Hydrographical and Biological Conditions in the North Sea as Indicated by Plankton Organisms.

By

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Introduction.

FROM the beginning of the investigations of the International Council for the Exploration of the Sea the possibility of using plankton organisms as indicators (Leitformen) of water movements has been constantly borne in mind. This idea had already been suggested earlier by Cleve and Aurivillius, and was probably in the minds of most plankton workers, for when the habits of plankton organisms are known these organisms form ideal drift-bottles.

In the present review of the research on plankton indicators I shall restrict myself chiefly to work done in the North Sea area since the war, a brief historical survey having already been given previously (Russell, 1935 b, p. 13). It will be sufficient here to give the references to the publications of earlier workers such as those of Gran (1902), Gough (1905 a and b), Damas and Koefoed (1907), Ostenfeld (1908) and Bygrave (1911). In addition there is much important information to be found in the comprehensive *Bulletins Planktoniques* of the International Council.

But from the start it was fully realized that the problem could not be tackled satisfactorily until the full distribution of all species was worked out and until more was known about the life histories of the animals. Thanks to the co-operative work of the International Council and to the researches of individual workers both these aspects have received considerable attention. As a result the study of plankton indicators has shown a marked advance in recent years.

In the post-war period the first publications bearing on the use of plankton indicators were those of Bowman (1923 a and b), who instigated the study in Scottish waters, and of Hardy (1923) on the occurrence of certain plankton species off the east coast of England during the unusual hydrographical conditions of the year 1921.

In 1927 Kramp published his comprehensive work on the Hydromedusae of Danish waters, followed in 1930 by a paper on the Hydromedusae in the south-western part of the North Sea and the eastern part of the English Channel. Both these publications had as a major aim the association of the distribution of the Medusae with the movement of the water masses.

Meek (1928), by a study of the *Sagitta* population off the Northumberland coast, was the first to show that an examination of the relative abundance of the two species, *Sagitta elegans* and *S. setosa*, might produce valuable indications of hydrographical conditions.

Meanwhile Savage (1930), with his publication on the influence of *Phaeocystis* on the migrations of the herring, produced data which were to the followed by the important works on the distribution of phytoplankton patches in the southern North Sea, in collaboration with Hardy (1935) and with Wimpenny (1936). This work introduced a somewhat different type of observation in that the movements of whole patches of diatoms, chiefly *Rhizosolenia styliformis* and *Biddulphia sinensis*, were followed in successive years from 1921 onwards.

Wulff and Künne (1933), sponsored by Mielck, completed observations in the southern North Sea, which showed the relationships of both the microplankton and the larger plankton animals to the hydrographical conditions in that area.

At about the same time observations made at Plymouth and off the western end of the English Channel (Russell, 1935 a, 1936) showed the importance of certain of the larger plankton animals as indicators, and carried Meek's work on *Sagitta* a stage further. This was followed, in a review of zooplankton research (Russell, 1935 b) by remarks on the value of this type of work and a list of animals likely to be of use in different areas, compiled from the observations of earlier and recent workers.

Since that date further important works on certain indicator species have been published. Künne (1937 a) followed up his earlier research with a paper on the indicators in the southern North Sea in winter and also (1937 b) in the Baltic. In the latter paper Künne gives lists of those species which can be regarded as visitors (Fremdlinge) to the different regions of the Baltic.

Fraser (1938 and 1939) has given data on the distribution of Chaetognatha, including *Sagitta elegans* and *S. setosa*, and of other plankton animals in the northern North Sea and Scottish waters; and Furnestin (1938) compared the distributions of species of *Sagitta* with the salinity in the whole North Sea area.

During this period a number of shorter notes had been published on the occurrence of certain organisms which might prove of value as indicators in different areas; Russell and Kemp (1932) on *Velella* and *Ianthina* south-west of the British Isles; Lucas (1933) on *Dolioletta gegenbauri* in the northern North Sea; Russell and Hastings (1933) on the occurrence of salps and doliolids in the

English Channel; Russell (1934) on the siphonophores *Muggiaea atlantica* and *M. kochi* in the western end of the Channel; and Beatson, Nicol and Elton (1936) on *Ianthina*, *Velella* and *Lepas* on the west coast of Scotland. In addition a number of valuable notes are to be found in the annual reports of the Fishery Board for Scotland.

This list of workers would not be complete without mention of the work of A. C. Hardy and his collaborators[1]) on the distribution of plankton studied by means of his continuous recorder and the indicator disks supplied to fishermen. For it seems probable that Hardy's continuous recorder will prove to be one of the most valuable means of obtaining a broad picture of the distribution of indicator organisms over the whole area. As a result of this more recent work we are now in a position to differentiate more clearly between a number of plankton communities which typify the water masses in which they occur. Furthermore these water masses or "types of water" usually differ one from the other in origin or immediate past history, in so far as their salt content and temperature allow their more immediate origin to be deduced. Our knowledge of the different areas will be outlined below, and a resulting generalized picture drawn of the conditions over the whole North Sea area.

I have limited myself as much as possible to literature mainly concerned with plankton indicators, and have omitted detailed reference to hydrographical work as this would have unduly lengthened the list of literature. Much help has, however, been obtained by a study of the hydrographical publications, and among the works especially consulted are those of J. N. Carruthers, H. W. Harvey, J. R. Lumby, D. J. Matthews, and J. B. Tait. It may appear, perhaps, that I have over-simplified the story. The complexity of the water circulation must be fully realized, but in so short an account the qualifications necessary in describing any one area would have destroyed the clarity of the picture.

The Indicators for Different Areas.

Southern North Sea.

The following "types of water" are recognized in this area (see Fig. 1).

1. Northern water, brought into the area from the north, and especially from the north-west. This water is drawn from mixed oceanic and coastal water from the north, which is reduced in the southern North Sea to a salinity less than 35 ‰. It goes partly into the south-west Dogger Bank swirl, and also in part southwards along the east coast of England, turning finally in an easterly direction.

The northerly elements of the plankton which are indicators of the presence of this northern water are (Künne, 1937 a):—

[1]) Marshall, N. B. North Sea plankton recorder survey, 1938: Zooplankton other than Copepoda. Hull Bull. Marine Ecol. (In the press).

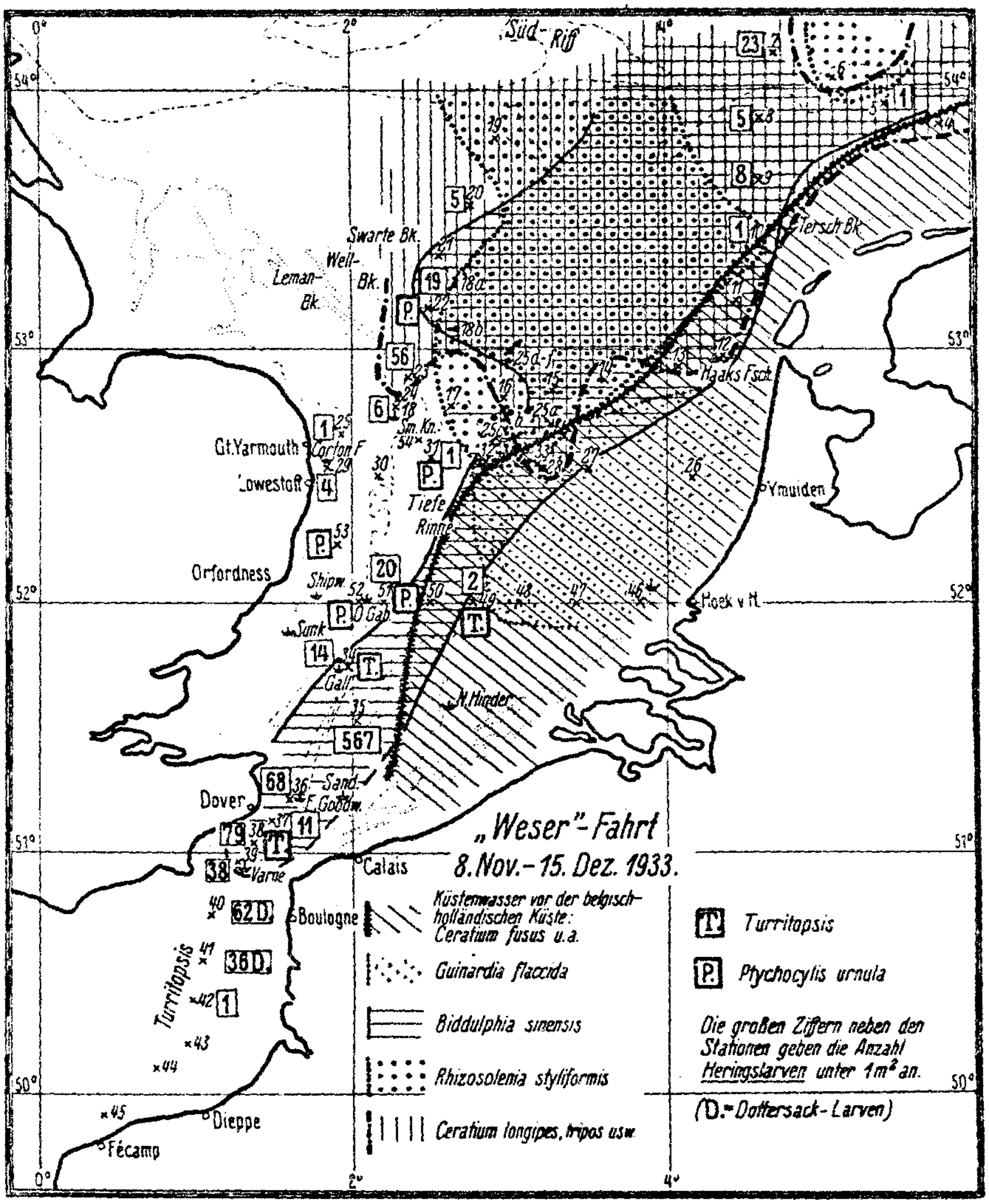

Fig. 1. Distribution of microplankton in southern North Sea. (From Wulff, 1933).

Hydromedusae: *Tima bairdi*, *Cosmetira*[2]), *Aglantha*[2]), and the siphonophore *Agalma elegans*.
Chaetognatha: *Sagitta elegans elegans*.

[2]) *Turritopsis*, *Cosmetira*, and *Aglantha* are here designated by generic names only. Künne identifies the first two as *Turritopsis polycirrha* Keferstein and *Cosmetira megalotis* (Maas). They are probably synonymous with *Cosmetira pilosella* Forbes and *Turritopsis nutricula* McCrady, (see Russell, 1938). *Aglantha* in the area under discussion is the small form known by some as *A. digitalis* f. *rosea* and by others as *A. rosea;* they are the same Medusa.

Crustacea: the euphausians *Nyctiphanes couchi, Thysanoessa gregaria,* and other species, and the amphipod *Themisto abyssorum* (= *Parathemisto oblivia*).
Pteropods: *Clione limacina* and *Limacina retroversa.*
Echinoderms: *Luidia sarsi* larvae.
Appendicularia: *Oikopleura labradoriensis.*

2. Channel water, entering the southern North Sea through the Straits of Dover. It may be composed of pure Channel water, or of mixed oceanic and coastal water from the western mouth of the Channel. Both these waters may become mixed together in the Dover Straits region. The water may reach a salinity of 35 ‰ or more. It passes north-east towards the Jutland coast.

The indicators of Channel water are:—

I) Pure Channel water.
Microplankton (Wulff, 1933): *Biddulphia sinensis.*
Macroplankton (Künne, 1937 a).
Hydromedusae: *Turritopsis*[2]) and *Gossea corynetes.*
Mollusca: *Lamellaria perspicua* larvae.

II) Mixed oceanic and coastal water (see English Channel and South Ireland area below).

3. Flemish coast water, occurring along the Belgian and Dutch coasts. It becomes mixed along its offshore boundary with Channel water and moves in a north-easterly direction along the Jutland coast.

The indicators of this water are:—

Microplankton (Wulff, 1933): *Paralia sulcata,* small *Coscinodiscus, Bellarochea malleus, Guinardia flaccida, Thalassiothrix nitzschioides, Ceratium fusus* and *Ceratium furca.*
Macroplankton (Künne, 1937 a): the pelagic hydroid *Clytia*[3]).
This water is also notable for the amount of detritus it carries.

4. Remaining coastal waters, found close into the coasts along the east coast of England and the Belgian, German and Dutch coasts, especially in the regions of the river mouths. It has a low salinity and carries much detritus.

Its indicators are:—

Eastern English coast.
Microplankton (Wulff, 1933): *Biddulphia mobiliensis* f. *regia* and *Ptychocylis urnula.*
German Bight.
Macroplankton (Künne, 1937 a): the Medusa *Sarsia tubulosa.*

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[3]) Künne uses the name *Clytia pelagica* for this hydroid. There seems to be little doubt that it is the same species as *Clytia johnstoni,* the hydroid of the Medusa *Phialidium hemisphaericum.* They are probably colonies regenerating in the plankton from fragments broken off from the sea bottom.

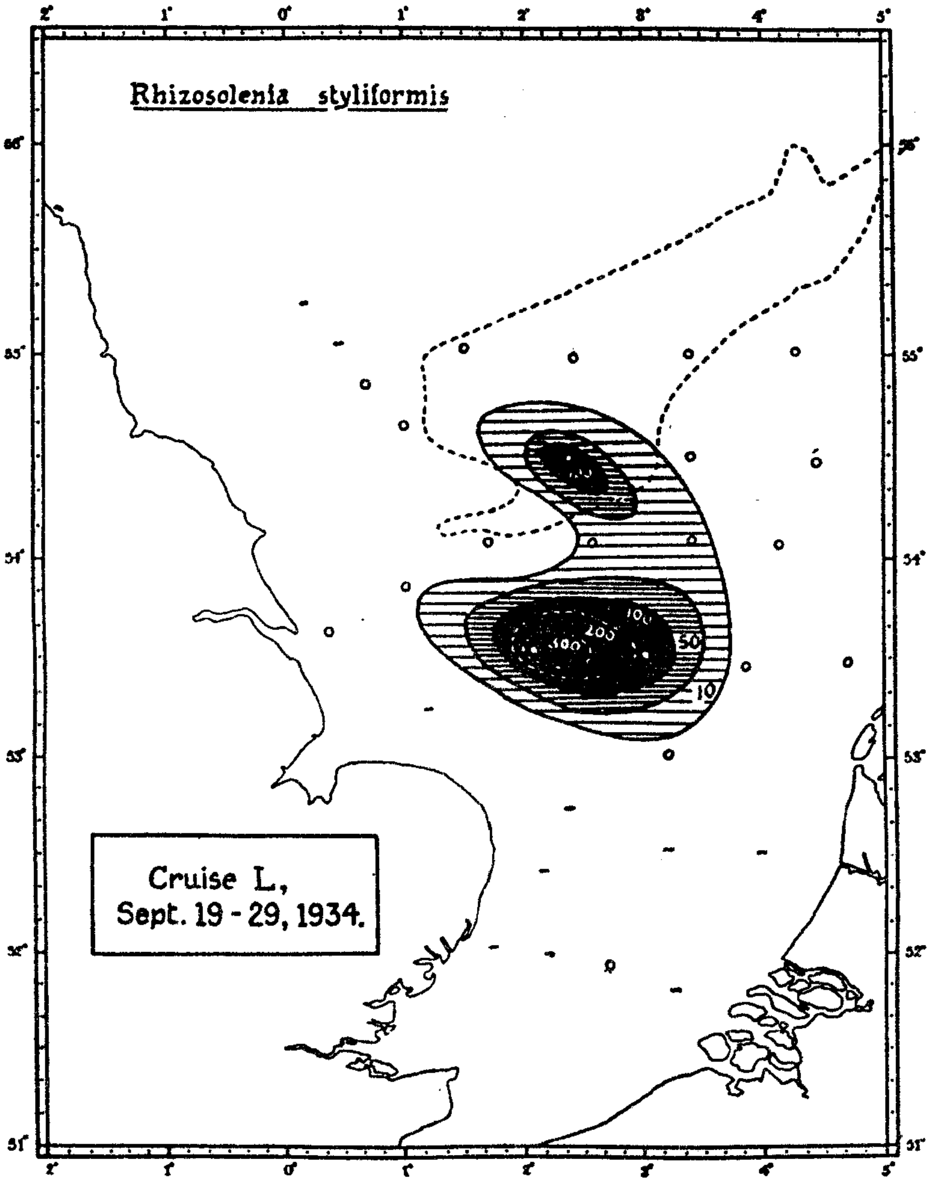

Fig. 2. Distribution of *Rhizosolenia styliformis* in southern North Sea in region of south-west Dogger Bank swirl; contoured in thousands of cells per cubic metre. (From S a v a g e and W i m p e n n y, 1936).

5. S w i r l w a t e r s. Most noteworthy in this region is the south-west Dogger Bank swirl (see Fig. 2).

It appears to draw its planktonic indicators entirely from the north, without admixture of Channel forms.

Its indicators are:—

Microplankton (W u l f f, 1933): *Rhizosolenia styliformis, Ceratium longipes, C. macroceros, C. tripos* and *C. bucephalum.*

Macroplankton (K ü n n e, 1937 a): those given above for northern water.

In considering the southern North Sea from the point of view of plankton distribution it must be realized that conditions are continually changing, as indeed they are in all areas. But perhaps in this area conditions are liable to more sudden alteration from effects of wind (e.g., Savage, 1932, on movements of *Pseudocalanus* swarms) and of outflow of fresh water from the land after heavy rainfall (e.g., Graham, 1938).

It is interesting to note here also that *Sagitta elegans* may occur in the Thames estuary (Wells, 1938).

Northern North Sea.

The information is taken from Fraser (1938, 1939).

1. Oceanic water entering in the extreme north through the Fair Isle Channel and mostly north of the Shetland Islands.

This water contains a mixture of warm and cold water species varying in their proportions according to the degree of influence of arctic water from the north and the Atlantic drift water from the south-west.

Among the indicator forms of this water are the following:—

I) Cold water.
Hydromedusae: the siphonophore *Dimophyes* (= *Diphyes*) *arctica*.
Chaetognatha: *Sagitta maxima* and *Eukrohnia hamata*.
Crustacea: the copepods *Calanus hyperboreus* and *Metridia longa*.
Pteropoda: *Limacina helicina*.

II) Warm water.
Hydromedusae: the siphonophores *Physophora hydrostatica*, *Agalma* (= *Agalmopsis*) *elegans* and *Galeolaria* (= *Galetta*) *truncata*.
Chaetognatha: *Sagitta serratodentata*.
Crustacea: the copepod *Rhincalanus nasutus* and several other species.
Pteropoda: *Clio pyramidata*.
Tunicata: various salps and doliolids.

2. Mixed oceanic and coastal water (see Fig. 3).
Hydromedusae: *Neoturris pileata*, *Laodicea undulata*, *Halopsis ocellata*, *Cosmetira*, *Tima bairdi*, and *Aglantha*.
Chaetognatha: *Sagitta elegans*.
Crustacea: the amphipod *Themisto*.
Pteropoda: *Limacina retroversa*.

This is a rich, often fatty, plankton, with abundant *Calanus finmarchicus*.

3. North Sea water. Its only indicator is:—
Chaetognatha: *Sagitta setosa*.

This plankton is usually not of a rich nature.

The sequence of events as we pass from north to south is as follows (Fraser, 1937, p. 313).

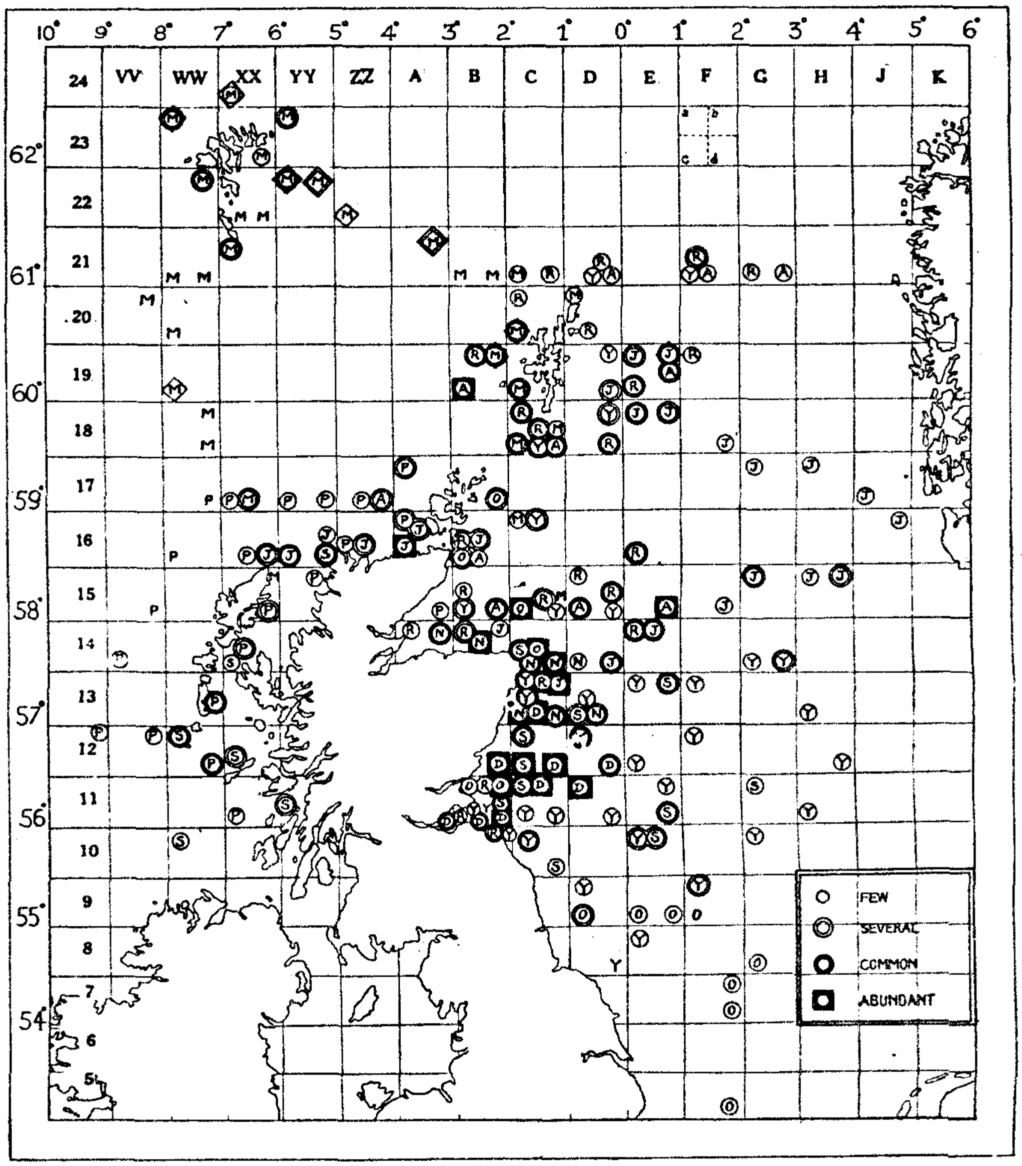

Fig. 3. The distribution of *Sagitta elegans elegans* (circles) and *S. elegans arctica* (diamonds) in Scottish waters in 1937. Letters indicate months. Unringed letters indicate absence of *Sagitta*. R. = March, P = Apr., M = May, J = June, Y = July, A = Aug., S = Sept., O = Oct., N = Nov., D = Dec. (From Fraser, 1939).

"As this mixed fauna moves round the north of Scotland the pure warm-water Atlantic forms gradually perish, but there is a further addition of arctic forms between Faroe and Shetland. These, too, gradually perish and the fauna is replaced by a growing admixture of coastal and neritic forms from the Scottish coasts, Shetland and Faroe, and this together with a probable replenishment from the Norwegian Deep south of 61°N. forms a very rich, often fatty, plankton with abundant *Sagitta elegans*, *Calanus finmarchicus*, and many Medusae.

Thus the fauna of the entering Atlantic stream becomes completely changed in quite a short space and time. In exceptionally favourable circumstances a few of the original forms persist and are carried into the North Sea as exotics, but as a rule only those forms which are capable of very rapid breeding (such as salps and doliolids in the asexual phase) are found in numbers in the North Sea."

Transition Area.

The Transition area is that region of the North Sea lying between the basin of the North Sea and the Baltic proper, comprising the Skagerak, Kattegat and Danish waters. It is a region of very marked hydrographic differences. The water masses involved are:—

1. Baltic water, of low salinity, flowing out as a surface layer and running north along the Norwegian coast.

2. Water of the Jutland current, entering the area in the deeper layers. This is formed of the mixtures of southern North Sea and coastal waters.

3. North Sea and oceanic waters entering in the deeper layers and varying in relative proportions.

The Medusa fauna of this area has been fully discussed by Kramp (1927). It is a very complex area and much experience in distinguishing the different plankton elements is required, since indications are mainly based on abundance or poverty of certain species. The more oceanic elements, however, such as the siphonophores *Physophora hydrostatica, Galeolaria truncata* and *Dimophyes arctica* are sufficiently obvious when they occur.

English Channel and Southern Ireland.

In this area the following types of water are recognized (Russell, 1936 b) (see Fig. 4).

1. Channel water, occupying the Channel proper. This water is characterized by a general paucity of plankton and its only indicators are:—

Hydromedusae: *Turritopsis.*
Chaetognatha: *Sagitta setosa.*

2. Mixed oceanic and coastal water, which forms a large swirl off the mouth of the Channel south of Ireland, and may at times be carried into the Channel. The indicators of this water are rather similar to those of the same type of water in the northern North Sea, but the more northern species are absent; they are:—

Hydromedusae: *Laodicea undulata, Cosmetira, Aglantha* and the siphonophores *Agalma elegans* and *Stephanomia bijuga.*
Chaetognatha: *Sagitta elegans.*

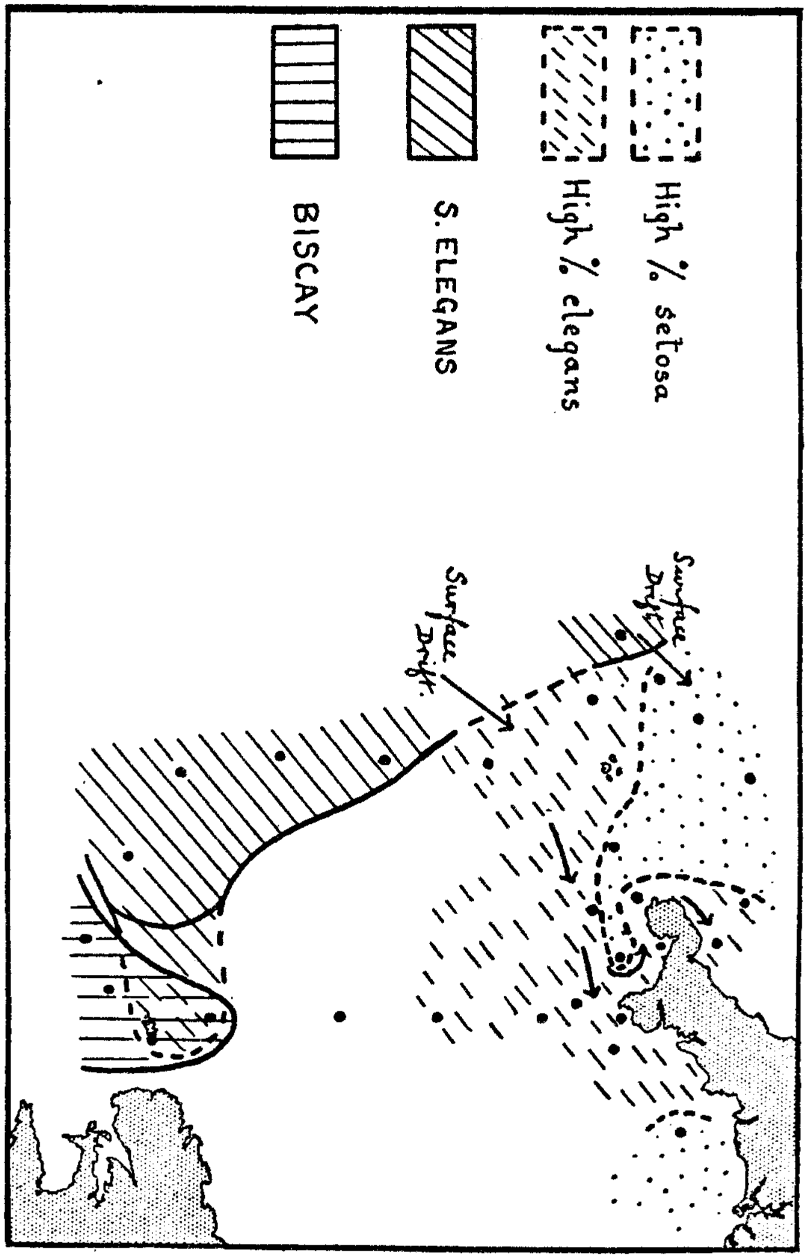

Fig. 4. Distribution of water masses in mouth of English Channel as shown by plankton collections in July, 1935. (From Russell, 1936 b).

Crustacea: the euphausians *Meganyctiphanes norvegica, Nyctiphanes couchi,* and *Thysanoessa inermis,* and the amphipod *Themisto gracilipes.*

Pteropods: *Clione* spp.

The plankton of this water is rich, and often of a fatty nature. The purely oceanic elements, as indicated by *Sagitta serratodentata* may occur mixed with the *S. elegans* plankton in proportions varying with the degree of oceanic influence. A mixed assembly of this plankton and the warm oceanic water species given below may also occur, similar to that described by Fraser for the northern North Sea.

3. W a r m o c e a n i c w a t e r, coming from a south-westerly direction; the indicators are:—

Hydromedusae: *Liriope tetraphylla* (= *exigua*), and (?) the siphonophores *Muggiaea atlantica* and *M. kochi.*

Crustacea: the copepod *Euchaeta hebes.*

Tunicata: various salps and doliolids.

In addition to the three types of water mentioned above there is possibly a fourth type. For several years water in the western end of the Channel has been characterized by a great number of pilchard eggs and a general poverty of plankton indicators, including both species of *Sagitta.* This water has been called provisionally "pilchard water" and the nature of the water has not yet been worked out.

The general principles of the circulation of water in the area are as follows:—

"Through oceanic circulation and wind effects there is a resultant flow of water through the Straits of Dover into the southern North Sea. The supply from which this water is ultimately drawn enters the mouth of the channel either from the west or south-west. It is generally conceded that more water enters the Channel than can pass through the Dover Straits, and this surplus probably drifts north-west or north past the Scillies—Land's End region, though the actual state of affairs here is not clear. To the west of the mouth of the Channel is a cyclonic swirl lying over the shallow continental plateau south of Ireland. This swirl varies in its extent and position; at times it appears to block the mouth of the Channel and at others apparently retreats farther north, thus laying the Channel mouth open to more oceanic water from the south and south-west. When there is a strong flow through the Dover Straits, water may move up Channel past Plymouth either from the swirl or from the ocean according to conditions existing off the Channel mouth. In the Channel itself there must be a body of water constantly being added to from the west and dissipated to the east, or hemmed into the coast to allow for passage of more oceanic water. The circulation of water in the Channel itself is clearly very variable from time to time." (R u s s e l l, 1938, p. 414).

It should also be mentioned that the water entering from the south-west may be of different types. Sometimes it is pure oceanic water; at others it may be coastal water of low salinity entering the Channel round Ushant (cf. P o o l e and A t k i n s, 1929).

Irish Sea and Western Coasts of British Isles.

Apart from the water flowing out from the rivers the Irish Sea draws its main supply of water from the complex existing off the mouth of the English Channel.

Its plankton appears to be mainly characterized by the *S. elegans* association. *S. setosa* occurs, however, in the Bristol Channel (R e e s, 1939) and in the Morecombe Bay area[4]). Some *S. setosa* are probably carried out round the north of Ireland (R u s s e l l, 1935 a; F r a s e r,

[4]) E. L. P i e r c e — private communication.

Fig. 5. Generalized picture of the distribution of plankton in the North Sea area. The conditions shown are such as might be expected at one moment in the autumn of a year in which the influx of Atlantic water into the North Sea from the north was strong.

//// mixed oceanic and coastal water containing the *Sagitta elegans* plankton association. EL., *S. elegans:* RH. ST., *Rhizosolenia styliformis* in the south-west Dogger Bank swirl.

|||| BID., Channel water with patch of *Biddulphia sinensis.*

≡ Coastal waters; CL; *Clytia;* S. TUB., *Sarsia tubulosa* (in late winter and spring).

\\\\ Oceanic water entering the Channel from the south-west.

The remaining area left white in the North Sea, Channel and Irish Sea is characterized by *Sagitta setosa;* SET., *S. setosa.* On the outer western edge of the *S. elegans* water is the pure oceanic water characterized by *Sagitta serratodentata* (SER.). The arrows indicate the general water circulation. It should be realized that there may in places be isolated patches of *S. setosa* water in the *S. elegans* areas.

1938); this species may also appear at times on the south coast of Ireland (F u r n e s t i n, 1938). It might also be expected to occur at places along the Welsh coast, since another associated indicator, *Turritopsis*, has been recorded from Tenby.

Along the outer western coasts of Ireland and Scotland, where the oceanic water comes in close to the coasts, the immediate coastal area carries a typical *S. elegans* community.

The North Sea Area as a whole.

With the information now available it is possible to construct a generalized picture of the distribution of plankton over the whole area. This I have attempted to do in Figure 5. The different types of water are inserted in this figure as they might be expected to be distributed at one moment in the autumn of a year in which the influx of Atlantic water into the North Sea from the north was strong. This figure is admittedly idealized and much simplified, but it is based fairly closely on the distribution shown in the different areas by the workers already cited. The general circulation of the water as shown by hydrographical observations has been indicated by arrows. The dependence of the plankton distribution on the general circulation of the water is at once obvious.

With such a diagram it becomes possible to visualize the picture as a whole and realize how changes going on in one area are linked with those in any other area.

The main points are that there is a large bay, the North Sea, containing water to which fresh water is added from the land and flowing out from the Baltic. At the same time the whole bay is open to the influx of water of oceanic origin from the north, and through a bottle-neck, the Straits of Dover, in the south. The surplus water flows out to the north. The so-to-speak resident plankton population of the North Sea water is characterized by *Sagitta setosa,* except in the coastal fringes of less saline water. The incursion of oceanic water gives rise to conditions in which a different plankton community, typified by *Sagitta elegans*, flourishes; and upon the extent of this incursion the variations in the configuration of the whole picture largely depend. Of first importance in this scheme is the fact that the mixture of oceanic water may produce a considerable enrichment of nutrient salts.

Although nutrient matter comes into the area off the land, e.g., the outflow from the Thames (G r a h a m and H a r d i n g, 1938), there can be little doubt that the whole area is chiefly dependant for variations in its productive capacity on the extent of exchange with water from the north and south-west.

The far-reaching effects of this penetration are exemplified by the productive area of the south-west Dogger Bank swirl in almost the extreme southern part of the North Sea. This swirl is notable for the development at times of intensely thick patches of diatoms, especially

Rhizosolenia styliformis. The origin of the nutrient salts which give rise to this diatom growth has been examined by Graham (1938). His charts compared with those of Savage and Wimpenny (1936) slow clearly that in 1934 this region was provided with higher phosphate concentration during the summer than the rest of the area examined. The source of this phosphate is the northern part of the North Sea, the rich water passing through the "gateway" between the Doggerbank and Flamborough.

This conclusion appears also to be backed by plankton observations, the indicators in the south-west Dogger-Bank swirl being exclusively of northern origin (Künne, 1937 a). It is also supported by Wimpenny's (1937) observations on the plankton of the Flamborough region, for here *S. elegans* is in evidence and the crustacean plankton has a characteristically high fat content.

In order that the story may not appear too simple it will be as well to give further details of Graham's work. It was indicated that the Silver Pit was also a source of phosphate-rich water, apparently owing to regeneration of phosphate in the deeper layers during periods of temporary stability. Also, while the source of phosphate enrichment is to be traced to the northern North Sea Graham found that in the summer of 1936 large areas of the southern North Sea were well supplied with phosphate. Thus he concludes that apart from the Atlantic water there is an accumulation of phosphate beneath the thermoclines, the concentration of phosphate showing more relation to the thermocline than to the salinity.

It is reasonable, therefore, to suppose that a year of strong influx of rich Atlantic water may so enrich the area that its effects will be felt for several succeeding years. The heavy production of plankton made possible will, on death, give up a supply of nutrient salts to the deeper layers. In addition there may be an increased abundance of small bottom invertebrates due to successful survival of young in the rich year or even to the incursion of large numbers of larval stages with the rich water.

Graham also gave an indication that the stability of the *Rhizosolenia* patch may be related to rainfall and its influence on the outflow of fresh water from the Humber and perhaps the Wash. If this outflow is heavy the source of supply of rich water coming through the "gateway" is blocked, and the fresher water pushed into the swirl, leading to the cessation of diatom growth.

It seems reasonable to suppose that the degree of productivity in the whole North Sea area ultimately depends upon the amount of upwelling on the continental edge, which brings nutrient salts from the store in the deeper oceanic layers. It is thus self-evident that if at any time the main supply of water should be drawn from depleted surface oceanic waters, a poverty will ensue. This effect, also, as suggested above for rich water, may last for several years until the whole volume of water has been dissipated away into the ocean and replaced once more by richer water. In this connexion it must be supposed that a considerable body of water may remain in one area for a long period of time in the form of an eddy or swirl. Otherwise it is difficult to account for the continued existence of a pure association of *S. elegans* plankton in such an area as that south of Ireland. Orton (1937) has drawn attention to the possibility of the importance of such areas for the settling of the larvae of bottom-living animals.

Plankton Indicators in Relation to Fishery Research.

With this general picture of plankton distribution in mind it is clear that the movements of rich or poor water may have far-reaching results on the fish population. On first thoughts we can realize that the plankton conditions may operate in two ways.

1. By influencing the survival of recently hatched young.
2. By causing the alteration of the routes of migrating fish.

The literature contains examples of both possibilities.

1. An example of the apparent effects of rich *S. elegans* and of poor *S. setosa* plankton is furnished by work at Plymouth.

For a number of years observations have been made at regular intervals on the phosphate content of the water, on the numbers of planktonic young fish, and on the changes in the *Sagitta* population. These results have been summarized by Russell (1936 b) and by Kemp (1938). They can be shown best in the following table which is that of Kemp, brought up to date.

Year	Phosphate in preceding winter %0 deviation from mean[1])	Young fish (less Clupeids)		*Sagitta*		
		summer spawners	spring spawners[2])	Total No. ÷ 1000	*S. elegans* %	*S. setosa* %
1924	+ 27	696	2133	—	—	—
1925	+ 9	140	1510	—	—	—
1926	+ 36	909	2051	—	—	—
1927	— 2	170	1014	—	—	—
1928	+ 23	—	—	—	—	—
1929	+ 23	321	502	—	—	—
1930	—	403	1114	91·5	94·1	5·9
1931	— 7	230	1395	117·3	16·7	83·3
1932	—16	197	1359	118·3	6·2	93·8
1933	— 5	117	1220	117·4	4·7	95·3
1934	—14	79	1065	94·5	3·5	96·5
1935	—25	37	393	48·2	3·6	96·4
1936	—16	115	372	24·0	39·7	60·3
1937	—14	174	382	26·1	3·8	96·2
1938	—16	135	315	20·4	1·5	98·5

[1]) Phosphate determinations made by Dr. W. R. G. Atkins and Dr. L. H. N. Cooper.

[2]) i.e., total young fish (less Clupeids) less summer spawners.

This table shows the correlation between the low numbers of young fish and the low phosphate content, coupled with the predominance of *S. setosa* off Plymouth. It is noticeable that the survival of the young of summer spawners was first affected.

2. The alteration of migration routes is best exemplified by the work of Hardy, Savage and Wimpenny on the influence of phytoplankton patches on the distribution of the herring shoals which give rise to the East Anglian fishery. These patches, which were chiefly *Rhizosolenia styliformis* or *Phaeocystis*, have been watched for a number of years, and they are an outstanding feature of the plankton in the area of the great herring shoaling. It was found that the position and intensity of these patches were apparently of great importance in the fishery, the landings being lowest in years of greatest concentration. On this evidence it was surmised that the dense phytoplankton has diverted the routes of shoaling fish.

Other indications of change in migration of herring which have not yet been confirmed are linked with the occurrence of *S. elegans* and *S. setosa*. E. Ford has followed the age composition of the herring shoals in the winter fishery off Plymouth for many years (for summary see Kemp, 1938). It has been a noteworthy feature that since 1931—2 there has been an absence of the younger year-classes of herring, the fishery in each successive year depending on an aging stock. As a result the fishery has now completely failed.

It is remarkable that just at the period of this change in the composition of the Plymouth herring population, a change took place in the composition of the *Sagitta* in the plankton. *S. elegans* gave way to *S. setosa* which has predominated ever since. There is a possibility that these herring results may be linked with other changes that have occurred in recent years. There have been indications of a northerly shift of the warm water fauna. At Plymouth the herring is near the southerly limit of its distribution, while the pilchard is on its northern limit. The occurrence of "Pilchard" water (see p. 181) off Plymouth may indicate that the herring have retreated farther north and the pilchard have taken their place.

We shall not be able to draw conclusions until the *S. elegans* conditions return once more off Plymouth, but it is perhaps significant that a similar herring-*Sagitta* correlation has been recorded off the Northumberland coast. Burton and Meek (1932) record that the herring fishery was poor in 1921 and 1926, in both of which years *S. setosa* was in evidence. It should, however, be noted that the herring off the Northumberland coast are feeding while those at Plymouth are spawning. The correlation with *Sagitta* off the Northumberland coast may therefore be accounted for by the large swarms of *Calanus* associated with *S. elegans* water.

In passing, it is interesting to note that the above authors also state that "There is a fairly definite positive agreement between the *S. setosa* periods and the Salmon catches of the Tyne".

These Northumberland observations deserve further comment, as they show that the Atlantic influx into the North Sea may be of different types in different years (see, e.g., Storrow, 1939). It appears that in recent years the *S. elegans* water has been close in along the eastern coasts of Scotland and northern England, yet in 1921, in which year the Atlantic influx was so marked, *S. setosa* predominated on the Northumberland coast. It seems possible that the axis of influx was in that year more centrally placed in the North Sea so that the *S. setosa* water was forced into the coast and the north-flowing branch of *S. elegans* water was absent along the Northumberland coast.

There seems also to be an interesting connexion between the *Sagitta* population on the Northumberland coast and the distribution of salps in Scottish waters. I am most grateful to Mr. J. H. Fraser for the information on salps which is as yet unpublished[5]). In 1920 and 1925 salps were very abundant in Scottish waters, and in 1921 and 1926 they were also abundant though less so. In both the years 1921 and 1926 *S. setosa* was in evidence on the Northumberland coast. Mr. Fraser tells me that there were differences in the type of distribution of the salps in the north in these years. Both in 1920 and in 1925 an invasion of salps flooded the Moray Firth, but in 1921 and 1926 the Moray Firth was free of salps. These relations between the salps and *Sagitta* may of course be coincidence, but this is at any rate the type of correlation worth watching for in future.

These few examples are sufficient evidence of the necessity for studying the movements of planktonic indicators, for it may be fairly said that they supplement the hydrographic observations. It is perhaps premature as yet to seek for further correlations until more detailed observations have been extended over a period of years. For future work it cannot be too strongly stressed that the distribution of the plankton-rich *S. elegans* water should be watched. The distribution and extent of this water will possibly be of considerable importance for the survival of the young of fish breeding in the area. It might perhaps, therefore, be expected that some such correlation will be shown for the haddock.

The year 1923 was an exceptionally good brood year for haddock and there is evidence that the plankton conditions were unusual in that year. The haddock fry appeared in unusual numbers in Danish waters where a good fishery resulted in the winter 1925—6. In 1923 the planktonic fauna in the Kattegat and Belt Sea was more oceanic than usual. The siphonophores *Physophora hydrostatica, Galeolaria truncata* and *Dimophyes arctica,* and euphausians were recorded. These conditions have been discussed by Kramp (1927, p. 183) who showed that a study of the Medusa fauna was of great assistance in understanding the relations and movements of the different water masses.

[5]) Fraser, J. H. The distribution of *Thaliacea* in Scottish waters, 1920—1938. Fisheries, Scotland, Sci. Invest. (unpublished).

The Practical Use of Indicators.

The more experienced the plankton worker, the wider is his knowledge of the species of the plankton as a whole. If he be a specialist in a large group such as the copepods he can recognize differences in the distribution of many species (see, e.g., Farran, 1920). In general, however, probably many of these species form the characteristic association of organisms which accompanies one or two more striking animals. It is these latter which should be selected as indicators, for it is essential for rapid examination of large numbers of collections that they should be easily seen.

The general association occurring with the few selected species should, however, be borne in mind, for under certain circumstances it may afford a valuable clue as to the type of water. It is possible, for instance, for the chosen indicator species to be itself absent. Thus pure *S. elegans* water may be recognized in some areas by the presence of large numbers of *Cosmetira, Laodicea, Aglantha, Themisto* and euphausians and the absence of indicators of other types of water, even though *S. elegans* itself be absent; for even the holoplanktonic species may show great seasonal fluctuations in their numbers.

Those species occurring in the plankton which have a bottom stage in their life history naturally show considerable seasonal fluctuations and are only of use as indicators in certain seasons. With a knowledge of the life histories and seasonal fluctuations in numbers of both holo- and mesoplanktonic animals a worker in one area will probably be able to see in his results much more than is at first obvious from the mere numerical data.

In regions of mixing it may not be so much the actual numbers of the indicators that are of importance, but rather the relative proportions of the indicators of the different types of water. The boundaries between waters of different types may sometimes be clearly defined by the plankton indicators. At other times there may appear to have been mixing over a considerable area. Unless collections have been made separately at different depths it will be necessary to examine the hydrographic data before any conclusions are attempted. A broad region of apparent mixing may be produced by water of one type overlying that of another type. An example may be found in the northern North Sea, where in the north-eastern area *S. elegans* and *S. setosa* may sometimes appear mixed. This has been shown by Fraser (1939) and Furnestin (1938) to be due to the presence of *S. elegans* water in the deeper layers.

A knowledge of the vertical distribution of the animals and of their habits of vertical migration must also be taken into consideration.

In practice it is probable that the larger plankton animals are more useful as indicators than unicellular organisms which reproduce very rapidly. An increased knowledge of the life histories and size changes of diatoms may, however, prove of value (see, e.g., Wimpenny, 1936, and Garstang, 1937).

In conclusion there are certain aspects connected with the use of plankton indicators to which future attention might profitably be directed.

The life histories of certain plankton animals have now been studied in detail and the differences in size of individuals of successive generations noted. To a certain extent it should thus be possible to follow the history of any one brood and its movements in the water masses from place to place. Such a study should be of great value in tracing the extent of the resultant water movement in a given time.

Some species also show structural variation according to geographical distribution and a detailed knowledge of these differences can be of value in tracing the origin of water masses. Possibilities in this direction have already been indicated by Fraser (1939) in a study of the varieties of *S. elegans*.

A close study should also be made of the mortality rates and reproductive capacities of different organisms as they are carried by water movements into areas in which their environmental conditions become changed.

All the above types of observation may prove of practical value, but they involve also problems of purely scientific interest, and if treated from the latter point of view they may in the end produce results of even greater practical importance. For bound up with the problems of variation, mortality, and reproduction is the question why certain organisms are apparently only able to survive in certain types of water.

One may postulate that in passing from the ocean to the coast changes in physical and chemical factors may gradually eliminate the purely oceanic species until a pure neritic community is reached. It is more difficult to suggest why this should act in the reverse direction, i.e., why neritic holoplanktonic organisms do not survive in pure ocean waters. These problems involve the study of the presence or absence of toxic or limiting substances, competition between species and their habits of life. Harvey's (1939) observation that the diatom *Ditylum* did not grow successfully in enriched natural sea water taken at certain times of year are significant. There are, however, many factors to be considered and it is beyond the scope of the present paper to discuss these.

It is at any rate certain that a study of the water from the biological viewpoint often throws quite a different light on observations made by more strictly hydrographical methods. In certain key localities also plankton indicators alone may prove of immense value as a guide to the general conditions. But the use of indicators should be regarded only as one more tool in the oceanographer's bag to help with other methods in picking the locks which bar us from knowledge of life in the sea.

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