 fathoms, that is below the limit of penetration of light. The inhabitants of this region have been regarded by many as likely to be found to be cosmopolitan. They have not been divided among the oceans in Table I as in many groups our knowledge of the true deep sea species is insufficient.

In those groups in which the division of species between arctic and sub-arctic, and antarctic and sub-antarctic, is uncertain the numbers in the Table have been placed centrally between the two columns in each region. Below they have been written arctic-subarctic, and antarctic-sub-antarctic.

COELENTERATA

The data for Medusae have been supplied by Dr. P. L. Kramp. The Medusae have been divided into the Mero-planktonic Antho-, Lepto-, and Scypho-medusae, and the Holo-planktonic Trachy-, and Narco-medusae.

SIPHONOPHORA. The data have been obtained *from Moser, 1925; Bigelow, 1911 and 1931; and* Lens and van Riensdijk, 1908, with the assistance of Mr. A. K. Totton.

The cold water species are:—

Sub-arctic, *Stephanomia cara* (A. Agassiz).

Antarctic-sub-antarctic, *Diphyes antarctica* Moser; *Crystallophyes amygdalina* Moser (? deep sea), *Pyrostephos vanhöffeni* Moser, and *Stephanomia convoluta* Moser.

Bipolar, *Dimophyes arctica* Chun.

It is still uncertain whether *Stephanomia cara* should be regarded as a distinct species from the warm water *Stephanomia bijuga* (della Chiaje).

The following are possibly deep-sea species, *Chuniphyes multidentata* Lens u. v. R., *Chuniphyes problematica* Moser, *Clausophyes ovata* (Kef. u. Ehl), *Thalassophyes crystallina* Moser, *Amphicaryon acaule* Chun, *Pterophysa (Bathyphysa) studeri* Lens u. v. R., and *Bathyphysa sibogae* Lens u. v. R.

CTENOPHORA. The data have been supplied by Dr. H. Mortensen, and the distribution in the oceans has been taken from Moser (1909). The cold water species are:—

Arctic, *Mertensia ovum* Fabr.; Arctic and sub-arctic, *Pleurobrachia crinita* Moser and *Bolina infundibulum* Martens; Sub-antarctic, *Callianira antarctica* Chun; Antarctic, *Callianira cristata* Moser and *Beroe compacta* Moser.

Beroe cucumis Fabr. and *Pleurobrachia pileus* Fabr. occur both in the arctic and antarctic, but also in surface waters of warm latitudes and are cosmopolitan.

Moser (1909, p. 181) was of the opinion that the ctenophores in cold waters have undoubtedly evolved from a centre of species formation in warm waters.

The deep sea species are *Bathyctena chuni* (Moser), *Aulacoctena acuminata* Mrtsn., and *Beroe abyssicola* Mrtsn.

NEMERTEA. The Pelagic nemerteans are after Brinkmann (1917) and Wheeler (1934).

POLYCHAETA.

Tomopteridae. The data have been supplied by Prof. P. Fauvel.

The cold water species are:—

Sub-arctic, ? *Tomopteris helgolandica* Greef.

Antarctic-sub-antarctic, *Tomopteris carpenteri* Quatref., *T. rosea* Ehlers, ? *T. opaca* Treadwell, and ? *T. tentaculata* Treadwell.

T. septentrionalis Quatref. is regarded by Augener (1929, p. 281) as a bipolar species.

CHAETOGNATHA. The data have been supplied by Dr. S. T. Burfield. Ritter-Zahony's (1911) mesoplankton species have been regarded as deep sea. The cold water species are as follows:—

Antarctic-sub-antarctic, *Heterokrohnia mirabilis* Ritt.-Z. and *Sagitta gazellae* Ritt.-Z.; Bipolar, *Sagitta maxima* (Conant) (and deep sea), *Eukrohnia hamata* Möb.

S. gazellae and *S. maxima* are both very nearly related to the warm water species *S. lyra* Krohn. If they can be regarded as separate species, it is possible that *S. gazellae* has evolved in southern cold waters; and that *S. maxima* has evolved in cold northern waters and become bipolar. *S. planctonis* Steinhaus a deep water species appears in the Antarctic.

To the number of warm water species should also be added six species described by Oye (1918) from the Java Sea whose identity has not yet been confirmed, and *S. euxina* from the Black Sea. The deep-sea species are *Sagitta decipiens* Fowl., *S. lyra* Krohn, *S. macrocephala* Fowl., *S. planctonis* Steinhaus, *Eukrohnia fowleri* Ritt.-Z., and *Heterokrohnia mirabilis* Ritt.-Z.

Crustacea

CLADOCERA. The data have been taken from Rammner (1933). There are no purely arctic or antarctic cladocera, Sub-arctic, *Podon intermedius* Lillj.; Bipolar (sub-arctic and sub-antarctic) *Podon leuckarti* G. O. Sars, *Podon polyphemoides* Leuck., and *Evadne nordmanni* Lovén.

COPEPODA: all the data for copepods have been supplied by Mr. G. P. Farran.

The following is the tentative list of cold water and cosmopolitan species:—

Arctic and Boreal. *Calanus cristatus*, *Calanus hyperboreus*, *Pseudocalanus elongatus*, *Microcalanus pusillus*, *Gaidius brevispinus* (A), *Pareuchaeta glacialis* (A), *Pareuchaeta norvegica* (B), *Undinopsis similis*, *Undinella oblonga* (A), *Scolecithricella minor* (B), *Scolecithricella dentata*, *Temorites brevis*, *Heterorhabdus norvegicus* (B), *Augaptilus glacialis* (A), *Mormonilla polaris* (A), *Oncaea borealis* (A), *Acartia longiremis* (A).

Antarctic. *Calanus propinquus*, *Calanus acutus*, *Rhincalanus gigas*, *Stephus antarcticus*, *Chiridius antarcticus*, *Chiridius minor*, *Chiridius polaris*, *Gaetanus antarcticus*, *Euchirella rostromagna*, *Undeuchaeta spectabilis*, *Pareuchaeta austrina*, *Pareuchaeta erebi*, *Pareuchaeta rasa*, *Pareuchaeta antarctica*, *Pareuchaeta similis*, *Xanthocalanus tenuiserratus*, *Onchocalanus frigidus*, *Cephalophanes frigidus*, *Scolecithricella glacialis*, *Scaphocalanus impar*, *Scaphocalanus sub-brevicornis*, *Amallothrix* *polaris, Amallothrix incisa, Racovitzanus antarcticus, Metridia gerlachei, Metridia curticauda, Heterorhabdus austrinus, Heterorhabdus pustulifer, Haloptilus ocellatus, Paralabidocera hodgsoni, Oithona frigida, Oncaea curvata.*

Sub-antarctic. *Calanus simillimus, Eucalanus longiceps, Clausocalanus laticeps, Pareuchaeta biloba, Candacia cheirura.*

Bipolar. *Microcalanus pygmaeus, Scaphocalanus magnus, Metridia lucens, Metridia longa* (A), *Heterorhabdus compactus, Candacia falcifera.*

Cosmopolitan. *Calanus finmarchicus, Ctenocalanus vanus, Gaidius tenuispinus, Scaphocalanus brevicornis, Pleuromamma robusta, Pleuromamma borealis, Heterostylites longicornis, Oithona similis, Oncaea notopus, Oncaea conifera.*

A. With a tendency to be purely arctic.
B. With a tendency to be purely boreal.

AMPHIPODA. The data have been supplied by Dr. K. Stephensen.

Hyperiidea.

The cold water species are:—

Arctic, *Themisto libellula* (Mandt), *T. abyssorum* (Boeck) (mainly); Antarctic (? subantarctic), *Mimonectes setosus* Barnard, *Vibilia edwardsi* Bate, *Cyllopus lucasi* Bate, *Janira macrocephala* Dana, *Hyperoche capucinus* Barnard, ? *Hyperia macronyx* Walker, *Hyperiella dilatata Stebb.*, *Euprimno antartica* Stebb., ? *Brachyscetus antipodes* Bate, (*Hyperoche lutkenoides* Walker, and *H. cryptodactylus* Stebb. uncertain species).

Paralanceola anomala Barnard, and *Hyperiella antarctica* Bovall. are deep sea antarctic species.

Cosmopolitan, *Scina borealis* G. O. Sars, *Themisto gaudichaudi* Guer.

In addition to the 28 deep sea species given in Table I there are a further 25 species which should probably be regarded as deep sea. The number of warm water species would thus be proportionately reduced.

Gammaridea.

The cold water species are:—

Arctic-subarctic, *Cyclocaris guilelius* Chevreux (deep sea), *Pseudolibrotus glacialis* (G. O. Sars), *P. nanseni* (G. O. Sars), *Orchomonella lobata* Chevr. (deep sea), *Apherusa glacialis* (H. J. Hansen), *Eusirus holmi* H. J. Hansen, *Cleonardo microdactylus* K. Steph. (? deep sea,) *Hyperiopsis voringi* G. O. Sars, (deep sea).

EUPHAUSIACEA: the data have been supplied by Prof. W. M. Tattersall.

The cold water species are as follows: —

Antarctic, *Euphausia superba* Dana and *Euphausia crystallorophias* H. & T.; sub-antarctic, *Euphausia frigida* Hansen, *E. vallentini* Stebbing, *E. triacantha* Holt & Tattersall, *E. longirostris* Hansen, *E. hanseni* Zimmer, *Thysanoessa macrura* G. O. Sars, and *T. vicina* Hansen.

Thysanoessa gregaria G. O. Sars is bipolar in sub-arctic and sub-antarctic regions of the north and south Atlantic and north and south Pacific.

The genera *Euphausia* and *Thysanoessa* are cosmopolitan and upper layer genera on the whole. It seems likely that the cold water forms have evolved from the warm water species of the upper layers, as they are more nearly related to upper layer warm water species than to deep sea species.

PTEROPODA. Data taken from Meisenheimer (1905), Tesch (1904), Bonnevie (1913), Massy (1920), and Pruvot-Fol (1924).

Thecosomata. The cold water species are: —

Antarctic-sub-antarctic, *Limacina (Clio) australis* Eydoux and Souleyet; Sub-antarctic, *Cleodora sulcata* (Pfeffer) (See Mackintosh, 1934, p. 86) (*Limacina antarctica* Woodward has not been included since Meisenheimer suggested that its separation from *L. helicina* was not certain).

Bipolar, *Limacina helicina* Phipps.

Large numbers of *L. helicina* from the antarctic were examined by Massy (1920) and no reasons were found for regarding the arctic and antarctic forms as different. *Limacina balea* Möller may be bipolar in sub-arctic and sub-antarctic waters.

There are at least three deep sea species:—

Peraclis diversa Mont., *Limacina helicoides* Jeffreys, and *Clio falcata* Pfeffer.

Gymnosomata. The cold water species are:—

Arctic and sub-arctic, *Clione limacina* Phipps; Antarctic and sub-antarctic, *Clione antarctica* E. A. Smith; Sub-antarctic, *Spongiobranchaea australis* d'Orbigny (See Mackintosh, 1934, p. 86).

Clione limacina has been regarded as bipolar, but Massy (1920) regards the antarctic form *C. antarctica* to "be entitled to specific rather than varietal rank".

Heteropoda. The data have been taken from Tesch (1906). There are no purely cold water species.

TUNICATA: The data have been supplied by Miss A. B. Hastings.

Appendicularia: (supplemented from Lohmann and Bückmann (1926).

The cold water species are as follows:—

Arctic, *Oikopleura vanhöffeni* Lohm. and *Oikopleura chamissonis* Mertens; Arctic boreal, *Oikopleura labradoriensis* Lohm.; Antarctic-subantarctic, *Oikopleura gaussica* Lohm., *O. valdiviae* Lohm., *O. drygalski* Lohm., *O. weddelli* Lohm., *Fritillaria antarctica* Lohm. and *Fritillaria drygalski* Lohm.; Cosmopolitan, *Fritillaria borealis* Lohm., with several forms; Deep Sea, *Fritillaria aberrans* Lohm. *Chunopleura mirogaster* Lohm., and *Bathycordaeus charon* Chun are possibly purely deep sea species (Lohmann, 1931, p. 108).

In his Weddell Sea report Lohmann (1928, p. 71) gives the distribution of certain species as still uncertain: these have been included here with the warm water species.

Lohmann (1905) has shown that the polar species of Oikopleura are the most recently developed. For their origin he favoured Ortmann's hypothesis that they are the remains of a universal warm water population left at the poles when climatic changes set in, and which have since developed their own peculiar species. On the contrary he regarded *Fritillaria borealis* as the relic of the original polar stock which has given rise to warm water species.

Whatever the origin of the Oikopleura species in polar waters it is at any rate certain that there are no bipolar species. The Oikopleuras are essentially inhabitants of the upper layers and are dependant on the nannoplankton for their food supply. It is thus unlikely that any would survive sufficiently long in the deepest layers to have

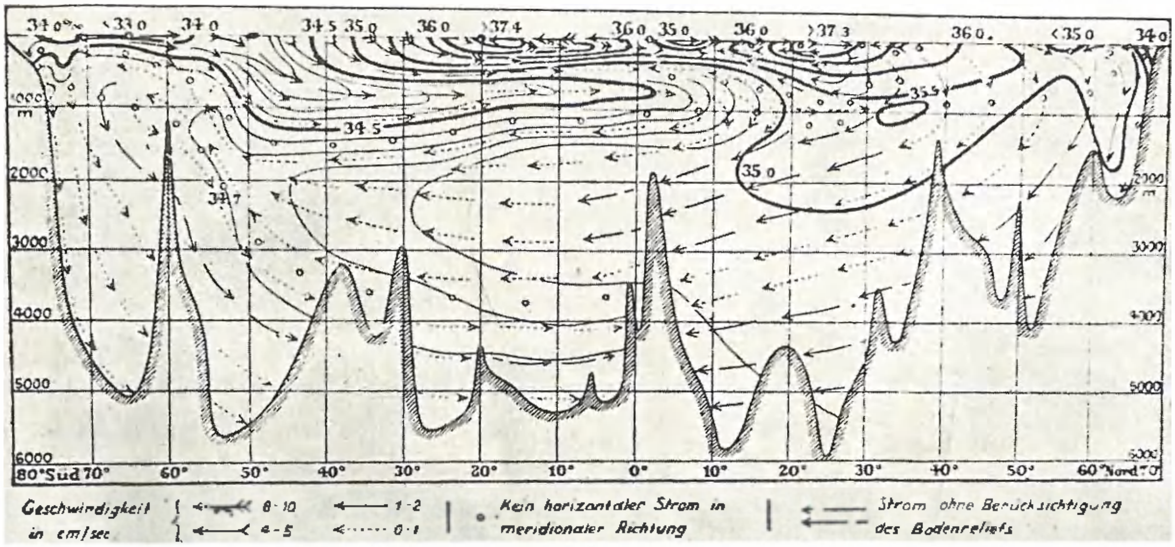

Fig. 2.
Circulation of the meridional component of the water movements in the Atlantic Ocean at 30° W. (after Defant, 1927, p. 365, Fig. 53).

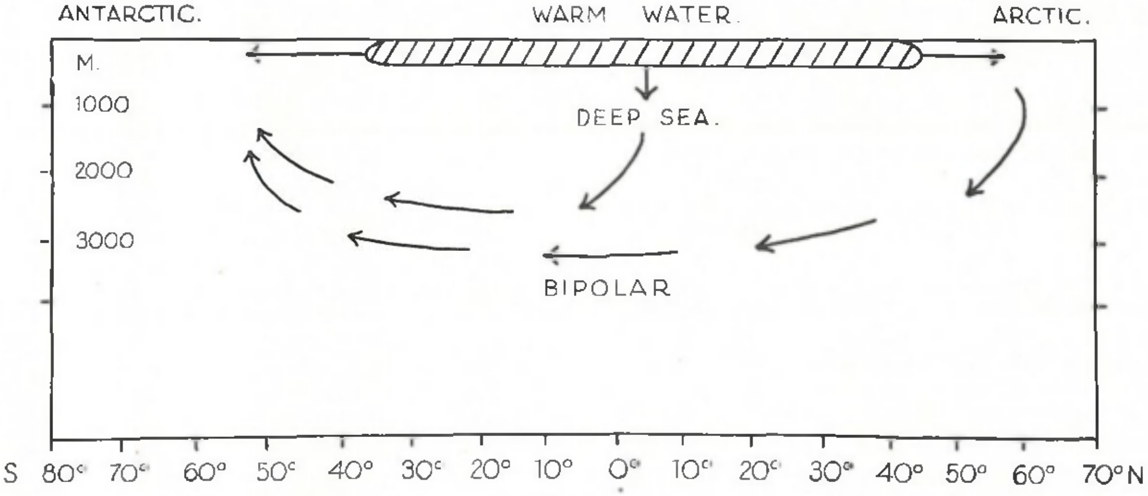

Fig. 3.
Diagram showing how cold water species that have evolved from warm water species in the Northern hemisphere will tend to be carried southwards in deep water to become bipolar-epiplanktonic. Species which have evolved as deep sea species and become adapted to low temperatures may also thus join the Antarctic community. The diagram is based on the circulation of water given in Figure 2.

allowed transport from the north polar regions to the antarctic. Lohmann (1931, p. 45) remarks however on the remarkable similarity between the northern *O. labradoriensis* and the southern species *O. gaussica* and *O. valdiviae* and suggests that they may be regarded as a bipolar group of species in the genus Oikopleura. *O. drygalski* on the other hand is most nearly related to the warm water species *O. albicans*.

Fritillaria borealis may on the other hand be a relic of past ages left at both poles as Lohmann suggested. If this be so it seems strange that they have not given rise to species peculiar to the poles. Another polar species *F. antartica* Lohm., is confined to the Antarctic and has been shown by Lohmann to be very closely related to the warm water species *F. fraudax* Lohm. It seems more likely that *Fritillaria borealis* is a cosmopolitan species, which is known to show many forms, and that the parallel development of forms has occurred in the cold waters of the north and the south.

Doliolidae. There are no purely cold water species except possibly *Doliolina resistibile* (Neumann) in the Antarctic. This species is however regarded by Garstang (1933, p. 213) as a variety of *D. intermedium* Neumann).

Salpidae. There is only one cold water, antarctic-sub-antarctic species *Apsteinia magalhanica* (Apstein); another species *A. racovitzai* (Berc. & Selys-Longchamps) has been described on the basis of a single specimen as slightly different from *A. magalhanica*, but until more specimens are obtained its identity remains doubtful. A form of *Salpa fusiformis* Cuvier also occurs in the Antarctic, viz. *S. fusiformis* form *aspera* (Chamisso).

regarded by some as Arctic. But, while observations made in the eastern Atlantic where the transition zone is wide lead to this conclusion, the distribution on the western side, where the transition from Atlantic to Arctic water is abrupt, seems to indicate that this species may justly be regarded as an Arctic species. The difficulty in demarcating the Arctic zone is clearly shown by an examination of the general oceanic circulation. In the north the main water movement in the deeper layers is southwards; thus representatives of Arctic water are carried in the deeper levels to lower latitudes. In Table I species regarded as purely arctic are those whose distribution on the western side of the north Atlantic indicates that their real home lies in Arctic waters.

In seeking to understand the distribution of species in the cold waters the vertical circulations of the ocean must be considered as well as the horizontal current systems. In Figure 2 is reproduced a diagram showing the type of vertical circulation in the Atlantic ocean (after Defant, 1927). It is evident that in the deeper layers the main body of water is moving in a southerly direction. Thus species evolving outwards into cold water from a warm surface species producing centre will form cold water northern and southern species (Fig. 3). But the ocean circulation is in favour of carrying any northern species that can withstand and reproduce under deep water conditions southwards to the Antarctic, so producing bipolar species. Thus it is likely that any species in the cold northern waters, whether a relic from past ages or one more recently evolved, may become bipolar, but not so antarctic species. In this way the number of pure cold water species is further reduced in the north. In this respect it is interesting that two of the groups with no bipolar species, Tunicata and Ctenophora, are essentially composed of surface living species.

Cold water species may also be evolved as deep sea species from the warm surface layers. Again taking the oceanic circulation into consideration the odds are in favour of polar species evolving from deep water species to the south rather than to the north for in the south existing species will be continually carried into antarctic waters. An examination of the data on Copepods kindly supplied by Mr. Farran rather bears this out. If the genera be divided into surface genera, (in which less than 50 $^{0}/_{0}$ of the species in a genus can be regarded as deep sea species), and deep sea genera (in which 50 $^{0}/_{0}$ or over of the species in a genus can be regarded as deep sea species) we find the following result.

	No.	Total No. of species	No. of Arctic and boreal spp.	No. of Antarctic and Sub-ant. spp.	No. of Bipolar spp.
Surface genera	76	525	13	19	5
Deep Sea genera	36	228	3	18	1

The great majority of cold water species belonging to "deep-sea" genera are found in the antarctic. Further support is also given by the fact that there are also relatively more bipolar species found among "surface" than "deep-sea" genera.

The actual number of bipolar epiplanktonic species is small compared with the total number of species of plankton animals. It seems probable that their bipolarity can be sufficiently explained by the conditions of the vertical circulation of the ocean without the necessity for regarding them as hypothetical relics of a past homogeneous fauna.

It is worthy of mention that the majority of epiplanktonic bipolar species occur in sub-arctic waters and are probably able to withstand a considerable range of temperature.

Space will not allow further discussion on problems raised by an examination of Table I. It is only necessary to call attention to the fact that our knowledge of the fauna of the Pacific and Indian oceans falls far short of that of the Atlantic ocean. The differences and phylogenetic relations between those species which are peculiar to the Atlantic and those peculiar to the Pacific also appear worthy of study. And certain groups of soft-bodied animals, such as the Ctenophores, Siphonophores, and Gymnosomatous Pteropods, which are difficult to preserve need special attention in the future.

The actual contents of Table I appear slight in proportion to the labour involved in its production, but it is surely a noteworthy tribute to the labours of workers in the past that it has been possible to produce such a table at all.

As regards future work Steuer (1933) has suggested that in the planning for further expeditions attention should especially be paid to the distribution zones in coastal regions and also to the Pacific ocean. There seems also to be some essential difference between the fauna of the western and eastern halves of the Atlantic worthy of closer study; and the examination of the deep-water faunas of the different ocean basins needs special attention.

For the study of geographical distribution, whether over large or over small areas, attention must also be drawn to the valuable results likely to be obtained by the use of the continuous plankton recorder invented by Hardy (1926).

It has been remarked that the distribution of the coastal forms needs further study. This leads us to examine the results of the plankton collections by the International Council. In no part of the world have the coastal waters received greater attention than in the area which comes under the *aegis* of this Council. The whole area bordering our coasts was examined for a period of years from 1902 to 1908. As a result it was possible to publish the Plankton Resumés in which detailed pictures of the distribution of most of our species have been reproduced. In the final summary of results Ostenfeld (1931) subdivided the plankton populations of the area covered into a number of convenient groups according to their distribution. While it is possible to pick out species that are truly representative of the different divisions there is naturally considerable overlapping among the majority of species. Examination of the distribution charts in the Plankton Resumés shows that there is a complete range of animals from those that are purely brackish water species to purely oceanic species. This range may be exemplified as follows (Fig. 4): —

Brackish water	e. g. *Eurytemora affinis*
Littoral and brackish water	e. g. *Acartia bifilosa*
Neritic, low salinity	e. g. *Oithona nana*
Neritic,	e. g. *Centropages hamatus*
Atlantic oceanic, existing all the year round under neritic conditions.	e. g. *Centropages typicus*
Atlantic oceanic, existing only part of the year in neritic regions,	e. g. *Aglantha digitalis*

These types also show the major geographical distributions outlined above, and overlap in range is likewise shown here. But whereas many species occur over rather a wide area, the boundaries for certain species coincide with the limits for certain water masses.

At the beginning of the International Council programme it was emphasized that "The study of the floating organisms had particular worth for the solution of hydrographical problems". While it has always been fully realised that it should be eventually possible to make use of plankton organisms as an aid to the study of water movements, the International survey did not appear to come fully up to expectation in this respect. There are various reasons to account for this. The identification of some species was not always certain. The collections were not always sufficiently regularly taken. Large nets were not used and therefore the larger animals were not caught in sufficient numbers. The results for each group were given to specialists to work up and the plankton has perhaps not been sufficiently studied as a whole. Examination of the report shows that only one or two species in any group are likely to be suitable as indicators; and it is often the *association* of these different species that gives the necessary indication. Owing to their very widespread distribution the majority of species are of little value in this respect unless examined in great detail. An indicator must be a *practical* indicator.

We owe the first idea of the use of plankton indicators chiefly to the work of Cleve and Aurivillius (1898). Gran (1902, pp. 98—106) showed that such sweeping generalisations as Cleve made could not hold good, because the composition of the plankton was modified as the conditions in the moving water mass altered, and because it changed with time of year. He also insisted that full use of plankton organisms as indicators could not be made until their life histories and habits were better known. In this latter respect Kramp (1927 and 1930) has ably shown how a thorough knowledge of the biology of hydroids and medusae may be of practical importance in the study of water movements.

There is no doubt that with our increasing knowledge much more use of plankton animals as indicators under certain conditions could be made at the present time. It is therefore worth examining the conclusions and observations of previous workers. Gran (1902, p. 104) has said "the characteristic forms of the regions can be used as indicators, in so far as they are dominant; there will however always be fairly wide boundary regions, where the characteristic forms of both current regions are mixed". "Species may be found outside their regions. When they occur as secondary constituents of the plankton together with indigenous species we can conclude that water from the distribution region of the visitors must occur as a mixture."

The results of the plankton collections of the Belgica expedition to the Greenland Sea were critically examined by Damas and Koefoed (1907) from the point of view of the use of plankton animals as indicators. They conclude that "the use of pelagic organisms as indicators of currents is a local science, based on the knowledge of the special habits of each form, in the region considered". "The same species can in fact be an excellent indicator for the polar current in the north and for the Atlantic current in the south".

They give two examples of circumstances under which the plankton can be employed with certainty as an indicator of currents.

1. An organism which, being totally absent in an ocean basin appears there suddenly and periodically. In the Greenland Sea this case is realised by the species, of southern origin, which the Gulf Stream brings from temperate and even tropical regions.

2. The occurrence of meroplanktonic organisms off shore. *Cyanea capillata* and the medusae born on the continental plateau of the Norwegian coast are good examples. They can be regarded as certain indicators for coastal water; this was also maintained by Gran (1902, p. 105).

Gran (1902, p. 106) has also pointed out that while plankton organisms may be reliable as indicators of surface waters, it is more difficult to make use of them for studying the water movements in the deeper layers owing to their habits of vertical migration.

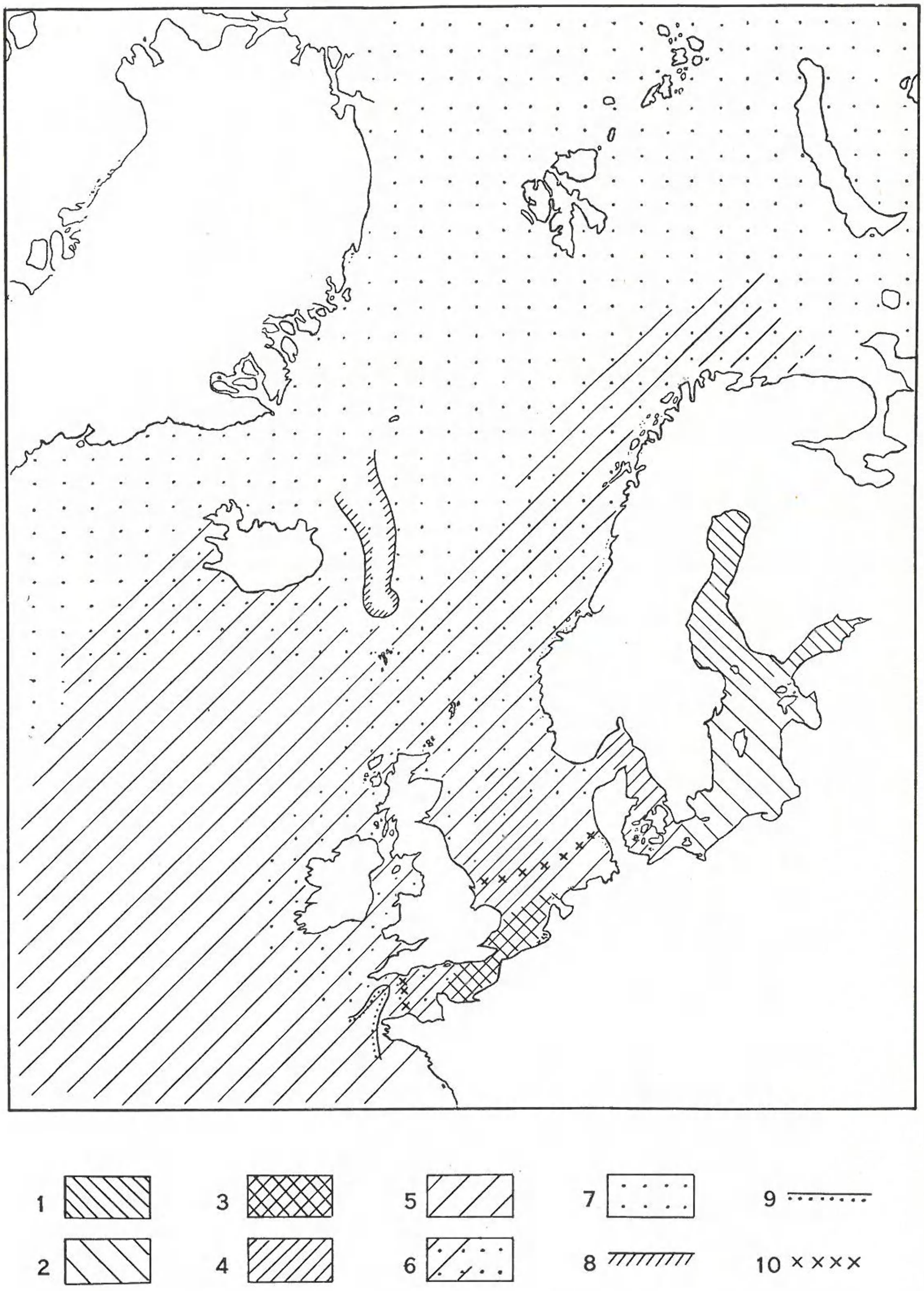

Fig. 4. (as to legend: see the following page).

Plankton animals must therefore be used with discrimination if they are to be employed as indicators, and they must be taken in their context. Thus we must be on our guard at times against drawing conclusions from the occurrence of a single indicator, owing to the possibility that an organism having been brought into the region some time previously finds conditions suitable for the establishment of a local race. But the appearance of a number of indicators together, with different habits, must be taken as an indication of influx of water (See also Kramp, 1927, p. 231).

Furthermore because doubt has been cast upon the use of an animal as an indicator in one locality it does not necessarily imply that the same animal may not be useful elsewhere.

Thus, as Gran (1902, p. 105) has pointed out, *Calanus hyperboreus* must be used with caution an an indicator of Arctic water in Norwegian waters, since it is indigenous in some Norwegian fjords, yet in other regions it may well be of value. Similarly *Clione limacina*, a boreal-arctic species, cannot be used *in name* as an indicator of Arctic water because it lives successfully in temperate Atlantic waters also. Yet in regions where there is no possibility of Arctic influence such as the mouth of the English Channel the species may be used as an indicator of Atlantic water. It is extremely likely however that with a thorough knowledge of its growth and size at maturity in Arctic and Atlantic waters it should be possible to discriminate between Clione of Arctic regions and those from Atlantic waters. This is a type of racial investigation so exemplified by the work of the late Prof. Schmidt, and by the studies by Steuer on copepods.

Fig. 4.

Distribution regions of coastal and oceanic plankton animals in north eastern Atlantic and adjacent waters.

1. Brackish water, *Eurytemora affinis*; region of greatest abundance in August and November (after Scott, plate XVIII).
2. Littoral and brackish water, *Acartia bifilosa*; region of greatest abundance (after Scott, 1911, Pl. XXII).
3. Neritic — low salinity, *Oithona nana*; region of greatest abundance (after Farran, 1911, Pl. XV.).
4. Neritic, *Centropages hamatus*; region of greatest abundance (after Scott, 1911, Pl. XVIII.).
5. Atlantic species, *Acartia clausi*, area of distribution (after Jespersen, 1934, p. 123.).
6. Arctic — boreal species, *Calanus finmarchicus*, showing southerly limit of abundant occurrence (after Farran, 1911, p. 83).
7. Arctic species e. g. *Limacina helicina*.
8. Area in which the Arctic species *Calanus hyperboreus* was recorded as abundant; this is in the East Iceland Polar Current (after Farran, 1911, p. 89 and Pl. XI, and Damas, 1905, Pl. I.).
9. Limit of area within which the warm water species *Euchaeta hebes* occurred on at least 20 % of the occasions on which observations were made (after Farran, 1911, Pl. XIV.).
10. Southern limit in North Sea and Eastern limit in Channel of Arctic-boreal species *Clione limacina* (after Paulsen, 1910, p. 53).

The occurrence of immigrants into an endemic Atlantic plankton community has been dealt with in detail in the Gulf of Maine by Bigelow (1926, pp. 51—69). In Figure 5 is reproduced a chart from his report showing the chief routes followed by planktonic immigrants entering the Gulf at different levels. This chart shows the course of circulation of the water masses as clearly as do hydrographic data. Bigelow says for instance that "The lines of dispersal followed, respectively, by *Sagitta serratodentata*, Eukrohnia, and *S. maxima* within the gulf correspond closely with the dominant drift of water at as many levels — that is, surface, mid, and deepest — as made evident by the physical data afforded by temperature and salinity and drift bottles" (1926, p. 64).

Bigelow stresses the value of knowing to what extent the immigrants are capable of living and reproducing under the new conditions (see Table II). He says (1927, p. 923) "Clearest evidence of the drift within the Gulf is afforded, of course, by such species as are comparatively short lived there and can not reproduce in its low (or high) temperature". Such knowledge would be of great value in judging how recent an influx had been and the age of the water masses.

It is especially valuable to watch for any correlations between the presence or absence of certain plankton animals with that of fish and larger swimming animals. Frost, Lindsay and Thompson (1934) have for instance shown a correlation between the abundance of Squid in Newfoundland waters and that *of Sagitta serratodentata*. This is of clear value for the cod fisheries. In the North Sea Meek (1928) showed that the two species of Sagitta, *S. elegans* and *S. setosa*, were apparently representative of different water masses. The study of the Sagitta populations has been carried a stage further at Plymouth, (Russell, 1935 a), and it has been found that *S. elegans* is an indicator of Atlantic water and *S. setosa* of Channel water. In association with *S. elegans* we find the typical Atlantic community consisting of Aglantha, Cosmetira, Stephanomia, Clione, Meganyctiphanes, and Luidia larvae. These or closely allied species are the indicators that Künne (1934) has given for the south west Dogger Bank swirl. It is thus possible that the two species of Sagitta may prove of great importance as aids to the study of the distribution and movements of water masses in the North Sea. In the Channel the two Sagitta populations appear to sway to and fro past Plymouth according to the strength of flow of Atlantic water into the North Sea from the North. This is in agreement with Carruthers' theory that the Straits of Dover act in buffer relationship between the waters of the North Sea and the

Table II.

List of Plankton Animal Indicators.

Arctic water.

1. A high temperature is fatal and they soon perish. (1)[1]

Ctenophore	Mertensia ovum.	Gulf of Maine (1)
Medusae	Ptychogena lactea	,, ,, ,, (1)
	Sarsia princeps	Labrador Current (20)
Pteropod	Limacina helicina	Gulf of Maine (1) Barents Sea and North of Iceland (3)
Tunicate	Oikopleura vanhöffeni	Gulf of Maine (1) Newfoundland (2)

2. Able to survive for a considerable period and even reproduce to some extent. (1)

Copepods	Calanus hyperboreus	East Iceland Polar Current (4, 5, 18) Gulf of Maine (1)
	Metridia longa	East Iceland Polar Current (4) Gulf of Maine (1)
Pteropod	Clione limacina	,, ,, ,, (1)

Mixed arctic and atlantic water.

Species unable to breed in high (or low) temperatures (1)

1. Surface layers.

Chaetognath	Sagitta serratodentata	Gulf of Maine (1, 19)
Euphausian	Nematoscelis megalops	,, ,, ,, (1)

2. Intermediate layers (say below 50 m.)

Chaetognath	Eukrohnia hamata	,, ,, ,, (1, 19)
Siphonophore	Diphyes arctica	,, ,, ,, (1)

3. Deepest layers (150 m. or deeper)

Chaetognath	Sagitta maxima	,, ,, ,, (1, 19)

Entering north western North Sea

Euphausian	Thysanoessa longicaudata	North Sea (6)

In Newfoundland waters (2) a relation has been shown between the abundance of *Sagitta serratodentata* and that of the squid *Illex illecebrosus* during the years studied, 1931, 1932 and 1933.

Atlantic water.

Water entering north western North Sea round north coast of Scotland.

Euphausians	Meganyctyphanes norvegica	North Sea (6)
	Thysanoessa inermis (in winter only)	,, ,, (6)

In regions away from influence of Arctic water.

Medusae	Aglantha digitalis var. rosea	S. W. Dogger swirl (7) Channel (8)
	Cosmetira megalota	S. W. Dogger swirl (7)
	Cosmetira pilosella (in spring and summer only)	Channel (8)
Siphonophore	Agalma elegans	S. W. Dogger swirl (7)
	Stephanomia bijuga	Channel (8)
Chaetognath	Sagitta elegans (should probably also prove of value in southern N. Sea)	Channel (8)
Euphausians	Meganyctiphanes norvegica	Channel (8)
	Thysanoessa inermis	Channel (8)
	Nyctiphanes couchi	S. W. Dogger swirl (7)
Pteropod	Clione limacina	Channel (8) S. W. Dogger swirl (7)
Echinoderm	Luidia sarsi young	Channel (8) S. W. Dogger swirl (7)
Tunicate	Oikopleura labradoriensis	S. W. Dogger swirl (7) Newfoundland (typical of mixed temperate water) (2)

---

[1] Numbers in brackets are those of the references at the foot of the table.

Warm atlantic water.

Tunicates	Salpa fusiformis	North Sea (9, 10, 11), Channel (8), Gulf of Maine (1)
	Salpa democratica	Ditto
	Cyclosalpa bakeri	North Sea
	Doliolum nationalis	North Sea, Channel (8)
	Doliolum gegenbauri	North Sea (12), Channel (8)

N.B. There are no boreal or arctic salps or doliolids; the presence of any species in these groups may therefore be regarded as an indication of water from warmer latitudes.

Medusae	Liriope exigua	Channel (8)
Siphonophore	Muggiaea atlantica	Channel (13)
	Muggiaea kochi	Channel (8)
	Physophora borealis	North Sea and Norwegian coast (17, 18)
	Cupulita sarsi	„ „ „ „ „ (17, 18)
Actinia	Arachnactis larvae	„ „ „ „ „ (17)
Cirripedia	Lepas fascicularis	„ „ „ „ „ (17)
Copepoda	Anomalocera patersoni	Norwegian Sea (18)

Coastal water.

Medusae	Cyanea capillata	Norwegian Ocean (14, 17)
	Cyanea lamarcki	North Sea (17)
	Sarsia princeps	Spitzbergen (17)
	Sarsia flammea	„
	Catablema eurystoma	„
	Bougainvillea superciliaris	„

Any meroplanktonic species with a fixed bottom stage in its life history is indicative of coastal water, and its distance off shore is dependant on its length of life in the planktonic stage (14, 18).

Chaetognath	Sagitta setosa	Channel (8) (probably also North Sea)

The coastal water of the Channel (8) and southern North Sea (7) is also distinguishable from Atlantic water by its poverty in animal plankton.

Certain species are given by Kramp (15) as likely to be carried into the southern North Sea *via* the Channel.

Medusae	Turritopsis nutricula, Amphinema dinema, Slabberia halterata, Gossea corynetes, Octorchis gegenbauri, Cosmetira pilosella.
Euphausian	Nyctiphanes couchi.

Of these Cosmetira and perhaps Nyctiphanes will have been carried in Atlantic water.

Eastern and Southern Kattegat.

Kramp (16) gives as visitors introduced from the north:—

Medusae	Bougainvillea britannica, Laodicea undulata, Staurophora mertensii, Melicertum octocostatum, Mitrocoma polydiademata, and Cosmetira pilosella.

References.

1, Bigelow (1926); 2, Frost, Lindsay and Thompson (1934); 3, Paulsen (1910); 4, Farran (1911); 5. Damas (1905); 6, Kramp (1913); 7, Künne (1934); 8, Russell (1935); 9, Schmidt (1909); 10, Bowman (1923); 11, Apstein (1911); 12, Lucas (1933); 13, Gough (1905); 14, Damas and Koefoed (1907); 15, Kramp (1930); 16, Kramp (1927); 17, Damas (1909); 18, Gran (1902); 19, Huntsman (1919); 20, Kramp (1926).

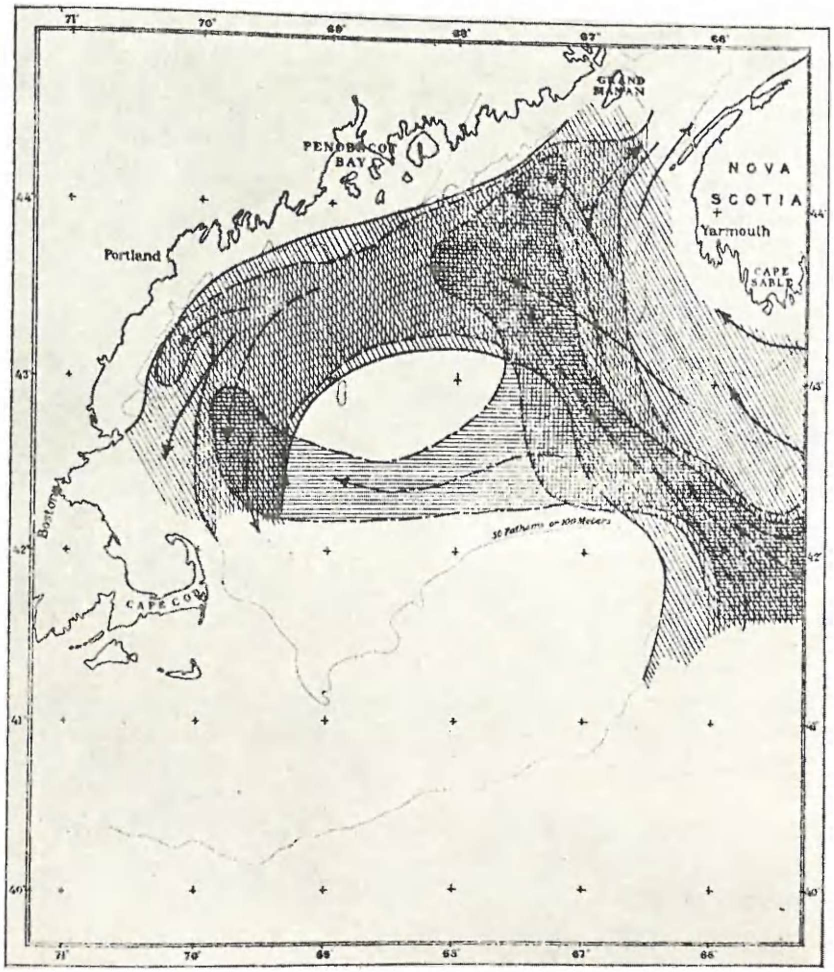

Fig. 5.
Chief routes followed by planktonic immigrants entering the Gulf of Maine at different levels. ▨, immigrants at surface; ||||, immigrants at intermediate levels; ≡, immigrants at the deepest level. (After Bigelow 1926, p. 65, Fig. 33).

Channel. Thus a correlation appears to be shown between the occurrence of *S. setosa* off Plymouth and the presence of concentrations of Rhizosolenia in the southern North Sea studied by Savage and Hardy (1935) (Russell, 1935). When the Atlantic flow from the North is strong *Rhizosolenia styliformis* and phosphate rich water is carried into the southern North Sea and *S. elegans* is pushed westward in the Channel so that *S. setosa* appears off Plymouth.

From the knowledge now available I have drawn up in Table II a list of certain plankton animals and the water masses of which they can be regarded as indicators in certain regions. In this list I have included only those animals that are sufficiently large and easily identified to be practical indicators. At this stage the list is tentative but it should be the aim of future research to produce a similar table in greater detail.

Especial attention should be paid to a study of the life histories of some of the larger arctic-boreal species such as *Sagitta elegans* and *Clione limacina.* It is characteristic of species with this wide type of distribution that they show quite considerable differences in the size to which they grow and at which they mature both from place to place and season to season. Our knowledge of the life histories of such species should then be brought together and comparisons made between different water masses. It will probably be possible then to distinguish between different types of growth and maturity for the different waters. A species such as *Calanus finmarchicus* is also well known to show similar characteristic variations;

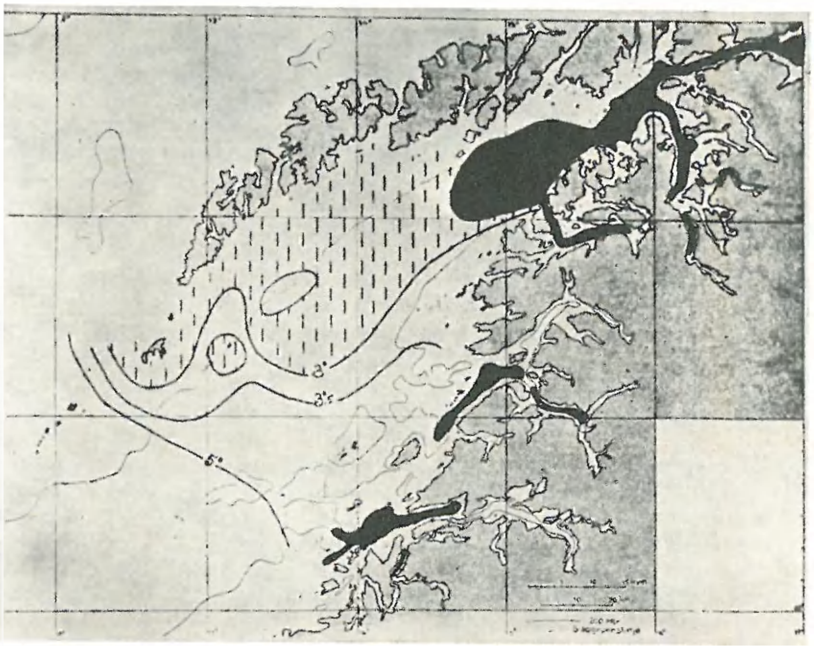

Fig. 6.
The Lofoten area with the surface temperatures for March to April 1922. The darkened areas show the centres where rich hauls have been made during winter time for both species investigated, and to which the spawning of *Calanus hyperboreus* is limited. The area shaded is the cold area into which most numbers of *Calanus hyperboreus*, females and larval stages, are carried after spawning time,and where the main spawning of *Calanus finmarchicus* takes place (after Sømme, 1934, p. 9. Fig. 1).

but if we are to fix upon indicators they must be *practical* indicators and therefore species that do not require microscopic examination for identification or measurement. Owing to the use of small silk nets in the International Investigations the larger species were not caught in sufficient numbers to show their utility.

From the point of view of fishery investigations it must be realised that plankton indicators are of extreme importance. If correlations can be shown to hold consistently for a number of years it should be possible to predict certain conditions in the fisheries. Large plankton indicators can be seen at a glance and the delay necessary for the detailed analysis of water samples is avoided.

It would seem that these larger plankton animals should prove of much greater value as aids to hydrography than the nannoplankton organisms. In charting the distribution of water masses it is the boundaries along which the masses mix that we wish to have demarcated. With their rapid rate of reproduction nannoplankton organisms will quickly increase in numbers in water which has only been seeded with individuals carried either in wind borne surface layers or in small eddies at intermediate depths. A false impression would thus be produced; whereas by the change in numbers of the larger animals it should be possible to gain some idea of the quantities of water of different origin that have been intermingled. But as has been stressed by Gran and Kramp it is first essential that the life-histories and habits of the animals should be thoroughly known.

The different stages in the life histories of many of the commoner plankton animals of north European waters have now been described from the morphological point of view. For the life histories of the copepods we are indebted especially to such workers as Oberg, Grobben and With, while Lebour has gone a long way towards describing many of the planktonic larval stages of bottom animals. But we still know very little of the habits and biology of the different developmental stages in the sea. It is a remarkable fact that the actual yearly sequence in the succession of broods of our commonest plankton animal, *Calanus finmarchicus*, was only demonstrated in detail for the first time in 1933 by Nicholls at Millport. The early work of Damas and Koefoed on the copepods in northern waters has now been carried considerably further by the work of Ruud, Jespersen, and Sømme. The life story of *Calanus hyperboreus* in Norwegian waters has been made especially clear by Sømme. The length of life and seasonal occurrence of many Hydromedusae have been worked out by Kramp in Danish waters. The growth and breeding of *Sagitta elegans* and *Sagitta setosa* are now known at Plymouth (Russell, 1932—33). These are a few examples (see Fig. 9); but still the number of species that have received such detailed attention remains surprisingly few. This is an aspect of zooplankton research that needs to be especially developed, for advance in other directions is still likely to be prevented by lack of this necessary knowledge. An understanding of the biology of individual species may throw quite unexpected light on obscure problems. For instance Sømme (1934) has shown how the differences between the horizontal distribution of *Calanus finmarchicus* and *Calanus hyperboreus* in offshore Norwegian waters are the results of slightly different habits of spawning and in the time of their vertical migration after the winter months. After migrating from the deep layers the species are carried away in the surface waters "from the winter localities out over the coastal banks" (Fig. 6).

But if the biology of plankton animals is to be fully understood, it is necessary also to know their relations with their environment. We must know their food supply, their enemies, and the nature of the balance that exists in the community in which they live; and also their relations with the physical and chemical factors of their environment. It is only by gaining this knowledge that we can study the question of production of life in the sea, which may be intimately bound up in one of the greatest problems of marine biology, namely the causes of the fluctuations in the populations of our food fishes. When we consider the relations amongst the animals themselves we find that we have at our command a considerable knowledge that should be put to greater use in the future. Largely through the researches of Lebour (1918—1923) we have a very detailed knowledge of the food of most of our commoner plankton animals and young fish. The work especially of Bullen (1908 and 1912), Jespersen (1928), Savage (1931), and Hardy (1924) has shown to what extent the different plankton animals are preyed upon by fishes. But the interactions of the plankton animals upon one another have been little explored. Lohmann (1908) by his great work in Kiel Bay gave a picture of the total plankton production throughout a year under the conditions there existing. Since then the work has not been repeated in other regions. This is perhaps largely because we have been awaiting the development of method. It is now possible to measure plant production much more rapidly by chemical methods, and possibly we shall soon be able to say the same for the measurement of total zooplankton (see Cooper, 1934). But the necessity for a study of the interactions between species still remains, and this was not dealt with by Lohmann because life histories were insufficiently known. We have also been held back by the lack of methods for comparing the numbers of plants and animals from known volumes of water. There has been great want of uniformity in the types of nets used in the past. Hensen, when he introduced quantitative methods into plankton research, devised a net on lines which he calculated would give greatest efficiency. In his examination of the fishing capacities of many different types of plankton nets Künne (1929 and 1933) has shown that Hensen's type of net is still the most efficient. With nets of coarse mesh for the capture of the larger plankton animals the filtration errors are likely to be small if the plankton is not very abundant. But with the finest silk required to retain the small copepod nauplii the errors due to filtration will be large. The filtration coefficient of the net varies widely according to the amount of plankton present and may be anything up to as high as 6 or over (Kokubo and Tamara, 1931).

We have therefore always hesitated to regard catches with fine meshed plankton nets as worthy of exact treatment. But recently a net has been designed by Harvey (1934) which gives an actual measure of the volume of water that has passed through the net. The meter can be used with silk of any required mesh, and with simultaneous hauls it should be possible to use it for the calibration of large coarse meshed nets. As a result of the introduction of this net it is now possible to examine the relations between the phytoplankton crop *retained by the net* and the animals grazing upon it. But the work can be carried a stage further. The effects produced by the ravages of predatory plankton animals on the plant feeding population should be observed. Such animals as medusae, ctenophores, and chaetognaths, are notably voracious, and unusual abundance of any of these will lead to a considerable decrease in the food available for post-larval fishes as well as to the destruction of the fish themselves. (Russell, 1935 b.). The balance of life would be soon upset by a sudden increase in the numbers of these predators and the increasing demand for food as they grew in size.

As Hardy (1924, p. 33) has said "It is only by having some concrete representation of the normal marine community that one can attempt to predict the effect which an abnormal increase of one or other particular form — — — may have in the balance of the whole". He produced an instructive diagram reproduced here (Fig. 7) which gives a good illustration of the lines on which this aspect of research should develop.

When we see a sample of plankton caught from a given body of water at a given time we must realise that this does not represent a static condition. We are looking at a cross section at one moment in one place of a continuous phenomenon moving both in time and in space. The sample is the result of past history and possesses the potentiality for future history. It will consist of a population of producer plants, of plant consumers,

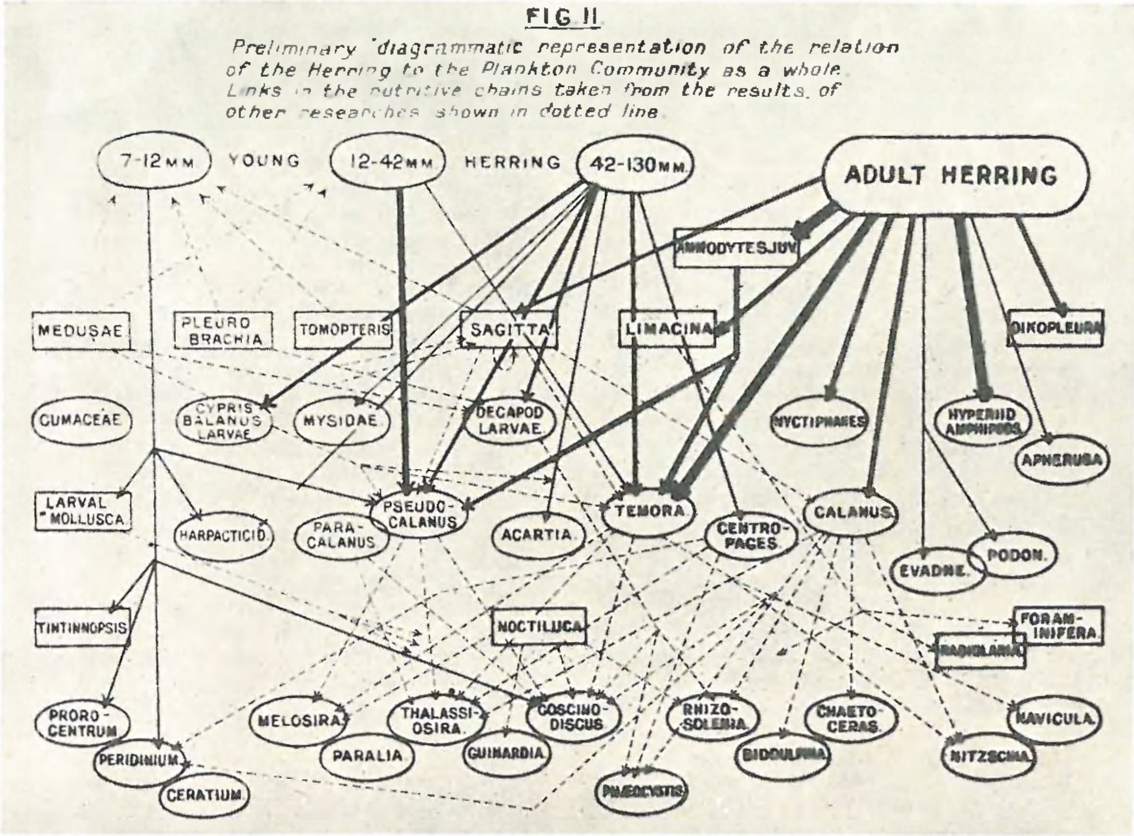

Fig. 7.

Preliminary representation of the relation of the herring to the plankton community as a whole (after Hardy, 1924, Fig. 11).

and of predatory carnivores. The population will be made up of the balance of plants composed of the original stock plus the sum of the increase by reproduction and the decrease by death and consumption; and similarly the balance of consumers resulting from their interactions with the carnivores. Bigelow (1931, p. 131) has rightly pointed out that "As yet we know little of the interrelationships of different species or groups of animals in the sea beyond the obvious fact that some prey on others, but we may be certain" he says "that in many cases interrelationships of less obvious sorts are vital links in animal economy".

But although we know something of the type of food devoured by most plankton animals, it is difficult to visualise the course of events between successive samples because little is known about the actual *food requirements* of the animals. The theory of Pütter that plankton animals must draw a large proportion of their food supply from dissolved organic substances in the water has recently been critically reviewed by Krogh (1931). He concludes that "there is no convincing evidence" that dissolved substances are taken up in significant amounts. Indeed it is likely that all metazoan plankton animals depend mainly for their food supply on particulate living or detrital matter and on colloidal material (see Gellis and Clarke, 1935). Recent observations by Marshall, Orr, and Nicholls (1935) on the respiration of *Calanus finmarchicus* have confirmed the earlier observation by Ostenfeld and Knudsen (1913, p. 424) on *Calanus hyperboreus* which indicated that the figures put forward by Pütter were too high. Pütter estimated that in general Calanus required as food 39 $^0/_0$ of its body weight daily in summer. Marshall, Nicholls and Orr found that for stage V Calanus this figure lay between 6.2 and 7.6 $^0/_0$ in summer. In a recent survey of the phytoplankton and zooplankton collected with Harvey's measuring net at Plymouth it was concluded that the summer zooplankton per cubic metre required daily 120,000 diatoms of average size. The daily production of this quantity of vegetation could reasonably be expected. It is a quarter of the average diatom population caught in the measuring net during this period, a net which undoubtedly lets many very small plant organisms pass through it. This is in agreement with Lohmann's conclusions for Kiel Bay that during the spring and summer months the producer plankton was in excess. The problem of the food requirements of plankton animals is open to attack in two ways. Direct observation may be made in the laboratory on the amount and type of organisms that any species will eat. Work of this nature has already been started at Woods Hole by Clarke and Gellis (1935) and also in Professor A. C. Hardy's laboratory at Hull. Such work indeed as the notable research on the rearing of planktonic crustacean and molluscan larvae by Lebour (1924—34) and polychaete larvae by Wilson (1928—33) at Plymouth was originally made possible by the work by Allen and Nelson (1910) on the culture of marine diatoms, which are now used so largely as food in rearing experiments. On the other hand observations may be made on the rate of respiration under controlled conditions in the laboratory. In order that this second method can prove applicable to conditions in the sea it will be necessary to know the weights and chemical composition of the different plankton organisms. Such work is already started and was foreshadowed many years ago by Brandt (1898). Observations on the weight and chemical composition of a number of plankton crustacea have already been made, notably by Orr, Wimpenny, and Klem (1929). The vitamin content of plankton oils is also being investigated (Drummond and Gunther, 1934). Studies on the weights of copepods by Bogorov (1932—34) see the inauguration of an extensive programme on the part of Russian biologists to assess the total quantity of life in the sea at any time from quantitative counts on the basis of a knowledge of the weights and composition of the different species. At first sight it would appear that the task of weighing and analysing all the plankton animals is likely to be excessive. Indeed it is not so great as it appears, the number of species are limited and once the necessary data have been obtained for any one species the results are final and need but to be tabulated for future reference. These results could no doubt be further simplified by classifying the species into size categories somewhat after the style of Hentschel's (1934) recent suggestion. Admittedly the work is not exciting to the zoologist. But the various attempts to obtain the necessary information such as the calculation of displacement by volume of models by Lohmann (1908), and the recent suggestions by Gunther (1934) and Hentschel (1934) emphasize the need for agreement on some form of standard data.

It will be suitable at this stage to draw attention to the need for more experimental work on the physiology of plankton animals. Such knowledge is most necessary to explain some of the types of behaviour that we now know to be shown by animals in the sea. Perhaps in no way does the plankton animal give indications of changes in physiological state better than in its habits of changing vertical distribution. The migration towards the surface at night is our first indication of direct reaction to some external or internal stimulus. We now know that not only are there these nightly wanderings, but that the animal also exhibits changes throughout its life history according to its age. At times also the animals become apparently irresponsive to external changes; at different times of year we find the same species behaving in a different manner, pointing to physiological differences between different broods. The external factors affecting the behaviour of the animals as shown by vertical distribution, namely salinity, temperature, oxygen content, and hydrogen ion concentration have been investigated in the past. It is only recently, however, largely through the pioneer work of Poole and Atkins, that we have obtained the means of determining the variation in intensity and composition of that most important factor, light. In the vertical distribution of the same species in regions many latitudes apart there is no doubt that the main controlling factor is that of temperature. If an animal is adapted to live within a certain range of temperatures the lethal effects of temperatures above this range and the temperatures limiting successful reproduction must naturally overweigh the possible disadvantages that may arise owing to abnormal light conditions. But the changes shown from day to day and season to season in any one place are undoubtedly manifestations of physiological change which affects the animal in its response to light conditions. Until the post war period our knowledge of the vertical distribution of plankton animals was largely confined to the gross differences shown by the results of collecting from widely spaced depths in ocean waters, and the conditions in coastal waters had not been systematically studied. Yet the general facts of daily and seasonal migrations were fully recognised. In recent years the study of this problem has been carried out on a finer scale in shallow waters (Russell 1925—1934), and similar work in deep ocean waters is now being done at Woods Hole (Leavitt, 1935). As a result of the accumulated knowledge and ideas of past workers and of my own researches at Plymouth it became possible to draw hypothetical diagrams showing the distribution to be expected at any time of day of animals requiring optimum light intensity conditions and migrating under the stimulus of light (Russell, 1927). It can be realized that by varying the scales of length of day, strength of light, depth of optimum, transparency of the water, and swimming speeds of the animals any number of such diagrams can be drawn to fit the different kinds of movements. Support in favour of this theory has come from field work. The behaviour of female *Calanus finmarchicus* as shown by Nicholls (1933) fits the hypothetical diagram to a remarkable degree. The study is now being carried further by Clarke (1933 and 1934 a) at Woods Hole with simultaneous observations of distribution and light conditions (Fig. 8.).

But it is no longer agreement with theory that

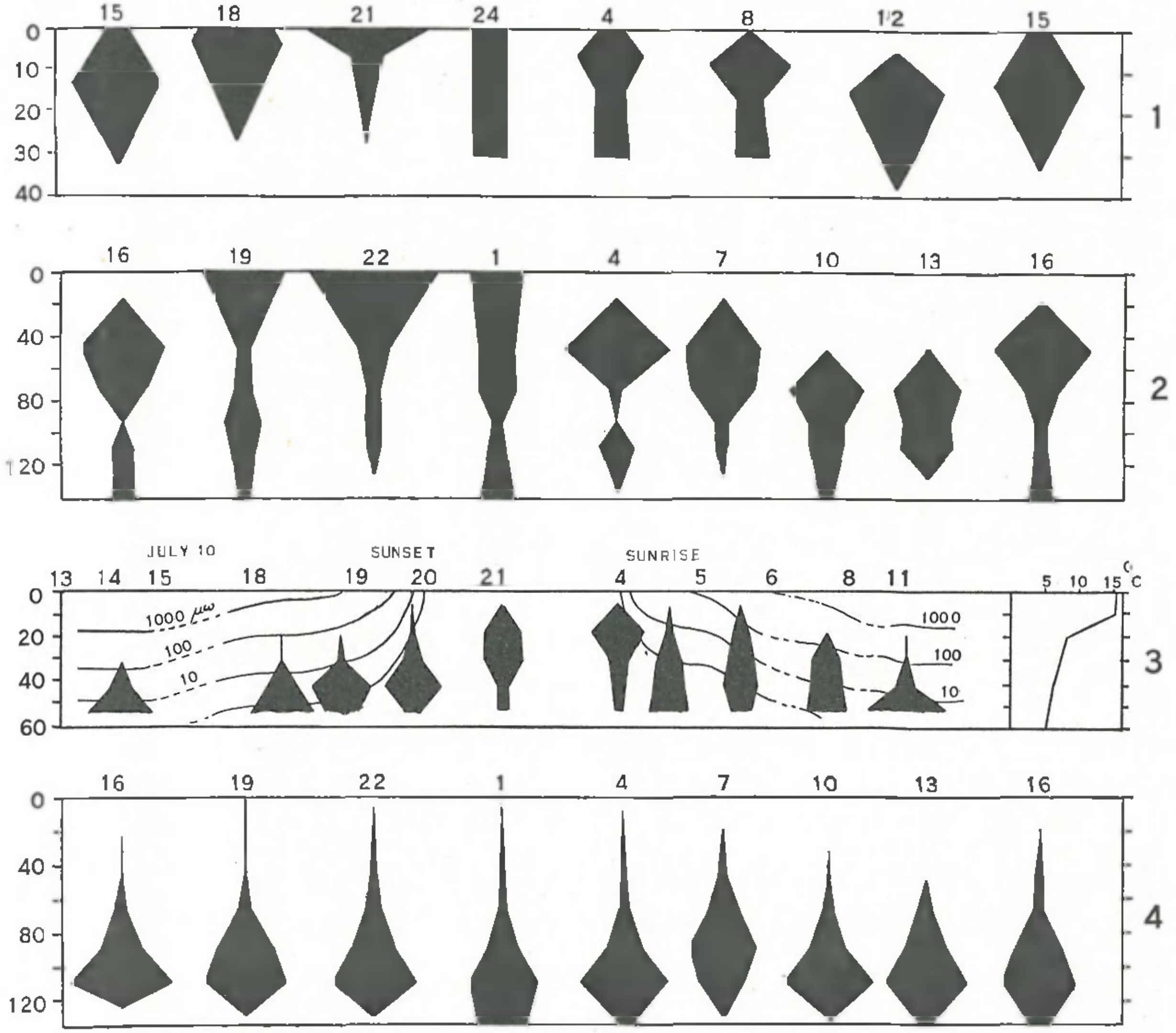

Fig. 8.

Vertical Distribution of Plankton Animals.

1. Hypothetical vertical distributions at different times in the twenty-four hours to illustrate the behaviour of a population of a species such as *Calanus finmarchicus* in its diurnal movements, (after Russell, 1927, p. 237, Fig. 4).
2. Diagram showing vertical distribution of female *Calanus finmarchicus* at 3-hourly intervals during 24 hours on January 25th—26th, 1932; sunset 4.27 p.m.; sunrise 8.57 a.m. (after Nicholls, 1933, p. 150, Fig. 4).
3. Diurnal migration of adult females of *Metridia lucens* in the Gulf of Maine, July, 1932. The changes in light intensity are indicated by the lines representing the depth at which 1000, 100 microwatts etc. occurred (one microwatt may be taken as approximately equal to three metre-candles). The temperature curve at the right shows that migration right to the surface at night was prevented by the thermocline (after Clarke, 1933, p. 426, Fig. 5).
4. Diagram showing vertical distribution of Stage V *Calanus finmarchicus* at 3-hourly intervals on Jan. 25th—26th, 1932 (after Nicholls, 1933, p. 148, Fig. 3).

we wish to observe. It is by seeking for disagreements that advances are made. For it is where behaviour is contrary to this theory that we shall find the clues to the differences in the physiological state of the animals themselves.

It has been mentioned previously that at times the animals appear to be irresponsive to light changes. A very good example of this has been shown for the fifth copepodid stage of *Calanus finmarchicus* (Nicholls, 1933). The possible significance of this state is worth consideration. The gonads of a copepod do not usually mature until the moult into the adult stage is completed. The fifth copepodid stage is the final stage of immaturity and immediately on developing into the adult stage the gonads start to ripen. After moulting into the adult stage or possibly even immediately before this moult the copepod becomes once more responsive to light conditions and exhibits typical migrational movements. After the successive production of the spring and summer broods, the offspring surviving from the final brood have to pass the winter months. It is in this irresponsive fifth stage that Calanus exists for the long period from August until the following February, when the final moult into the adult takes place. These animals thus have to survive a period when there may be a prolonged deficiency of their diatom food. Orr (1934; Marshall, Nicholls, Orr, 1934) has shown that the Stage V individuals of *Calanus finmarchicus* are loaded with fat in the late summer. They must therefore live to a certain extent on these reserves. But they will obviously benefit if they can reduce their metabolic activity to a minimum. A daily wandering up and down under the stimulus of changing light conditions will be unnecessary waste of energy when no supply of food is being produced in the surface layers. Light itself may have an effect upon the rate of metabolism, although the results of Marshall, Nicholls and Orr (1935) seem to show that it is doubtful whether this effect will be felt much below a depth of five metres. One of the most obvious ways for a plankton animal to reduce its expenditure of energy is thus by seeking the deeper layers and becoming irresponsive to the stimulus of changing light conditions. In this respect the observation made by Sømme (1934, p. 81) that copepods kept in the dark are dull and sluggish compared with those exposed to subdued light seems very significant.

Evidence is not wanting that many plankton animals seek deeper layers in winter. It was long ago shown by Gran (1902) and Nordgaard that *Calanus finmarchicus* might be found in the winter in the deep water layers at the bottom of the Norwegian fjords. This habit has been examined more fully by Sømme for *Calanus finmarchicus* and *C. hyperboreus*, and it has been shown that a considerable stock of both these species survives the winter in these deep layers near the coast undergoing migrations towards the surface layers after the winter (see Fig. 8). Sømme also remarks that near Tromsø these species do not undertake extensive daily vertical migrations during the winter time. Beebe (1934) in his dives in the bathysphere below the photic zone has remarked that in the regions of perpetual night the plankton and pelagic animals did not appear to show those phototropic responses to his search light so characteristic of animals of the surface fauna. Possibly these deep sea organisms are permanently irresponsive; but if this were so it would be difficult to understand the function of the light emitting organs; it may have been that his search light was too powerful, or that the animals are only stimulated by rays from phosphorescent light.

The habit of some plankton animals to seek the deeper levels in winter is possibly quite comparable with that of hibernation of animals on land. Indeed this habit may be largely responsible in deciding to what degree an animal shall be oceanic. Unless an animal can find the required depth in the winter months it will not survive. Thus we can draw the distinction between an animal that can in certain coastal regions find sufficiently deep water such as *Calanus finmarchicus*, which dies down to a meagre band of survivors during winter in shallow waters; one such as *Calanus hyperboreus* which requires greater depths but may still be found in the deepest fjords; and an animal which is possibly even more oceanic such as Aglantha the last summer brood of which may not be able to survive the winter in shallow water. Kramp (1927, p. 160) in discussing the occurrence of Aglantha in the Belt Sea says: "I think myself it is rather the slight depth of this water which renders it less suitable as a permanent habitat for Aglantha". Such oceanic animals when brought once more into coastal waters after their vertical migration in the early months of the year can reproduce and thrive under coastal conditions so long as the summer lasts; but during the hibernation period they must seek the depths or perish.

It must not be overlooked also that at times certain plankton animals may live actually on or in the bottom (Clarke, 1934, b; Russell, 1932—33). In Figure 9 are shown typical sequences of life histories.

Enough has been said to show how a full knowledge of the biology of the different species of plankton animals is essential to explain the differences in their abundance and distribution from time to time. In this respect it is not sufficient to base conclusions on results obtained in another locality. It has been found that the same species of animal appears to show a different behaviour in one region from that which it shews in another. For instance in the waters off Plymouth the brood

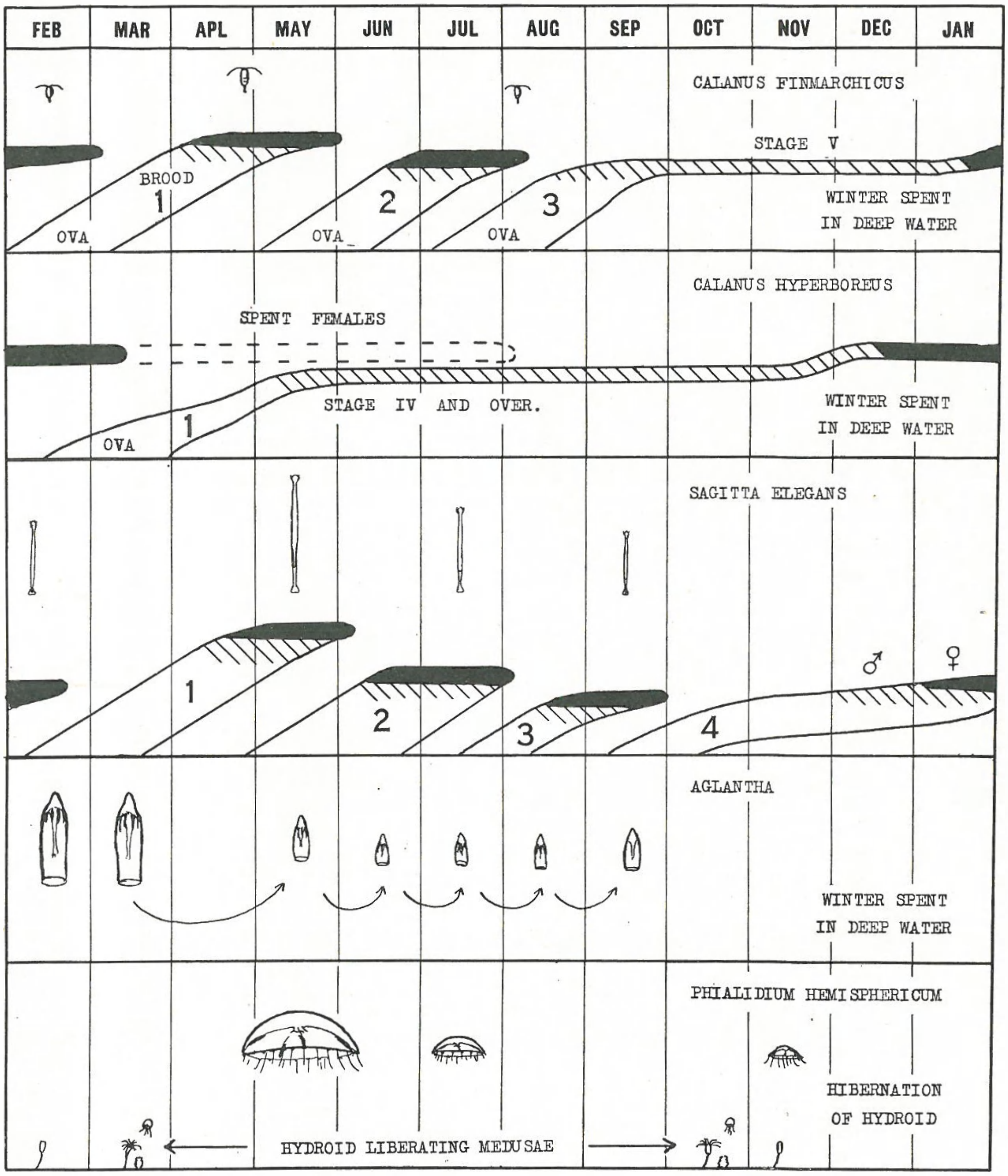

Fig. 9 (as to legend: see following page).

of *Calanus finmarchicus* maturing in July lives very much nearer the surface in the daytime than do the preceding broods. Whereas in the Clyde Sea area (Marshall, Nicholls and Orr, 1934) and in the North Sea (Gardiner, 1933) the brood maturing in May appears to live nearest the surface. This seems to point to some essential difference in the animals themselves.

The seasonal behaviour and production of successive broods of plankton animals needs to be studied in polar and tropical regions, and also in the deep waters of the ocean. The stimulus of external temperature conditions has been largely regarded as responsible for deciding the time of onset of maturity and spawning. It is however difficult to understand how this factor can decide the delay in the development of the sexual organs shown in the last summer brood of many plankton animals — that is the brood which survives the winter. It seems almost that we must regard the successive annual production of broods as comparable with the annual breeding cycle of an animal that may live for a number of years. That is, after a prolonged period of reproduction a period of recuperation is necessary. In temperate waters this recuperative period falls apparently for most species during the winter months. May it not be that some essential factor has been removed from the water during the summer which becomes available again only after a period of time or is perhaps lacking in the diminishing food supply?

Fig. 9.

Diagrammatic representation of the life histories of *Calanus finmarchicus*, *Calanus hyperboreus*, *Sagitta elegans*, Aglantha and *Phialidium hemisphaericum*. These are examples of species in which several broods are produced during the year, and of a species which produces only one brood a year. *Sagitta elegans* and *Calanus finmarchicus* are Arctic-boreal species. The diagrams represent their life histories under boreal conditions. It is probable that in Arctic waters they produce only one brood a year as the arctic species *C. hyperboreus*. In the diagrams the period of full maturity is indicated in black and the state immediately preceding maturity is shown by shading. This latter period corresponds to copepodid Stage V in the copepods and the ripening of the male sexual organs in Sagitta.

The height of the diagram for each brood give an indication of the size to which the adults grow, and above each brood is given a life size representation of the animal itself. The noteworthy feature is the prolonged existence in the final immature state during the winter and the retirement to deep water.

A. Succession of Broods of *Calanus finmarchicus*. This is based on the results of Marshall, Nicholls and Orr (1933—35) at Loch Striven. There are three main breeding periods in the year covering the periods February—March, April — May — June, July — August. Spawning does not take place with the same intensity throughout a whole period, but in any one year it is likely to be most intense in one month, e. g. February, May and July. Individuals of the first brood, developing during the coldest period of the year grow to the largest size and weight. Thereafter they decrease in size as the temperature rises. The first born in any brood are generally the largest for that brood.

In 1933 the last brood which was hatched mainly in July had established the autumn-winter stock of Stage V by August 14th. These persist mostly as Stage V and moult into adults in January and February.

The work of Farran (1927), Russell, and Bogorov (1934, a) shows that this sequence is essentially the same in the waters south of Ireland and in the western end of English Channel.

Maximum length.

Females.	Median length of cephalo-thorax.		Dry Weight.
Loch Striven			
(Marshall-Orr)	2.76 mm.	(24.iv.33)	0.28 mg.
Plymouth			
(Russell)	2.82[1])	(19.v.26)	
(Bogorov)	2.89[1])	(22.v.30)	0.252[2])
Minimum length.			
Loch Striven	2.26	(28.viii.33)	0.135
Plymouth	2.46[1])	(26.vii.26)[3])	
	2.26[1])	(16.x.30)	0.10[2])

The copepods grow larger in cold waters than in warm, e. g. Bogorov gives for Barents Sea:

Females.	Average total length.	Temperature.
69°30′ N — 75° N.	3.22 mm.	4.7° C.
75° N. — 77° N.	3.78	1.08°
North of 77° N.	4.57	—0.50°

Adler and Jespersen (1920) and Jespersen (1934) have given the following variations in length of cephalo thorax

Eastern North Sea	ca. 1.9—2.7 mm.
West Greenland Waters	2.4—4.5 „

The percentage of fat is highest in Stage V: in 1933 the autumn winter stock in September had 6 % more fat than the corresponding individuals in the previous January to March.

Sømme has shown that in Norwegian waters the majority of *C. finmarchicus* spend the winter at depths greater than 200—300 metres. After the winter there is an annual vertical migration completed about the middle of March; development of the eggs takes place *after* this vertical migration.

B. Seasonal cycle of *Calanus hyperboreus*. This is based on Sømme's (1934) results for Norwegian waters.

There is only one brood in the year. Spawning takes place in February and March. The earliest developmental stages are passed through by April, after which specimens earlier than copepodid Stage IV are not found. A few females start to ripen in November, but the majority do not do so until mid-December and January. The males are found only between December and the beginning of May, mostly in January and February. After spawning in February and March some of the spent females may survive until the following August.

---

[1]) Originally given as total length, converted into cephalo-thorax length by factor 0.8 (see Clarke 1934 p.00).

[2]) Formalin preserved material; there will have been some slight loss in weight.

[3]) No observations later than Sept. 22nd.

The winter is passed in deep layers mostly below 200—300 m. and deeper than *C. finmarchicus*. The annual vertical migration after the winter months is completed by the middle of April; the development of the eggs takes place *before* this vertical migration.

As there is only one brood there is no seasonal dimorphism in size.

The copepods grow larger in cold waters than in warm, e. g. Bogorov gives for the Barents Sea:—

Females.	Total Average Length.	Wet weight.	Temperature.
69°30′ N.—75° N.	6.0 mm.	4.0 mg.	4.7° C.
75° N.—77° N.	7.1	8.6	1.08
North of 77° N.	8.0	13.4	—0.50

A similar type of life history is shown by *Calanus tonsus* (Campbell, 1934) in the Strait of Georgia on the Pacific Coast of North America.

C. Succession of broods of *Sagitta elegans*. This is based on the results of Russell (1932—33) at Plymouth.

There are probably four main breeding periods during the year, i. e. February, May, June—July, and September. Individuals of the first brood developing at the coldest time of the year grow into the largest adults. Thereafter they decrease in size in the successive broods as the temperature rises.

Approximate average length of adults:—

May (1930)	19.5—20 mm.
June—July	13 —14.5
September	10 —10.5
February (1931)	12 —12.5

The offspring arising from the September spawning do not start to mature until December when the male sexual organs start to ripen. The female sexual organs do not start to ripen until January. There is an indication that there is a descent to deeper water during the winter.

D. Probable succession of broods of *Aglantha digitalis* var. *rosea*. This is based on results of Russell at Plymouth (unpublished). Development is direct, without a hydroid generation. Large individuals 12 to 18 mm. in height, which have survived the winter living probably in deep water, spawn in February and March. The adults of this first brood grow to about 6 or 7 mm. in height. During the summer months successive broods of small individuals, 5 or 6 mm. in height, are produced. There is an indication at Plymouth that there are at least three such broods. The offspring from the last spawning in August or September grow into the larger sized individuals which survive the winter and spawn the following February.

E. Biology of the Medusa *Phialidium hemisphaericum* in the plankton. Based on results of Russell (unpublished) and Orton (1920) at Plymouth.

The medusae are produced from the hydroid *Clytia johnstoni*. The hydroid starts producing medusae in numbers in March. The medusae liberated early in the year grow to a large size, individuals being found in May up to 19 mm. in diameter with as many as 32 tentacles. During the summer the successive adults are smaller and smaller until in September they have a diameter of only 5 or 6 mm. with usually about 16 tentacles. In November the hydroid polyps die down and the hydroid "hibernates" until the following March. (Compare also, Kramp, 1927).

References.

Adler, G. and Jespersen, P. 1920. Variations saisonnières chez quelques Copepodes planctoniques marins. Medd. Komm. Havund., Ser. Plankton, Vol. 2.

Allen, E. J. and Nelson, E. W. 1910. On the Artificial Culture of Marine Plankton Organisms. Journ. Mar. Biol. Assoc., N. S., Vol. VIII, No. 5, pp. 421—474.

Apstein, C. 1906. Die Salpen. Deutsche Südpolar-Exped. 1901—1903. Bd. IX, Zool. Bd. I., Heft III, pp. 159—203.

— 1911. Tunicata. Résumé des observations sur le Plankton des Mers explorées par le Conseil pendant les Années 1902—1908. Cons. Perm. Internat. Explor. Mer. Bull. Trim. Pt. II. pp. 150—162.

Augener, H. 1929. Die Polychaeten der Weddellsee. Int. Rev. d. ges. Hydrobiol. Hydrog., Bd. 22, pp. 273—312.

Aurivillius, Carl W. S. 1898. Vergleichende Thiergeographische Untersuchungen über die Plankton-Fauna des Skageraks in den Jahren 1893—1897. Kungl. Svenska Vetenskaps-Akad. Handl. Bd. 30. No. 3, pp 1—426.

Beebe, William. 1934. Half Mile Down. Harcourt, Brace & Co., New York.

Bigelow, Henry B. 1911. The Siphonophorae. Rep. Sci. Res. Expedition to the eastern tropical Pacific ... by the U. S. Fish Commission Steamer "Albatross". Mem. Mus. Comp. Zool. Cambridge, Mass. XXXVIII, No. 2, pp. 173—402.

Bigelow, Henry B. 1926. Plankton of the Offshore Waters of the Gulf of Maine. Bull. Bur. Fish. Washington. Vol. XL. 1924 Pt. II. Doc. No. 968. pp. 1—509.

— 1927. Physical Oceanography of the Gulf of Maine. Bull. Bur. Fish. Washington. Vol. XL. 1924. Pt. II, Doc. No. 969, pp. 511—1027.

— 1931. Oceanography. Its Scope, Problems and Economic Importance. Chapman & Hall, Ltd. London. pp. 1—263.

— 1931. Siphonophorae from the Arcturus Oceanographic Expedition. Zoologica. Sci. Contrib. New York Zool. Soc. VIII, No. 11, pp. 525—592.

Bogorov, B. G. 1932. Materials on the Biology of the Copepods of the Barents and the White Seas. Bull. State Oceanogr. Inst. U. S. S. R. No. 4, pp. 1—16.

— 1933. Modifications in the Biomass of *Calanus finmarchicus* in accordance with its age. Bull. State Oceanogr. Instit. No. 8, pp. 1—16.

— 1934 a. Seasonal changes in Biomass of *Calanus finmarchicus* in the Plymouth area in 1930. Journ. Mar. Biol. Assoc., N. S., Vol. XIX, No. 2, pp. 585—612.

— 1934 b. On the term "biomass of a plankton organism". Bull. All-Union Scient. Res. Inst. Mar. Fish. Oceanogr. No. 2, p. 28.

Bogorov, B. G. & Preobrajenskaya, E. 1934. On the weight characteristics of the plankton organisms of the Barents Sea. II. Copepoda. Bull. All-Union Scient. Res. Inst. Mar. Fish. Oceanogr. Nr. 2, pp. 1—25.

Bonnevie, Kr. 1913. Pteropoda from the "Michael Sars" North Atlantic Deep-Sea Expedition 1910. Rep. Sci. Res. "Michael Sars" N. Atlantic Deep-Sea Exped. 1910. Vol. III. Pt. 1. pp. 1—69 (Reprinted 1933).

Bowman, A. 1923. The Biological Interchange between the Atlantic and the North Sea. Rep. Brit. Assoc. Adv. Sci., London, 1922, p. 367.

Brandt, K. 1898. Beiträge zur Kenntniss der chemischen Zusammensetzung des Planktons. Wiss. Meeresunt., Abt. Kiel., u. f. 3, pp. 45—90.

Brinkmann, August. 1917. Die Pelagischen Nemertinen. Bergens Mus. Skrift. Bd. III. No. 1, pp. 1—180.

Bullen, G. E. 1908. Plankton studies in relation to the western Mackerel fishery. Journ. Mar. Biol. Assoc., N. S., Vol. VIII No. 3, pp. 269—302.

— 1912. Some notes upon the feeding habits of mackerel and certain Clupeoids in the English Channel. Journ. Mar. Biol. Assoc., N. S., Vol. IX, No. 3, pp. 394—403.

Campbell, Mildred H. 1934. The Life history and post-embryonic development of the copepods, *Calanus tonsus* Brady and *Euchaeta japonica* Marukawa. Journ. Biol. Board Canada, Vol. I, No. 1, pp. 1—65.

Clarke, George L. 1933. Diurnal Migration of Plankton in the Gulf of Maine and its correlation with changes in submarine irradiation. Biol. Bull. Vol. LXV, No. 3. pp. 402—436.

— 1934 a. Further Observations on the Diurnal Migration of Copepods in the Gulf of Maine. Biol. Bull. Vol. LXVII, No. 3, pp. 432—455.

— 1934 b. The Diurnal Migration of Copepods in St. Georges Harbor, Bermuda. Biol. Bull. Vol. LXVII, No. 3, pp. 456—460.

Clarke, G. L. and Gellis, S. S. 1935. The Nutrition of Copepods in Relation to the Food-Cycle of the Sea. Biol. Bull., Vol. LXVIII, No. 2, pp. 231—246.

Collin, G., Drummond, J. C., Hilditch, T. P., and Gunther, E. R. 1934. Observations on the Fatty Constituents of Marine Plankton. II. General character of the Plankton oils. Journ. Exper. Biol., Vol. XI, No. 2, pp. 198—202.

Cooper, L. H. N. 1934. The Determination of Phosporus and Nitrogen in Plankton. Journ. Mar. Biol. Assoc., N. S., Vol. XIX, No. 2. pp. 755—759.

Damas, D. 1905. Notes Biologiques sur les Copépodes de la Mer Norvégienne. Cons. Perm. Int. Explor. Mer, Publ. Circ. No. 22, pp. 1—23.

— 1909. Contribution à la biologie des Gadides. Cons. Perm. Int. Explor. Mer., Rapp. Proc. Verb. Vol. X., No. 3, pp. 1—277.

Damas, D. et Koefoed, E. 1907. Le Plankton de la Mer du Grönland. Croisière Océanographique accomplie à bord de la Belgica dans la mer du Grönland 1905, pp. 347—453.

Defant, A. 1927. Über die wissenschaftlichen Aufgaben und Ergebnisse der Expedition. Die Deutsche Atlantische Expedition auf dem Vermessungs- und Forschungsschiff "Meteor". Zeits. Ges. Erdkunde zu Berlin. Nr. 7/8, pp. 359—369.

Drummond, J. C. and Gunther, E. R. 1934. Observations on the Fatty Constituents of Marine Plankton. III. The Vitamin A and D Content of Oils derived from Plankton. Journ. Exper. Biol. Vol. XI, No. 2, pp. 203—209.

Farran, G. P. 1911. Copepoda. Résumé des observations sur le Plankton des Mers explorées par le Conseil pendant les Années 1902—1908. Cons. Perm. Internat. Explor. Mer., Bull. Trim. Pt. II. pp. 81—105.

Farran, G. P. 1927. The reproduction of *Calanus finmarchicus* off the south coast of Ireland. Cons. Int. Explor. Mer. Journ. du Cons. Vol. II, No. 2, pp. 132—43.

Frost, N., Lindsay, S. T. and Thompson, H. 1934. Plankton. Annual Report Year 1933. Rep. Newfoundland Fish. Res. Comm. Vol. II, No. 2. pp. 47—59.

Gardiner, A. C. 1933. Vertical Distribution in *Calanus finmarchicus*. Journ. Mar. Biol. Assoc., N. S., Vol. XVIII, No. 2, pp. 575—610.

Garstang, Walter. 1933. Report on the Tunicata. Part I. — Doliolida. Brit. Antarct. ("Terra Nova") Exped., 1910. Nat. Hist. Rep. Zool., Vol. IV, No. 6, pp. 195—251.

Gellis, S. S. and Clarke, G. L. 1935. Organic matter in dissolved and in colloidal form as food for *Daphnia magna*. Physiol. Zool., Vol. VIII, No. 2, pp. 127—137.

Gough, Lewis Henry. 1905. On the Distribution and the Migrations of *Muggiaea atlantica*, Cunningham, in the English Channel, the Irish Sea, and off the South and West Coasts of Ireland, in 1904. Cons. Perm. Int. Explor. Mer., Publ. Circ. No. 29, pp. 1—13.

Gran, H. H. 1902. Das Plankton des Norwegischen Nordmeeres von biologischen und hydrographischen Gesichtspunkten behandelt. Rep. Norweg. Fish. Mar. Invest. Vol. II. No. 5, pp. 1—217.

Gunther, E. R. 1934. Observations on the Fatty Constituents of Marine Plankton. I. Biology of the Plankton. Journ. Exper. Biol., Vol. XI, No. 2, pp. 173—197.

Hardy, A. C. 1924. The Herring in Relation to its Animate Environment. Part I. The Food and Feeding Habits of the Herring with Special Reference to the East Coast of England. Min. Agric. Fish., Fish. Invest. Ser. II. Vol. VI. No. 3, pp. 1—53.

— 1926. A New Method of plankton research. Nature, Vol. 118, p. 630.

Harvey, H. W. 1934. Measurement of Phytoplankton Population. Journ. Mar. Biol. Assoc., N. S., Vol. XIX, No. 2, pp. 761—773.

Hensen, Victor. 1895. Methodik der Untersuchungen. Ergeb. d. Plankton-Expedition d. Humboldt-Stiftung. Bd. I, B. pp. 1—200.

Hentschel, Ernst. 1934. Eine Methode zur Untersuchung von Copepodenbevölkerungen. Cons. Perm. Int. Explor. Mer., Rapp. Proc. Verb., Vol. LXXXIX, pp. 93—97.

Huntsman, A. G. 1919. Some Quantitative and Qualitative Plankton studies of the Eastern Canadian Plankton. Canadian Fish. Exped., 1914—1915, pp. 405—485.

Jespersen, P. 1928. Investigations on the Food of the herring in Danish Waters. Medd. Komm. Havund., Ser. Plankton. Vol. II.

— 1934. The Godthaab Expedition 1928. Copepoda. Medd. Grønland Komm. Vid. Undersøgels. Grønland, Bd. 79, Nr. 10, pp. 1—166.

Kokubo, S. and Tamara, I. 1931. A Quantitative Investigation of the Plankton of Aomori Bay, as studied comparatively by Pump and Net Collection. Sci. Rep. Tôhoku Imper. Univ. 4th. Ser. Biol. Vol VI. No. 3, pp. 491—531.

Kramp, P. L. 1913. Schizopoda. Résumé des observations sur le Plankton des Mers explorées par le Conseil pendant les Années 1902—1908. Cons. Perm. Internat. Explor. Mer., Bull. Trim. Pt. III. pp. 539—556.

— 1926. Medusae. Part. II. Anthomedusae. Danish Ingolf-Expedition, Vol. V, Pt. 10, pp. 1—102.

Kramp, P. L. 1927. The Hydromedusae of the Danish Waters. Kgl. Danske Vidensk. Selsk. Skrift., Naturvid. Math. Afd. 8. R. XII. 1. pp. 1—290.

— 1930. Hydromedusae collected in the south-western part of the North Sea and in the Eastern part of the Channel in 1903—1914. Mém. Mus. Roy. d'Hist. Natur. Belgique. Mem. No. 45, pp. 1—55.

Krogh, August. 1931. Dissolved substance as food of aquatic organisms. Biol. Reviews, Vol. VI, No. 4, pp. 412—442.

Künne, Cl. 1929. Vergleich der Fangfähigkeit verschiedener Modelle von Plankton-Netzen. Cons. Perm. Int. Explor. Mer., Rapp. Proc. Verb. Vol. LIX, pp. 1—37.

— 1933. Weitere Untersuchungen zum Vergleich der Fangfähigkeit verschiedener Modelle von vertikal fischenden Plankton-Netzen. Cons. Perm. Int. Explor. Mer., Rapp. Proc. Verb., Vol. LXXXIII, pp. 1—35.

— 1934. Bericht über die Teilnahme an einer Fischereischutzfahrt der "Weser" zu Untersuchungen über die Verbreitung der Heringslarven in der südlichen Nordsee und dem Kanaleingang. 5. Die Verbreitung des Grossplanktons. Deutsch. Wiss. Komm. f. Meeresforsch. N. F. Bd. VII. Heft 3.

Leavitt, Benjamin B. 1935. A quantitative study of the Vertical Distribution of the larger zooplankton in deep water. Biol. Bull. Vol. LXVIII, No. 1, pp. 115—130.

Lebour, M. V. 1919—1921. Various papers on the food of young fish, in Journ. Mar. Biol. Assoc., N. S., Vol. XII.

— 1922—1923. The Food of Plankton organisms. Journ. Mar. Biol. Assoc., N. S., Vols. XII and XIII.

— 1924—1934. Various papers on the Development of Crustacea and Mollusca, in Journ. Mar. Biol. Assoc., N. S. Vols. XIII—XIX, and Proc. Zool. Soc. 1928—35. London.

Lens, Albertine D., and Van Riemsdijk, Thea. 1908. The Siphonophora of the "Siboga" Expedition. Siboga-Expeditie. IX, pp. 1—130.

Lohmann, H. 1905. Die Appendicularien des arktischen und antarktischen Gebiets, ihre Beziehungen zueinander und zu den Arten des Gebiets der warmen Ströme. Zool. Jahrb. Suppl. VIII, pp. 353—382.

— 1908. Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. Wiss. Meeresunter. N. F. Bd. X. Abt. Kiel. pp. 131—370.

— 1928. Beiträge zur Planktonbevölkerung der Weddellsee nach der Ergebnissen der Deutschen Antarktischen Expedition 1911—1912. II. Die Appendicularien-Bevölkerung der Weddellsee. Int. Rev. d. g. Hydrobiol. Hydrogr., Bd. 20, Heft 1/2, pp. 13—72.

— 1931. Die Appendicularien der Deutschen Tiefsee-Expedition. Wiss. Ergebn. "Valdivia" 1898—1899, Bd. XXI, pp. 1—158.

Lohmann, H. and Bückmann, Ad., 1926. Die Appendicularien. Deutsche Südpolar-Exped. 1901—1903, Bd. XVIII, Zool. X. pp. 65—231.

Lucas, C. E. 1933. Occurrence of *Dolioletta gegenbauri* (Uljanin) in the North Sea. Nature, Vol. 132, p. 858.

Mackintosh, N. A. 1934. Distribution of the Macroplankton in the Atlantic Sector of the Antarctic. Discovery Reports, Vol. IX, pp. 65—160.

Marshall, S. M., Nicholls, A. G. and Orr, A. P. 1934. On the Biology of *Calanus finmarchicus*. V. Seasonal Distribution, Size, Weight and Chemical Composition in Loch Striven in 1933, and their relation to the Phytoplankton. Journ. Mar. Biol. Assoc., N. S., Vol. XIX. No. 2. pp. 793—827.

Marshall, S. M., Nicholls, A. G. and Orr, A. P. 1935. On the Biology of *Calanus finmarchicus*. Part VI. Oxygen Consumption in Relation to Environmental Conditions. Journ. Mar. Biol. Assoc., N. S., Vol. XX. No. 1, pp. 1—27.

Massy, Anne L. 1920. Mollusca. Part III. Eupteropoda (Pteropoda Thecosomata) and Pterota (Pteropoda Gymnosomata). British Antarctic ("Terra Nova") Exped. 1910: Nat. Hist. Rep. Zool. Vol. II. No. 9. pp. 203—231.

Meek, Alexander. 1928. On *Sagitta elegans* and *Sagitta setosa* from the Northumbrian Plankton, with a Note on a Trematode Parasite. Proc. Zool. Soc. London. pp. 743—776.

Meisenheimer, Johannes. 1905. Pteropoda. Wiss. Ergeb. Deutsch. Tiefsee-Exped. "Valdivia" 1898—1899. Bd. IX. Lief. 1, pp. 1—314.

Moser, F. 1909. Die Ctenophoren. Deutsche Südpolar-Exped. 1901—1903, Bd. XI, Zool. III. Heft. II, 1, pp. 117—192.

Moser, F. 1925. Die Siphonophoren der Deutschen Südpolar-Expedition, 1901—1903, zugleich eine neue Darstellung der ontogenetischen und phylogenetischen Entwickelung dieser Klasse. Deutsche Südpolar-Expedit. Bd. XVII, Zoologie, Bd. IX, pp. 1—541.

Neumann, Günther. 1913. Die Pyrosomen und Dolioliden der Deutschen Südpolar-Expedition 1901—1903. Deutsch. Südpol.-Exped. Bd. XIV. Zool. Bd. VI. Heft 1, pp. 1—34.

Nicholls, A. G. 1933. On the Biology of *Calanus finmarchicus*. I. Reproduction and Seasonal Distribution in the Clyde Sea-Area during 1932. Journ. Mar. Biol. Assoc., N. S., Vol. XIX, No. 1, pp. 83—109.

— 1933. On the Biology of *Calanus finmarchicus*. III. Vertical Distribution and Diurnal Migration in the Clyde Sea-Area. Journ. Mar. Biol. Assoc., N. S., Vol. XIX. No. 1, pp. 139—164.

Orr, A. P. 1934. On the Biology of *Calanus finmarchicus*. Part IV. Seasonal Changes in the Weight and Chemical Composition in Loch Fyne. Journ. Mar. Biol. Assoc., N. S., Vol. XIX. No. 2. pp. 613—632.

Orton, J. H. 1920. Sea-Temperature, Breeding and Distribution in Marine Animals. Journ. Mar. Biol. Assoc., N. S., Vol. XII. No. 2. pp. 339—366.

Ostenfeld, Carl Hansen. 1913. De Danske Farvandes Plankton i Aarene 1898—1901. Phytoplankton og Protozoer. (avec un résumé en français). Kgl. Danske Vidensk. Selsk. Skrift. 7. Række, Naturvid. Math. Afd. 2, pp. 117—478.

— 1931. Résumé des observations sur le Plankton des Mers explorées par le Conseil pendant les Années 1902—1908. Cons. Perm. Int. Explor. Mer., Bull. Trim. Pt. IV, pp. 601—672.

Oye, Paul van. 1918. Untersuchungen über die Chaetognathen des Javameeres. Contributions Scientifiques de Buitenzorg's Lands Plantentuin, Fac. IV. pp. 1—61.

Paulsen, Ove. 1910. Pteropoda. Résumé des observations sur le Plankton des Mers explorées par le Conseil pendant les Années 1902—1908. Cons. Perm. Intern. Explor. Mer., Bull. Trim. Pt. I, pp. 52—59.

Pruvot-Fol, Alice. 1924. Étude de quelques Gymnosomes Méditerranéens des pêches d l'"Orvet" en 1921 et 1922. Arch. Zool. Expér. Génér., Tome 62, pp. 345—400.

Rammner, Walter. 1933. Die Cladoceren der "Meteor"-Expedition. Wiss. Erg. Deutsch. Atlant. Exped. "Meteor" 1925—1927. Bd. XII Biol. Sond. Lief. 2. pp. 111—121.

Ritter-Zahony, R. von. 1911. Revision der Chätognathen. Deutsche Südpolar-Exped. 1901—1903, Bd. XIII, Zool. V, Heft. I, pp. 1—71.

Russell, F. S. 1925—1934. The Vertical Distribution of Marine Macroplankton. Parts I—XII. Journ. Mar. Biol. Assoc., N. S., Vol. XIII—XIX.

— 1927. The Vertical Distribution of Plankton in the Sea. Biol. Reviews. Vol. II, No. 3, pp. 213—262.

— 1932—33. On the Biology of Sagitta. Parts I—IV. Journ. Mar. Biol. Assoc., Vol. XVIII.

Russell, F. S. 1935 a. On the Value of Certain Plankton Animals as Indicators of Water Movements in the English Channel and North Sea. Journ. Mar. Biol. Assoc., N. S., Vol. XX, No. 2.

Russell, F. S. 1935 b. The Seasonal Abundance and Distribution of the Pelagic Young of Teleostean Fishes caught in the Ring-Trawl in Offshore Waters in the Plymouth Area. Part II. Journ. Mar. Biol. Assoc. N. S. Vol. XX, No. 2.

Ruud, Johan T. 1929. On the biology of copepods off Möre, 1925—1927. Cons. Perm. Int. Explor. Mer., Rapp. Proc. Verb., Vol. LVI. pp. 1—84.

Savage, R. E. 1931. The Relation between the Feeding of the Herring off the East Coast of England and the Plankton of the surrounding waters. Min. Agric. Fish., Fish. Invest. Ser. II. Vol. XII. No. 3, pp. 1—88.

Savage, R. E. and Hardy, A. C. 1935. Phytoplankton and the Herring. Part I. 1921 to 1932. Min. Agric. Fish., Fish. Invest. Ser. II. Vol. XIV. No. 2. 1934, pp. 1—73.

Schmidt, J. 1909. The Distribution of the Pelagic Fry and the Spawning Regions of the Gadoids in the North Atlantic from Iceland to Spain. Cons. Perm. Int. Explor. Mer., Rapp. Proc. Verb., Vol. X, No. 4, pp. 1—229.

Scott, Thos. 1911. Copepoda. Résumé des observations sur le Plankton des Mers explorées par le Conceil pendant les Années 1902—1908. Cons. Perm. Intern. Explor. Mer., Bull. Trim. Pt. II. pp. 106—149.

Sømme, Jacob D. 1934. Animal Plankton of the Norwegian Coast Waters and the open Sea. I. Production of *Calanus finmarchicus* (Gunner) and *Calanus hyperboreus* (Krøyer) in the Lofoten Area. Rep. Norweg. Fish. Mar. Invest. Vol. IV. No. 9, pp. 1—163.

Steuer, Adolf. 1933. Zur planmässigen Erforschung der geographischen Verbreitung des Haliplanktons, besonders der Copepoden. Zoogeographica, Bd. I. Heft 3, pp. 269—302.

Stiasny, G. 1934. Das Bipolaritätsproblem. Archiv. Néerlandaises Zool., Tome I, pp. 35—53.

Tesch, J. J. 1904. The Thecosometa and Gymnosometa of the Siboga-Expedition. Siboga Expeditie, LII. pp. 1—92.

— 1906. Die Heteropoden der Siboga-Expedition. Siboga-Expeditie, LI. pp. 1—110.

Wheeler, J. F. G. 1934. Nemerteans from the South Atlantic and Southern Oceans. Discovery Reports Vol. IX, pp. 215—294.

Wilson, Douglas P. 1928—33. Various papers on the Development of Polychaetes, in Journ. Mar. Biol. Assoc. N. S., Vols. XV—XVIII.

— 1932. On the Mitraria larva of *Owenia fusiformis* Delle Chiaje. Phil. Trans. Roy. Soc. London. Ser. B. Vol. 221. pp. 231—334.

Wimpenny, R. S. 1929. Preliminary Observations on the Fat-Content of the Plankton on the English herring grounds in the North Sea. Min. Agric. Fisheries, Fish. Invest., Ser. 2 Vol. XI, No. 5, pp. 1—23.

A/S L. IHRICH, KBHVN.