

MIGRATION IN BIRDS AND FISHES

BY

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INTRODUCTION

Our knowledge concerning the periodical movements in animals called migrations is chiefly based on observations on birds. By and by, however, a number of facts concerning migration in other animal groups have been assembled and it seems worth while to compare them with those known for birds. There is the more reason to do so here because the victim of this jubilee is interested in birds and fishes alike. Though I shall not restrict myself to these two groups they will take more place than the rest.

In the following I shall deal with North to South and South to North migrations chiefly. In the hope to succeed and make my ideas comprehensible to those who are not specially acquainted with this particular field I shall begin with a very short description of the migration of some animals in the sea, which may be used as a starting point for the comparison which follows next. These animals are the cuttlefish (*Sepia officinalis* L.), two species of fish: the anchovy (*Stolephorus encrasicholus* (L.)) and the tunny (*Thunnus thynnus* (L.)) and, finally, a mammal: the humpback (*Megaptera novaeangliae* (Borowski), one of the whales.

OBSERVATIONS

I—THE CUTTLEFISH (*Sepia officinalis* L.)

The cuttle of the European coast of the Atlantic in winter inhabits the continental slope south of England. In spring and summer the animals revive the french coast and part of them enter the North Sea. Here they spawn in the southern part where the temperature of the shallow coastal water rises to about 17-21° maximally. As they are restricted to this southern part and, moreover, they arrive somewhat earlier in the Scheldt estuary than near Den Helder there is little doubt that they enter the North Sea through the Straits of Dover and not in the North. At first sight it may appear somewhat strange to expect migration of a southern species around Scotland, but this is a quite common route for other species, as will follow below.

The first animals near Den Helder are regularly caught in the first decade of May. Dates of arrival for the different years are omitted here, because the migration of this species will be dealt with more fully in a separate paper. These early animals are 3-4 years old or perhaps partly older. Their main migration takes place during May; part of them is caught up to July. The animals of 2 years old reach us from the middle of May onward; they are most numerous in the first half of June, not a few are found up to the middle of July, most of them have disappeared before September. The one year old animals, finally, reach the surroundings of Den Helder from the beginning of July onward; their maximum lies in the first half of August, after that they diminish, generally speaking to disappear before October. After a period of rest small numbers of cuttlefish are regularly caught, especially during the onset of cold weather, in December and January.

It is of interest that on an average the males of *Sepia* arrive somewhat earlier than the females.

The cuttlefish can well be compared with a bird returning to us from the South in spring, an arbitrary song bird or a lapwing (*Vanellus vanellus* (L.)), for instance. Here too we find a more or less constant date of arrival; here too the males often arrive before the females and the old before the young. In *Sepia* we even find differences in the time of arrival of 1, 2, and 3-4 years old animals, a fact which, I think, is new in relation to birds. In many bird species, just as in the cuttlefish, the one year old animals partake in migration though they are not sexually mature. We even find in *Sepia*, as in birds, a revival of migration at the onset of cold weather in winter (the so called rushes of EAGLE CLARKE), apparently of animals which remained behind in favourable places.

Beside these points of agreement there is a point of difference between the migration of the cuttle and that of birds: northward migration of the cuttle continues until August, whereas bird migration in northern direction ends in the first half of June already. We will find this to be a general rule: migration in the sea is much later than that on land due to the shifting of water temperature when compared with that of the air.

2—THE ANCHOVY (*Stolephorus encrasicholus* (L.))

More or less comparable to *Sepia* is the anchovy.

This species too in winter inhabits the continental European slope south of England, to spawn near the coast in spring and enter the North Sea. Like *Sepia* the anchovy's spawning grounds remain restricted to the southern part of the North Sea (especially the Dutch waters), but after spawning the species may be found even near Norway and Scotland. As the northern North Sea is not populated before midsummer or autumn there is little doubt the animals enter the North Sea by way of the Straits of Dover. Part of them probably leave it around Scotland, however.

So called first dates of arrival of this economically valuable species of fish are known for a long series of years. The mean date for the Scheldt is April 14, but there is much difference from year to year, the species arriving much later in cold than in warm springs. The extremes range from April 1st to about April last. In the northern Zuyderzee and in the Waddenzee the early animals appear some 9 days later, a difference the isotherm of 6.5° centigrade needs to move from off the Zeeland coast to the North Sea off Den Helder. According to REDEKE the anchovies left the Zuyderzee from July onward, but in 1948 their numbers decreased in the Waddenzee near Texel in the end of May already. Most adult (i.e. two years old) animals as a rule left the Zuyderzee before September, but young were regularly found in October and sometimes in November. Near Den Helder and in the southern part of the North Sea the species during years of great abundance may be rather common in October and November, winter 1948-'49 some few were caught in December and one in the beginning of February; in this connection it should not be overlooked that the species in 1948 was exceptionally abundant and that winter '48-'49 was very warm. This occurrence in late winter is also known for the northern North Sea, where the species in summer is absent. In Oslofjord it was especially found in October, along the Scottish eastcoast the animals were found between November and January, data for the Scottish westcoast are known for the months of January and February. For references the reader is referred to a later paper.

The anchovy may well be compared with a bird like the chiffchaff (*Phylloscopus collybita* (Vieill.)), arriving rather early in spring and therefore in its arrival being more or less dependent on the temperature of each particular year; the chiffchaff too exceptionally may be observed till mid-winter.

But the anchovy's migration shows a peculiarity which at first sight appears new in the light of bird migration. The data show that it moves north after spawning and gradually fills the North Sea so to speak, finally to disappear around Scotland. That these animals in the North come from the South is, except by the dates of occurrence, made probable by the find of young specimens (born that same summer) in Oslo Fjord. COLLETT's supposition (1905) that these can have been born there seems improbable. I think they came from the Zuyderzee. Anyhow, we have the remarkable instance here of a species entering the North Sea in the South, spawning there and after spawning migrating northward. Even from the point of view of bird migration, however, this is not so remarkable, as we find just the same northward movement after breeding in the guillemot (*Uria aalge* (Pont.)) from Heligoland, which is found along the Norwegian south and west coast especially in October and November (DROST 1930b, STECHOW 1938). It is further wellknown that such a northward migration after breeding plays a rôle in herons, sea swallows and some other species of birds (TOWNSEND 1931, and others).

3—THE TUNNY (*Thunnus thynnus* (L.))

The tunny is indigenal in the Mediterranean and the Atlantic Ocean outside it. It there propagates in April-May, migrates northward after spawning and appears in most summers in the northern part of the North Sea, along the Norwegian westcoast up to Bergen (exceptionally the Lofoten), and in the Skagerrak and Kattegat. Its southern limit in the North Sea runs from about Smith's Knoll to the Doggerbank and the Skaw, the species is not found in the southern and southeastern part and there is no doubt it enters the North Sea in the North only. It also leaves the North Sea there. References will be given in a later paper.

According to RUSSELL (1934) the first tunnies on their way northward appear off the western entrance to the English Channel in the end of June. Because they are such enormous swimmers there is little difference in the times of arrival within the northern North Sea (the Norwegian west coast and the Kattegat included), which is invaded in July (LE GALL 1927 and 1929). According to WOLFE MURRAY (1932) the Doggerbank is reached from the second half of July onward, his extremes for 9 years being July 17 and August 2. It follows from this that the distance from the English Channel to the Doggerbank (around Scotland) may be covered in some 3 weeks and that the distance Gibraltar-Doggerbank may take some 6-8 weeks. The tunnies practically disappear from the North Sea about the end of September, WOLFE MURRAY's dates for latest animals range from September 26 to October 12, with one observation for November 1. In the Kattegat (JENSEN, 1937) they have been observed up to November, but several times the animals from October or November were dead or dying; I suppose that low temperatures combined with low salinities may have caused death in these cases. Along the Norwegian coast late animals have been seen till the end of November and even in the beginning of December (COLLETT, 1902). Schools of tunnies on their way southward have been seen in November and December along the margin of the continental slope west of the English Channel (LE GALL, 1927).

In the tunny we find a northward migration after spawning in an extreme form. This species makes a trip of some 6-8 weeks to the North and back again with the result that it can stay there for some 3 months during the warmest period of the year. In entering the North Sea it does not take the shortest route through the Channel and Dover Straits, but makes its way around Scotland.

Incidentally, SANZO's observation should be mentioned that the young arrive later on the Norwegian coast than the old animals (see RUSSELL, 1934).

4—THE HUMPBACK (*Megaptera novaeangliae* (Borowski))

Details on the humpback's migration in northern Atlantic waters have been published by INGEBRIGTSEN (1929). The northern population of this species

has its breeding grounds in the Atlantic Ocean north of the equator, where the calves are born in spring. The animals of the eastern Atlantic migrate north-eastward to pass the arctic summer along the edge of the polar ice. Nowadays the species is quite rare, but at the end of the 19th century they were captured in fair quantities. INGEBRIGTSEN's data especially refer to the waters between Finmarken and Bear Island. The animals arrived there from between Iceland and the Faroes (also the Shetlands) between the end of June (once June 5), and the second half of August (once the beginning of September, see INGEBRIGTSEN, p. 8). They disappeared towards the Northeast, in the direction of Frans Jozef's land, and remained in the high North during the period September to January. On their way back southwestward they passed Bear Island between February (earliest date January 25) and the beginning of April (latest date April 10). Only large, adult animals and calves (accompanying their mother) partook in these migrations; it seems that the non-mature animals (the calves excepted) did not make these long journeys.

The humpback forms a further instance of a species which propagates in the South and then migrates northward (in this case over enormous stretches) to pass the arctic summer in the high North. The fact that the times of migration fall so late in the year means that the arctic summer in this case must have shifted enormously. In connection therewith INGEBRIGTSEN points to the fact that the humpback of the western Atlantic, which migrated to New Foundland and Davis Strait, returned south at a much earlier date, as it was caught on the breeding grounds near the West Indies from February to April. This time difference between the arctic summer in the extreme eastern and western ends of the Atlantic Ocean be due to the enormous influence of the warm Atlantic current. But even if this difference between the warm Atlantic current in the eastern against the cold polar current in the western Atlantic is taken into account the arctic autumn cannot possibly have shifted to February-March if we limit ourselves to the surface water. The shifting of the seasons in a measure as demonstrated by these whale migrations can only be understood if we are concerned with the deeper waters, which may retain their heat so very long, see fig. 1-3. Apparently, then, these whales for their food depend more on the temperature of the deeper than on that of the surface water.

DISCUSSION

I will now use these data for a discussion of the following points:

- 1—the periodicity of migration;
- 2—the function of the migratory movements from South to North;
- 3—the migration route and the problem of orientation.

I—THE PERIODICITY OF MIGRATION

GROEBBELS (1928) and many others after him have worked with the inter-Bijdragen tot de Dierkunde, Afl. 28.

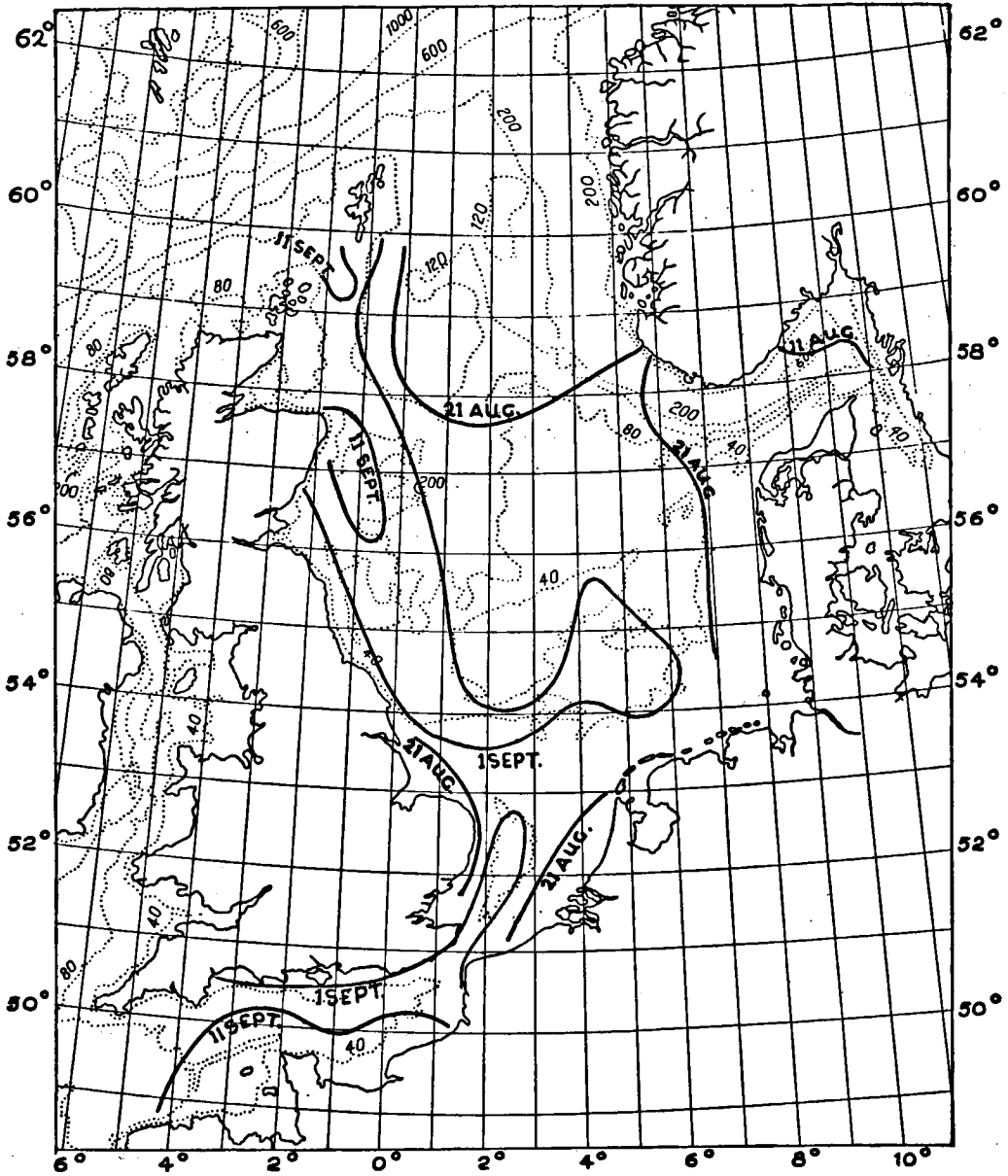


Fig. 1. Time of temperature maximum of the surface water within the North Sea (mean for the years 1902-'06). In the neighbourhood of land the maximum is found in the second half of August. In the western part, where the Atlantic water enters from the North, and continental influence is far away, it is found in the beginning of September. Data from Bulletin trimestriel Cons. Exploration Mer, Vol. 1906-'07, Supplement, plate XIII.

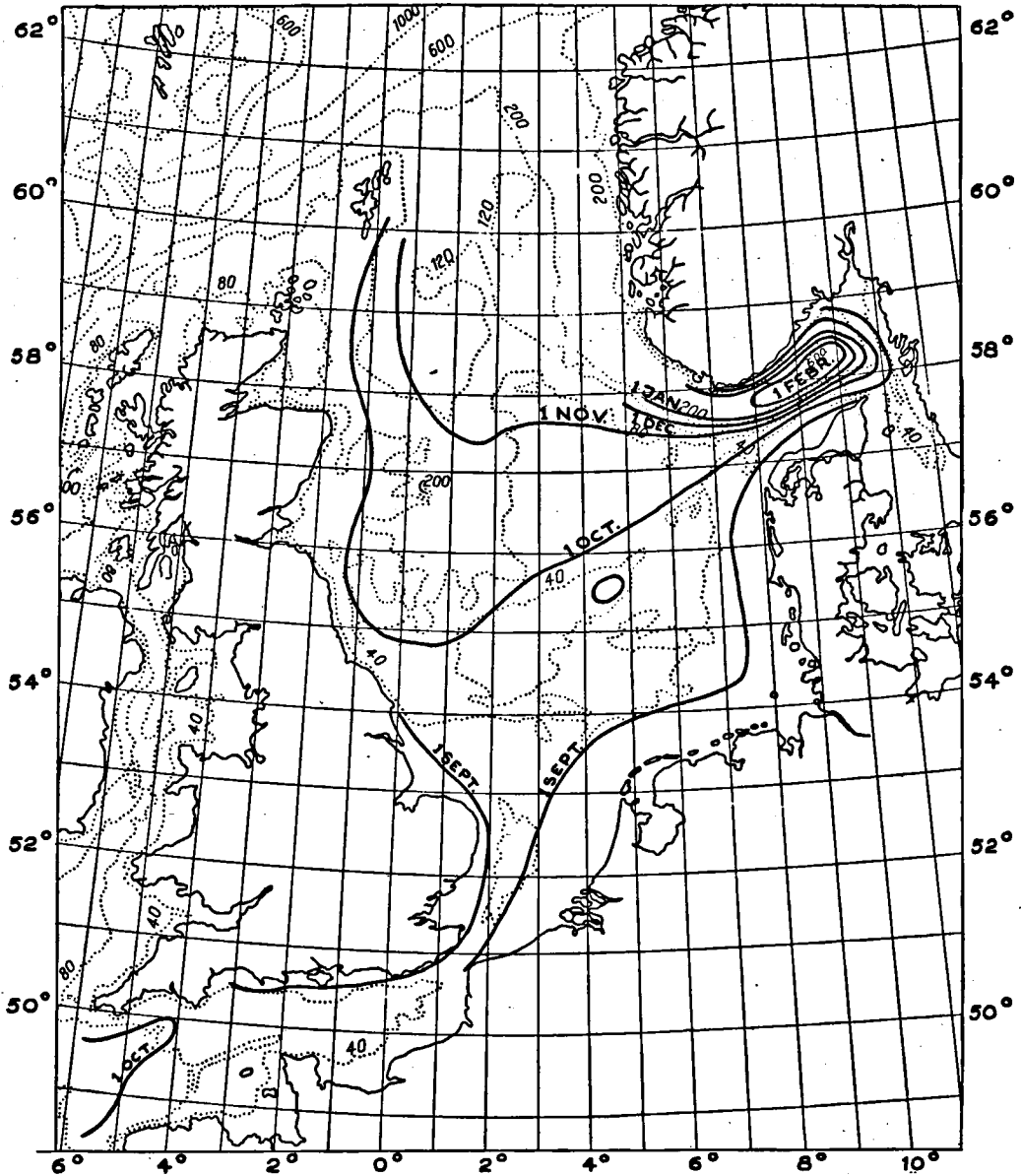


Fig. 2. Time of temperature maximum of the water near the bottom within the North Sea (mean for the years 1902-'06). The maximum shifts from medio August in close neighbourhood of the continental coast to January and even the beginning of February in the Norwegian Channel, where the depth exceeds 200 metres. Summer occurs in the coldest part of the year there. Source of data as in fig. 1.

pretation that the migratory instinct at a given moment may awake by the influence of some primary factors, whereas it would depend on factors of secondary importance whether migration really starts the moment the instinct awakes or not. GROEBBELS distinguished accordingly between "Zugdisposition" and "Zugstimmung". In terms of our present knowledge this would contain that the gradual increase in daylength in spring, so important in the physiology of reproduction and migration in birds and mammals, would awake the instinct (bringing the bird into Zugdisposition), but the cooperation of other

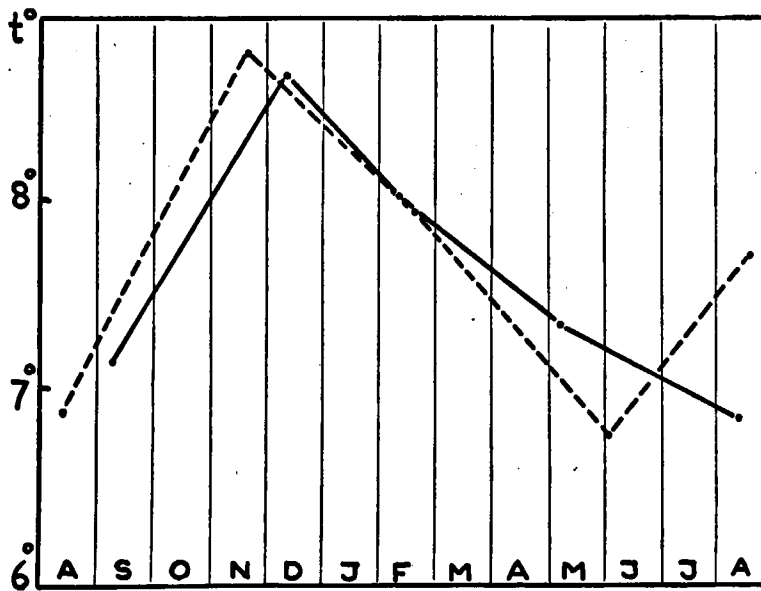


Fig. 3. Temperature of water at 200 metres depth in the northern part of the Norwegian Channel (long. $3^{\circ} 10' E$, lat. $61^{\circ} 32' N$) in August-September, November-December, February, and May-June of the years 1902-'04. Drawn line: 1902-'03, dotted one: 1903-'04. After OTTO PETTERSSON in: Svenska Hydrogr. Biolog. Kommiss. Skrifter, Vol. 2, p. 5-6, 1905. Summer and winter have reversed.

factors—certain components of the weather, the individual's physiological and psychological state at a certain moment—would be necessary to change the bird's Zugdisposition into its Zugstimmung.

I think we can better do without this distinction, in which the impulse to migrate awakes in two stages so to speak, and replace it by another interpretation, namely:

There are two groups of factors influencing the time of onset of migration: 1—the periodical factors like the gradual change in light and temperature; 2—the non-periodical factors like the components of the weather and other factors influencing the bird's physiological and psychological condition. These two groups of factors work at any moment as one indivisible whole. As one

whole they succeed (or do not succeed) in lifting the animal over the threshold, where migration starts. A distinction into two stages is impossible.

We must further assume, that the relative importance of each of these different factors is quite different in different seasons and at different moments of one season. Through the researches of ROWAN (1938) or for migration more especially of WOLFSON (1942) we know that light, in casu the increase of day length, is quite important when spring migration shall start and the bird must be unhooked from winter conditions. This does not mean that the components of the weather or the psychophysiological state of the bird would not be important too; generally speaking, however, their relative constancy in the bird's winter quarters may cause the relative importance of light. The latter, then, becomes the cause of the more or less constant first date of departure. When the bird is once on its way it is difficult to analyse what rôle the periodical and unperiodical factors play in relation to each other; one thing is certain, however: that bad weather conditions, especially a low temperature, may suppress the impulse altogether, and that favourable conditions, especially a high temperature, cause its increase. This has been shown both experimentally and through direct observations. Experimentally, by using the unrest of caged birds as an indication for the strength of the migratory impulse. PALMGREN (1937) and SCHILDMACHER (1938) have shown that a temperature rise in spring causes increased unrest in robins (*Erithacus rubecula* (L.)). But direct observations too are quite convincing. Not only do they show that migration is directly influenced by temperature (DROST, 1926 and 1930, SCHENK, 1929 and 1931, NICE, 1937, and others), there is a large amount of evidence in Europe as well as in America that favourable conditions give early and bad conditions late dates of arrival and that for that reason there is much dispersion in the first dates for different years, above all for species arriving in the earlier part of the season (see especially SCHENK, 1929, HAGEN's papers and NICE, 1937). The same follows from such maps as have been given by LINCOLN (1935) for America and SOUTHERN for Europe, in which lines of simultaneous arrival and certain isotherms are given for half a continent. SOUTHERN's map for the willow warbler (SOUTHERN, 1938) shows that the latter roughly follows the isotherm of 9° centigrade, also where the isotherms in certain areas remain behind so to speak¹). The connection is rough in so far that the birds lag behind in the South and are in advance of the isotherm in the North, a fact which has also been described (and that in a very convincing manner) for the songsparrow by Mrs. NICE; thus presumably showing that they need somewhat higher temperatures during the early than during the later part of their journey. Apart from this detail, it is clear enough that there is a direct

1) Data for the redbacked shrike (*Lanius collurio* L.) show quite different a behaviour (ECKE, 1936, SOUTHERN, 1941), the northwestern route through Europe hardly crossing the isotherms. Nevertheless, the connection between dates and temperature in the willow warbler and other species is certainly not accidental.

connection between time of arrival and temperature. But if the date of departure is fixed by light, favourable conditions cannot accelerate arrival in the North unlimitedly, and one would presume that the earliest dates of arrival of a series of years (occurring as a result of quite favourable conditions during the whole of the journey) must fall very little apart. The facts show that this does not hold in all cases and that for some species quite early dates may occur. Up till now I was inclined to assume that these were proof of an exceptionally early start of the journey, which would speak for temperature (besides light) influence on the first awaking of the impulse. SCHENK (1929) has given an instance, however, of very early arrival of the cuckoo in northern Europe in 1890, though arrival in southern Europe was not *so* early. This means that even this exceptionally early arrival may be explained through favourable conditions in Europe and not through an abnormally early departure from the winter quarters. The fact of these quite early arrivals, therefore, need not be in contradiction to our supposition that the first departure of these birds is influenced more by light than by temperature. For birds wintering at our own latitude one could imagine, however, that the rise of temperature in certain years can anticipate day length so to speak and that in such years temperature rather than light may awake the impulse. In that case extra-early dates of arrival in the North could result from temperature instead of light influence on the start. I know of no instance of this kind in birds, am inclined, however, to ascribe some few abnormally early dates of arrival for the squid (*Loligo vulgaris* Lam.) to this cause²). A similar reasoning may apply to the autumn migration, with the exception that decrease of day length has never been shown to awake the migratory impulse. We do know, however, that falling temperatures, which in spring certainly suppress the impulse, activate it in autumn. This has been shown by SIIVONEN and PALMGREN (1936) and WAGNER (1937) for the song thrush (*Turdus philomelos* L.), by MERKEL (1938) for the robin (*Erithacus rubecula* (L.)) and the white-throat (*Sylvia communis* Lath.). WAGNER also states that the unrest in autumn is not only increased by a fall, but also decreased by a rise in temperature. All this means that a rise or fall in temperature has quite different effects in different seasons and in this connection it is important that an aperiodical factor, viz. a sudden fall of temperature, eventually together with snow fall, without the help of a periodical factor at all, may cause migration in winter in the form of rushes at the onset of cold. This means that in last instance

2) The periodicity of *reproduction* in water animals is in favour of this supposition. Contrary to what is known for birds and mammals it is certainly governed by temperature, as many data point in that direction (see also BULLOUGH, 1939). There are also experiments with sticklebacks (*Gasterosteus aculeatus* L.), frogs (*Rana esculenta* L.) and newts (*Triturus viridescens* (Raf.)), which speak for temperature influence as the cause of the periodicity of reproduction (CRAIG-BENNETT, 1931, IFFT, 1942). If the periodicity of reproduction in water animals is caused rather by temperature than by light, however, the same may hold for the periodicity of migration.

the periodical influence of light or temperature may be wholly replaced by an aperiodical factor. And this, again, means that a distinction between Zug-disposition and Zugstimmung can better be replaced by the above interpretation³).

Notwithstanding all this the constancy of the dates of arrival is little less outspoken in water animals than in birds and the agreement in the phaenology of migration in water and land animals is striking. Not only does the constancy in dates attract attention. Just as in birds the dispersion of the dates in early spring (March-April) is much greater than later in the season (May); this is logical because we may expect sea animals and birds to react in a similar way to low temperatures. The agreement goes farther, however. In both birds and sea animals the old individuals often arrive earlier than the young ones. The cuttlefish forms an extreme instance in this respect, the young arriving some two months later than the old ones, and even two and three years old animals show a difference in their times of arrival. We find a later migration of the younger animals also in the squid *Loligo vulgaris* (Lam.) (TINBERGEN & VERWEY, 1945), the garfish (*Belone belone* (L.)) (COLLETT, 1903, p. 172), the tunny (*Thunnus thynnus* (L.)) (see above) and certainly many other species. All this means that old and young in sea animals as well as birds have different threshold values for the awaking of the migratory instinct with the result that on arrival the young ones meet with higher temperatures. It is probable that they need these for physiological reasons in general, as the young of many animal species seek higher temperatures also outside migration time⁴). The third point of agreement is the occurrence

3) To make my point of view better comprehensible the following concrete example be given. DROST (1929), in dealing with southward migrations at the onset of cold in spring says that such movements can only take place "solange der Zugtrieb nicht erloschen ist"; if it has been extinguished, DROST believes, the birds can no longer migrate and may be killed. DROST here supposes that the possibility to migrate may, for instance, remain from October to February, then to disappear. Several other remarks in the same paper are clearly based on the same interpretation. Displacement data for birds and other observations show, however, that the possibility to migrate is always present, but it depends on a number of factors whether the bird at any moment shall migrate or not. The main causes that birds sometimes do not partake in winterrushes and remain behind, gradually to starve from hunger and cold, are, I think: 1—that the animals especially react on *the change, the sudden fall* of temperature, or on *snowfall*, and are not (or little) activated by a *continuation* of frost or the *presence* of snow; 2—that in many cases the birds have suffered so much from the gradual worsening of winterconditions that it is no longer possible for bad influences (temperature fall, etc.) to bring them over the threshold for active migration. My conviction for the truth of both points rests chiefly on personal observations, but in connection with point 2 the researches and ideas of MERKEL (1937 and 1938) are specially valuable, whereas the observations of DROST, who gave much attention to these winter movements (DROST, 1929, 1937 and 1940) are of much importance.

4) In this connection it is interesting that in the herring (*Clupea harengus* L.) in the southern North Sea, which spawn during the period of sinking instead of rising temperatures, the younger animals arrive earlier on the spawning places than the older ones (HODGSON, 1934). The contrary seems to hold for the plaice, however (personal communication of A. C. SIMPSON to the writer).

of species in which the males arrive earlier than the females. *Sepia* forms a fine instance. The occurrence of different threshold values for migration in the two sexes of one species in so different animals as cephalopods and birds means that this physiological difference too must be important. L. TINBERGEN (TINBERGEN & VERWEY, 1945) has shown that in birds the earlier arrival of males has connection with the staking out of territories. We do not know whether this holds for the cuttlefish too, but the fact itself may form an indication in that direction.

Finally, besides all this agreement there is a great difference in land and sea migration. But this difference, again, is only logical. Migration in sea animals has shifted with the seasons in the sea. Spring migration does not start in January-February with skylarks (*Alauda arvensis* L.), starlings (*Sturnus vulgaris* L.), thrushes (*Turdus*), etc., but in the end of March with garfishes (*Belone*), red gurnards (*Trigla lucerna* L.), etc. It does not end in the beginning of June with the warblers and relatives (Sylviidae), but in August with the arrival of young *Sepia*'s. Autumn migration does not start in June with the migration of lapwings (*Vanellus vanellus* (L.)), curlews (*Numenius arquata* (L.)) and the like, but probably in August only with such species as *Sepia*, the squid (*Loligo vulgaris* Lam.) and others. The end of the autumn migration, on land as well as in the sea, is caused by spells of cold, but in deeper waters the seasons have shifted so far that we find the humpback migrating southward between February and April.

2—THE FUNCTION OF THE MIGRATORY MOVEMENTS FROM SOUTH TO NORTH

Reflecting about the spring migration of birds we see them before us striving towards their breeding haunts and we do not hesitate to consider the seeking of breeding places as the function of their migration. We fail to realize the fact that so many non-mature animals—especially Limicolæ—partake in these migrations without reaching their breeding grounds at all. We neither reflect about the fact that not a few birds migrate farther as soon as breeding is over, to turn South only late in summer or autumn.

In the sea matters are quite different. One is constantly impressed by the fact that so many of these South to North migrants make enormous journeys, which have nothing to do with reproduction. First of all, here too, there are many immature animals, for instance of the cuttlefish (*Sepia officinalis* L.), the John Dory (*Zeus faber* L.), the red gurnard (*Trigla lucerna* L.), and others, partaking in migration. Secondly, however, there are many species which travel northward though they propagate in the South: the whales, tunnies (*Thunnus thynnus* (L.)), basking shark (*Cetorhinus maximus* (Gunn.)), sunfish (*Mola mola* (L.)), swordfish (*Xiphias gladius* L.), John Dory (*Zeus faber* L.) and others.

What do all these animals seek in the North if their aim is not a breeding

place? There can be no doubt that the function of their travels is to seek areas in which food is abundant. The northern seas are inhabited in winter by few species only. After the long period of relative darkness they are rich in compounds which form the base for an upgrowth of new phytoplankton and animal life. These compounds have partly been brought there from the South, partly been formed in the North. The quantity of organic matter in summer is thus enormously increased. It would remain partly unused, if the small number of higher animals did not increase except by reproduction. Migration forms the way to fill the gaps. Through it the food quantities are exploited. This must mean that the northward migration of birds has a double function: migration to areas rich in food coincides with that to the breeding places. The breeding places are situated in the areas rich in food here.

Why then, however, are matters in the sea so different from those on land? Why do so many animals in the sea propagate in the South, to travel northward after the breeding season? The reason must lie in the shifting of the seasons, the slow rise (and fall) of the temperature of these enormous water masses. An instance may show this better than long reasoning. A southern species like the tunny, which needs a rather high temperature, certainly cannot visit the North Sea before June or July. One must well realize that June in the northern North Sea is colder than October, the mean surface temperature not reaching more than 10-12° centigrade. If, now, the tunny would use the North Sea for spawning, very little time would remain for the upgrowth of the brood (assuming the temperature would be sufficiently high for upgrowth, anyhow), and this would mean a constant danger to the species. Southern species therefore can better spawn in the South and migrate to the areas with abundant food when spawning is over. In that way we get two migrations: that to the spawning grounds and that to the North.

Part of the southern animals can spawn in the southern North Sea. Here the temperature rises much earlier than in the northern part and there remains a longer period for the upgrowth of the brood. Such species as the anchovy (*Stolephorus encrasicholus* (L.)), the cuttle (*Sepia officinalis* L.) and the squid (*Loligo vulgaris* Lam.) show, however, that even here circumstances are favourable for the upgrowth only in warm years and that even here many summers are much too cold. Moreover, however, the southern North Sea can be used for reproduction only by such species, which are not excluded from the possibility of inhabiting it. For the tunny, for instance, the salinity of the southern North Sea may be too low, whereas the depth may be too shallow.

I stated already that northward migration after the breeding season also occurs in birds. A fine instance form the guillemots of Heligoland, which in October and November are especially found along the Norwegian south and west coast (DROST, 1930b, STECHOW, 1938), where they feed on sprat (RÜPPELL, 1940). A northward migration after breeding has been described for American herons by TOWNSEND (1931); it also occurs in European herons

and some other species in Europe, but a good summary of facts has never been given. It is no accident, that most of these species are water birds⁵).

Before leaving this chapter mention should be made of the fact that part of these summer migrations to areas rich in food go in other directions than North. This is most clearly shown in the case of the guillemot. Not only Heligoland birds collect along the Norwegian coast, they mingle there with birds from Scotland (STECHOW, 1938). The reason is that these areas with plenty of food even in the North are more or less restricted. In the case of the guillemot its chief food (the sprat) is much more numerous along the coast of Scandinavia than somewhat farther west or in the Heligoland Bight. This means that the journey for the Heligoland guillemots is only directed northward, because Heligoland accidentally is lying to the South of these areas rich in sprat. As, generally speaking, the rich areas both in the sea and on land are lying in the North the chance that these summer movements are directed northward must be greater than that they are directed South, West or East. This does not alter the fact that in principle such migrations, if food is their chief object, may go in any direction, and it is in this light that we must consider the summer migrations of the starling (*Sturnus vulgaris* L.) from the Baltic States in westward direction (KRÄTZIG, 1936a and b, SCHÜZ, 1932), the migrations of the blackheaded gulls (*Larus ridibundus* L.) from mid-Europe to the Northwest, the movements of the Sheldducks (*Tadorna tadorna* (L.)) of part of western Europe to the German Bight, and those of other ducks to the Volga delta and similar places (HOOPERHEIDE & KRAAK, 1942, p. 15)⁶. Perhaps the early migrations of the lapwing (*Vanellus vanellus* (L.)), on which so much has been written (SCHÜZ, 1932, DROST and others, 1934, PUTZIG, 1938, KLOMP, 1947), may be seen in the same light, though, personally, I am not quite convinced that there is a more or less distinct pause between the early summer and autumn migration of this species, which could be used as an indication for the true character of these movements (see DROST and others, 1934).

It should finally be added that in ducks the summer areas mentioned, except for food, are certainly also valuable as grounds for quiet moulting. Moulting may even be the chief point here (HOOPERHEIDE & KRAAK, 1942). The fact that there is such a remarkable agreement between the migration to summer quarters in Sheldducks and guillemots makes one ask whether guillemots too

5) It is remarkable that in this northward migration especially young birds (born the same year) seem to partake (DROST, 1930b, DROST & DESSELBERGER, 1932, TOWNSEND, 1931, STECHOW, 1938).

6) In a species like the starling, large quantities of which in summer move from the Baltic States to the lowland plain of northern Germany, to remain there till the autumn migration, one may well ask what may be the reason that the number of breeding birds in northern Germany is not much greater, so that the food quantities present there could be exploited by breeding birds themselves instead of by Baltic starlings. Temperature, which plays such an important rôle in the North Sea, cannot be of influence here.

partly may seek the Norwegian coast for moulting. That this cannot hold follows from the fact that their moult falls late in summer, whereas they visit the Norwegian coast especially in October. Further, the majority of the guillemots (see above) are young, and these do not moult their primaries.

3—THE MIGRATION ROUTE AND THE PROBLEM OF ORIENTATION

Can our knowledge of migration in sea animals increase our insight into the migration of birds also in matters of routes and orientation? Can our knowledge about orientation in birds help us better to understand orientation in sea animals?

What at this moment is our view regarding orientation in birds?

I think, it is now generally agreed that we cannot do without the conviction that the young bird has inherited a certain direction in which it leaves its breeding quarters. This was supposed long ago, but the number of adherents to this supposition has gradually increased and no one doubts the fact since it was more or less proved for young storks (*Ciconia ciconia* (L.)) in Europe (THIENEMANN, 1931, SCHÜZ, 1934, KOEHLER, 1943, p. 178) and for young crows (*Corvus brachyrhynchos* Brehm) in Canada (ROWAN, 1946). Displacements of birds during migration have shown the same in those cases where the direction of their migration after displacement remained unchanged (young sparrowhawks: DROST, 1938, and KOEHLER, 1943, hooded crows: RÜPPELL, 1942 and 1944, RÜPPELL & SCHÜZ, 1948). Birdmarking has shown that this innate constant direction may be quite different for different populations of one and the same species. This direction leads the bird to its winter quarters, whereby concentration of birds against seas, lakes, coasts or mountains, and also ecological influences or tradition, may influence the route. Finally, in the South, we may suppose the animal to come to rest where milieu conditions are sufficiently favourable to extinguish the impulse.

When next spring the bird returns to its birth place, we could imagine that the same constant direction and the knowledge of the route passed in autumn may suffice to guide it. Transportation experiments of birds in the breeding season, however, have made us to assume that the old bird knows the geographical position of the place in question and that it could possess, except its sense of direction, also a sense of geographical position. Because this sense of geographical position represents something quite incomprehensible to us, there has been a constant search for a sense-organ, which could react on another form of energy than the organs known at present, up till now without result. GRIFFIN (GRIFFIN, 1944, GRIFFIN & HOCK, 1948) became the first serious opponent against this tendency. He tried to show that our interpretation of the results of transportation experiments may have been false and that the possibility of an orientation with the known senses should not be excluded. In this connection it is important that the knowledge

of the place of departure (the birth place) is not innate, but acquired⁷⁾. This is shown by experiments in which eggs or hatchlings were transported to other places, where the young birds grew up. The birds in these cases did not return to the place where they came into being as eggs, but where they grew up as young. Such experiments are known for ducks brought from England to Finland (VÄLIKANGAS, 1933), for woodducks (*Aix sponsa* (L.)) transported in America (McCABE, 1947; paper not seen by me), and for a swift (*Apus apus* (L.)), brought from Brunswick to Berlin (see SCHÜZ, 1931). All this means that if birds would be able to use the geographical position of a certain place as their aim they must have acquired its knowledge during their early life. In other words there cannot be a *sense* of geographical position, for this should be innate; there could only be a knowledge of the geographical position of the place in question, acquired during individual life.

I now come to water animals, especially fishes.

For them the problem is somewhat more complex, because during the first part of their life they are often for a shorter or longer period transported passively. In the young eel (*Anguilla anguilla* (L.)) this larval life takes some 2.5 years (SCHMIDT, 1922, '23, '24 and '35) and in my mind there can be little doubt that passive transportation covers the whole of this period, as the larvae after 2.5 years metamorphose near the continental slope of Europe, whereas the water must need a similar time to flow from the West Indies to the European coast.—After metamorphosis the young eels begin their migration. We know no more about it than that the animals appear in great numbers in the mouth of all our rivers. How did they reach them? From analogy to what is known for birds I suppose that they travel with the aid of an innate direction, which then for the European eels should be easterly. This innate direction would lead the animals to the continent, but as they concentrate in river mouths or sluices and according to the researches of TER PELKWIJK (unpublished) fail to appear on stretches of coast between these we must assume that they are helped by an innate preference for certain milieu factors. These would carry the young animals in optimal surroundings sufficiently favourable to extinguish the migratory impulse, just as was supposed above for birds. A similar reasoning could hold for the young of other species of fish with similar migrations, but too little is known about them.

After some years of life in inland waters the eels migrate back to the sea. If our assumption that birds may work with no more than a sense of direction would be right, the same may hold for fishes. In this connection it is important that transplantation experiments with fish (in casu salmon eggs) have shown that in fishes too the knowledge of the birth place is not innate, but is acquired during the first period of life (see E. S. RUSSELL, 1937, p. 329-334). Assuming

7) "Als Heimort gilt offenbar dasjenige Gebiet, wo der Vogel die ersten Eindrücke der Aussenwelt erhalten hat" (SCHÜZ, 1931).

that this holds for eels too it is not very probable that such a knowledge could be acquired by larval eels during the beginning of their passive journey near the West Indies. If knowledge about a certain place in the ocean would be acquired that place could at its most be the area of metamorphosis along the continental slope of Western Europe (the Western Mediterranean included); for it is this area which is comparable to the starting place of young migrating birds, as here migration of the young eel begins. For that reason I was up to a short time ago inclined to assume that the old eels must be able to find back the spawning grounds by using hydrographical factors, thereby eventually being helped by some knowledge of the route acquired since their metamorphosis. As to the use of hydrographical factors, I assumed that in fresh water the eels would travel *with* the current, whereas in the Atlantic Ocean they would travel against it. I supposed that especially the currents would guide the animals, because if the current was able to carry the larvae to Europe it should be sufficiently strong to be used by the adult eels to migrate against it. They would have to migrate along the bottom then, notwithstanding the weakness of the currents there. I overlooked the fact, that in many inland waters there is no current at all, and yet the eel passes them.

In connection with the above considerations it is quite important that marking experiments with eels have since shown that these animals on their way back to the ocean follow a constant direction. This discovery of MÄÄR (1947), relating to the Baltic, is especially valuable for different reasons.

The first and foremost of these is that this constant direction must be innate: a true sense of direction. My first reason to believe so is the above conclusion that the knowledge of the geographical position of the spawning places is not innate, but is acquired during individual life. It seems somewhat improbable, however, that the young eel could acquire the knowledge of its birth place during its passive transport as a larva. The only thing remaining, then, is the possibility of an *innate* constant direction. The second reason, which I owe to DEELDER, is more convincing still. MÄÄR concludes from his data that the direction of his eels in the Baltic is west to south. I think his data show that the direction varies between west to south and about southwest. Now, DEELDER (whose trains of thought are added at the end of this paper) points out that the direction southwest, if it is retained during the whole of the journey, leads to the Sargasso Sea, whereas if the animals would use the geographical position of the Sargasso Sea as their aim their direction in the Baltic should be north of west. In other words, the direction of these adult eels would be constant in relation to the compass.

If we may be sure, however, that adult eels are guided by a sense of direction, we may keep it for certain that young eels too possess such a sense and that they are able to find the continent with the aid of a constant direction, as was supposed above. Secondly, we can do away with the assumption that for adult eels returning to the spawning places hydrographical factors are needed,

or rather: we may suppose these to be of secondary importance. The sense of direction may guide the eels right through the Atlantic and only on the approach of the spawning places will hydrographical influences set at work and make them find optimal conditions for spawning, which will extinguish the migratory impulse, just as in birds. Thirdly, if fishes may find their spawning places with the aid of a sense of direction the chance increases that birds too may return to their breeding places with the aid of this sense, supported by an acquired knowledge of the place of departure. Only where this knowledge is missing is it impossible for the birds to return to their birth-place, and this, in my mind, is the reason why RÜPPELL's starlings, reared in captivity and transported to another place where they were set free, could not return to the place of origin (RÜPPELL, 1938, RÜPPELL & SCHEIN, 1941).

The true difficulty, however, begins, when we try to visualize on what this sense of direction may be based. It certainly means that we cannot do without the interpretation that water as well as land animals, at least fishes, birds and mammals (the whales included) so to speak constantly know the points of the compass. If now, with GRIFFIN, we try to understand this without assuming the existence of a separate sense we are obliged to enlist the help of, for instance, the relative movement of the sun, and eventually the capacity automatically to fly or swim a straight course over long distances, so that the points of the compass are retained during the sun's absence. The latter possibility, that of an automatical straight course, in my mind can be neglected, especially if we consider fishes (see also GULDBERG, 1897, JACCARD, 1926). In birds the maintenance of a certain direction during the sun's absence, without the help of such an automatical straight course, needs not give difficulties as long as they fly over land; but over sea, especially during dark nights, it seems difficult to believe in faultless navigation. They could use differences in the water's surface for orientation, or the direction of the wind in relation to fixed points of the water surface, or the like, a reasoning also given by LANDBOROUGH THOMSON, 1926 (p. 303), ALLARD, 1928 (p. 397 and 405), DROST, 1931a, THORPE and others, 1948. It seems not to be excluded that such factors give sufficient hold, because during oversea migrations birds regularly fly low over the water and preferently do not migrate in thick fog and complete darkness (see also DROST, 1935 and BESSERER & DROST, 1935). I think, however, that these precautions are not sufficient and that part of the migrations in wrong directions we can regularly observe in birds are due to mistakes made during changing winds or under other unfavourable circumstances. For fishes, the following of a straight course during the sun's absence would give no difficulties if they too during migration would keep to the bottom. MÄÄR's conclusion, however, is that eels during migration keep to the surface of the water rather than to the bottom. If this is right one does not understand how they can orientate themselves in dark nights. But as the bottom during such nights must be darker than dark still one may ask whether the

surface would not be the best of the two. At this moment the orientation of an animal like the eel forms a great obstacle to our further understanding, as migration in the surface water must be attended by a constant drifting away through currents, just as must occur in migrating birds in dark weather oversea through the wind. Notwithstanding these difficulties I prefer provisionally keeping to the sense of direction as a base for further work.

Till so far matters of orientation. The question becomes somewhat more complicated when we pay attention to the routes travelled.

I take the tunny as an instance. The migration of this species to its spawning places is no more difficult to understand than the migrations to the spawning or breeding grounds of so many other kinds of animals. But what to think about the journey of the tunny to the North Sea? It is probably made for the first time when the animals are some years old. Of course, we are obliged to assume that these tunnies, like all other migrants, are forced to travel by an impulse driving them northward. The knowledge of the North Sea cannot be innate, however, for they did never visit it before. It can neither be acquired. Therefore, they must find the North Sea quite accidentally or because they learn the route from older individuals. If accident plays a rôle, one must assume that the tunnies on their way northward reach areas with favourable conditions and that the North Sea makes part of these. We know something about the tunny's wants: it probably prefers a rather high salinity and not too low a temperature, possibly also not too small a depth. The favourable area, where the tunny migrates to, embraces the whole of the Norwegian coast from Stavanger to Bergen (exceptionally the Lofoten), the North Sea except its least deep and least saline southern part, the Skagerrak and the Kattegat. We may say that the tunnies here live within the branches of the Atlantic Current system and that they stop and turn where the salinity goes too much down through river influence (Southern North Sea, Kattegat), or the temperature, for instance in northern direction, decreases (coast of Norway). In this way their entering and leaving the North Sea through its wide entrance in the North would be comprehensible. One would further have to assume, however, that they do not enter the English Channel, because there too, as in the southern North Sea, conditions are unfavourable. Though I cannot disprove this supposition I am inclined to assume that neither depth nor salinity or temperature can be the cause that the Channel is not entered. The whole makes the impression on me that quite another factor is operating here, namely tradition. I think the younger animals may join the old and thus learn the route through them. If this would be right, we may compare the tunny's journey with other instances of angular migration, that of the stork (*Ciconia ciconia* (L.)) or the crane (*Megalongis grus* (L.)), etc., in which a fixed route is certainly passed on from old to young. The reason that nature here would work with tradition may lie in ecological factors. The journey of the tunny around Scotland for this more or less oceanic species may have the advantage that it does not leave oceanic

conditions, whereas the way through the Channel, moreover, would bring it into the southern North Sea, which is not favourable to the species. As to the stork I think it is now generally agreed that the southeastern route through Europe and around the eastern Mediterranean for this glider has aerodynamical advantages. What advantages could play a rôle for other species with an angular migration route I dare not say; *that* they are present is in my mind certain.

Tradition in the same way could play a rôle in the humpback, where the young follows the mother to the high North. It will be superfluous, of course, to say that the impulse to migrate in all these migrants is innate, and that it is the chosen route only, which may be influenced by tradition.

What, finally, about a case as that of the anchovy? It shows complete agreement with that of the John Dory (*Zeus faber* L.), the pilchard (*Alosa pilchardus* (Walb.)), and probably some other species, among which the mullet (*Mullus surmuletus* L.). All these enter the North Sea in the South, either propagate there (anchovy, pilchard, mullet) or not (John Dory), and in the course of summer move northward, finally to reach the northern part, where they may accumulate along the Scottish coast, to leave the North Sea in the North I think. Accumulation along the Scottish coast is certain for the anchovy (at least in certain years, see under observations) and the John Dory (THOMPSON, 1923). If we assume that here too the northward migration is the realisation of a true migratory impulse, the accumulation in the northern entrance along the Scottish coast should still be explained. I suppose that an important rôle is played here by hydrographical factors which during the period of falling temperatures may concentrate the animals in the relatively warm Atlantic water entering the North Sea in the North. Orientation on it would be the more effective the faster temperature falls, because then the great mass of Atlantic water lags the more behind. That is to say, the high temperature would activate the animals, the current would direct them. We have to assume, then, however, that the animals keep contact with the bottom or can use irregularities in the currents for their orientation. It is quite probable that they are also helped by being concentrated against coasts and following these. The recaptures of marked eels show us that these are accumulated in just the same way against coasts as birds. Eels are piloted out of the Baltic through following coasts which make an angle of more than 90° with their innate direction. It may be that they are helped here by their preference for certain hydrographical changes; we must not forget, however, that birds, in following gradually bent coastlines, may easily be made to fly in directions making angles of much more than 90° with their original ones, without the help of hydrographical factors whatever. Data for the Scottish coast show that the anchovies may be accumulated on the east coast in late autumn, on the west coast in winter. In my mind there is little doubt that they leave the North Sea around Scotland. I suppose they work their way southward along the English westcoast then; it seems they do

not enter the North Sea in the North next spring. The case reminds one of the blackheaded gulls (*Larus ridibundus* L.) which leave Switzerland or southern Germany to fly northward to the North Sea; they then follow the coasts of the latter on their way southward. There too surely a number of influences play a rôle: an impulse to migrate north- and later southward, concentration along coasts, ecological influences, eventually tradition. The more we get acquainted with these facts the clearer we realize the far reaching agreement between these migratory movements in sea and air animals.

In this chapter on routes and orientation one further point has to be dealt with. How did nature fix the directions north and south respectively? How is it that migrating animals do not go south in spring and north in autumn? It seems illogical to ask this, but I think the experiments of ROWAN (1930 and '32) and WOLFSON (1942) prove the contrary. They show that birds, kept under conditions of lengthening days in autumn, go north. ROWAN believed this to be due to the incretory activity of their gonads which had developed under the influence of the lengthening days, but PUTZIG's experiments with castrated crows show that they migrate northward in spring just as non-castrated individuals (PUTZIG, 1939 a and b). So the lengthening days may be the direct cause of their *northward* direction. If this is true we may expect shortening days to be the cause of southward migration, proof of which is wanting still. But there is more. In late winter, when northward migration of starlings (*Sturnus vulgaris* L.) and skylarks (*Alauda arvensis* L.) has already started, the direction of migration may at once turn under the influence of a fall of temperature or snow fall. I think, there can be little doubt that a strong fall or rise of temperature has the same influence as a change in day length: it does not only activate the bird, but also determines the sign of the direction in which it shall migrate. How must we interpret these facts? It is probable that lengthening days or temperature rise give northward, shortening days or temperature fall southward migration. This would hold for both spring and autumn with that restriction that temperature influence most of the year is overshadowed by the influence of light. I should like to assume, then, that the plane of the direction (north-south, northeast-southwest, northwest-southeast, etc.) is inherited, but that the sign of the direction (for instance north *or* south) depends on either falling temperatures and shortening days or rising temperatures and lengthening days.

DROST in a number of publications (DROST, 1929, 1930a, 1934, 1935, DROST & BOCK, 1931 a and b, DROST & RÜPPELL, 1932) has defended a different view. He supposes that the direction of migration (I think I may say the direction itself as well as its sign) is determined by movements of cold or warm air masses, and he presumes that the birds use the movement of these masses for their orientation⁸). In autumn, for instance, they would direct

8) In his paper of 1934 DROST, strictly speaking, even defends the view that birds would have no innate constant direction. In 1935 he drops this supposition again.

themselves against the movement of warm masses; they would also migrate southward *with* the cold masses. In spring they would move *with* the warm masses (or perhaps also against the cold ones). The advantage of this supposition is that it makes it easier to treat birds and fishes alike. In my mind, namely, there is little doubt that numerous water animals are not only quite sensitive to changes in temperature, salinity and current strength, but that to a certain extent they also use these for orientation. In by far the majority of cases it will not be possible for them directly to use a temperature or salinity gradient, but the change in temperature or salinity within a certain lapse of time may activate the animals to move *against* or *with* the current, with the result that they are guided by the watermasses. A similar reasoning could hold for birds and it seems not improbable that *their* route too is influenced by air movements to a certain extent. This is quite different, however, from what Drost supposes. Translated in terms of fishes he believes that tunnies migrate to the North Sea *with* warm or *against* cold currents and that they move back to the Mediterranean *with* cold or *against* warm currents. This, certainly, is more than improbable.

DROST quotes several facts in favour of his supposition, but I do not think they hold. First of all, the wellknown fact that waves of migrants in spring coincide with warm southwestern winds or foyn and that the birds in early spring may turn southward when cold northeastern winds set in (DROST, 1929) is no proof that the air masses indeed are used for orientation. On the contrary, strong waves of migrants are characteristic for hot days in May with movements of air from the east or southeast; yet the birds (at least in Holland) move in quite the same direction as in February, when heat is brought to us by southwestern winds. These facts simply speak for temperature influence on the strength of the migratory impulse and eventually on the sign of the direction, without telling anything about the way in which orientation takes place. DROST's second argument is an indirect one. He sees migration quite often take place in directions more or less perpendicular to the isotherms. This does not prove, however, that the isotherms, i.e. temperature gradients, are used; in most cases the temperature gradient will be much too small and also too much influenced by accident to make orientation on it possible. Moreover, SCHENK has called attention to the fact that the argument cannot hold for southeast-northwest migrants through Europe. That is probably the reason why DROST later restricted his supposition to part of the migrating species, a fact which weakened his point of view.-Further, DROST has called attention to the fact that the course of the isotherms during summer and autumn shifts in such a way that their gradient from southwest-northeast gradually changes to northwest-southeast. Therefore, species which leave us early would chiefly turn southeast, the later ones chiefly southwest. Even if this rule would hold it does not speak in favour of DROST's supposition, it would only mean that migration proceeds along a temperature gradient, without telling anything

about the way of orientation. DROST even believes (DROST & BOCK, 1931a) that the direction of migration of certain species shifts from southeast to northwest within one and the same season. I think, however, there are so many exceptions to this rule, that the fact in itself is far from general. Even if it were of somewhat more general occurrence, it would not *prove* that orientation on the movements of the airmasses involved takes place; but it would certainly speak in favour of DROST's supposition as long as no other ground for a shifting of the direction of migration within a certain species could be given. We may ask, however, whether the observations cannot be explained by the assumption that different populations with different innate directions are involved. DROST (DROST & BOCK, 1931 b, DROST & RÜPPELL, 1932) also believes that migration in Mid-Europe is more southeast than along the Atlantic and that the same holds for the temperature gradient. This, again, does not tell in favour of DROST's supposition, however, as it is only logical that migration routes, generally speaking, are directed along temperature gradients. Finally, DROST (DROST & BOCK, 1931a) believes that migration in wrong directions (i.e. north in autumn), as it may be observed on certain days, is directly conditioned by the transport of warm air from the North on such days. I was inclined to believe that this argument might hold. It would mean that, more or less *by way of exception*, air masses influence the direction birds take. KOCH (1934) has pointed out, however, that inverted migration regularly takes place on days with cold northeastern winds, when there is according to KOCH no question of movements of warm air from the North. This means that the birds in such cases do not fly *with* cold winds, as in autumn they should do, but that they fly *against* them. KOCH is of opinion that "masse-migration" in the wrong direction only takes place during the first days after a change in wind direction; after that migration becomes normal again. He therefore assumes it is the wind as such which temporarily influences the birds, which would be by no means the same as what DROST supposes⁹).

The result of all this is, I think, that there is little in favour of DROST's supposition that migrating birds would use the movements of air masses for their general orientation. Up till now there is even very little evidence that air masses are used for orientation anyhow (see GRIFFIN, 1944, p. 26-28). In view of its great importance the question deserves more attention than it has been given hitherto. To DROST must be given the credit to have brought the problem into discussion again and again.

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ADDENDUM

On the orientation of migrating animals

BY

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Mainly as a result of "homing experiments" the supposition has been made that animals may use two senses to reach their goal, viz. a "sense of direction" and (or) a "sense of geographical position". I here want to consider some consequences of this assumption.

"*Sense of direction*". An animal eventually migrating with the help of this sense will manage to keep the same direction, i.e. it migrates along a course which crosses the meridians with one and the same angle. Such a line is called a loxodromic line. It is rather simple to draw on a map with Mercator's projection since then it is represented by a straight line.

"*Sense of geographical position*". If an animal would possess this sense, we may assume it "feels" its goal and migrates to it. We must logically suppose that it does so along the shortest distance, as the "feeling" will be strongest then. The shortest distance between two places upon earth is given by the great circle, i.e. the intersecting line of the surface of the earth and the plane going through the two places and the centre of the earth. So our animal will migrate along the great circle going through start and finish of the migratory journey.

The course of such a great circle is rather difficult to plot. We need, therefore, some formulae of spherical trigonometry.

In fig. 4 WPE represents the surface of the earth.; P represents a pole, A and B two points upon earth, AVB the great circle going through them. At V the great circle is running east-west, so $\angle PVA = \angle PVB = 90^\circ$.

As the latitudes of A and B are known, we know also PA (= b) and PB (= a). As the longitudes are known, we know also $\angle P$. Therefore, $\angle A$ and $\angle B$ can be calculated with the formulae: $\text{tg } \frac{1}{2} (A + B) =$

$$\frac{\cos \frac{1}{2} (a-b)}{\cos \frac{1}{2} (a+b)} \cotg \frac{1}{2} P, \text{ and: } \text{tg } \frac{1}{2} (A-B) = \frac{\sin \frac{1}{2} (a-b)}{\sin \frac{1}{2} (a+b)} \cotg \frac{1}{2} P^{10}.$$

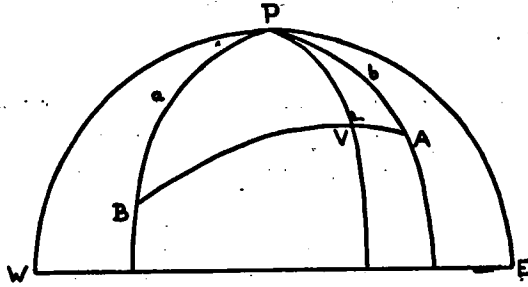
Longitude and latitude of V can be calculated with the formulae:

$$\cotg APV = \cos b \text{ tg } A, \text{ and: } \sin PV = \sin A \sin b^{10}.$$

10) I shall not prove these formulae, because this would fall beyond the scope of this article.

From the great circle AVB we know, then, the position of A, V and B, and the magnitude of $\angle A$, $\angle V$ and $\angle B$. With the help of these data we may construct the course of the line with sufficient accuracy.

From the foregoing we may draw a.o. two conclusions: first it will be clear that between two points on earth the loxodromic line and the great circle are two *different* lines. As an animal will migrate along one of them only, it can only be equipped with *either* a "sense of direction" *or* a "sense of geographical



position." Our second conclusion is that the possibility exists now to investigate with which sense an animal has been provided, assuming that its direction of migration is known. To show this possibility one example is given here. It deals with the migration of the eel (*Anguilla anguilla* (L.)) and has the advantage to be extra favourable for this calculation.

Several hundreds of eels have been marked and liberated along the Finnish and Esthonian coasts by MÄÄR (1947). Many have been recaptured. From these results the author concludes that the eels migrate in a certain direction (north about 120° west) and that no external, but only internal factors can be responsible for this phenomenon.

Now, we know the starting place (viz. the place where the eels were liberated) and the end of the journey (viz. the spawning place, described by SCHMIDT, 1923). Supposing that the eels would migrate with a "sense of geographical position" we find after calculation that they would have to start in a direction north about 80° west. On the contrary, if the eels would possess a "sense of direction" the direction in which they start would be north about 120° west, a value which fits well with the results of MÄÄR.

In my opinion this coincidence cannot be due to accident. For this reason I assume that eels migrate with the help of a "sense of direction".

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