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by L. Tinbergen and J. Verwey

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The biology of Loligo vulgaris IAM.

by

L. Tinbergen and J. Verwey

Zoological Station, Den Helder

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N.B. In this typescript, "quoted in the literature" should be read as "personal communication." —

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During 1932-1940, the Zoological Station of Den Helder bought large numbers of squid (Loligo vulgaris Lam.) from the local fishermen. Initially, this was done for faunal reasons, since this species was believed to be rare in the North Sea (TESCH, 1908, GRIMPE, 1925). However, it soon turned out that this was not the case for the Den Helder area, and that each year the animals arrive in large numbers to spawn in the coastal waters. VERWEY took advantage of this fact to study also other biological aspects of this species. His observations related mainly to growth, reproductive conditions, and migration. They comprised altogether 12000 individuals; size, sex, gonadal growth stages, and date of discovery were recorded. He left the evaluation of these data to TINBERGEN. It constitutes the subject of the present report which was written by TINBERGEN, with the cooperation of VERWEY.

This report is merely intended as a preliminary survey which, owing to the method used, shows a certain heterogeneity. The migrations of the squid have an important part in it; an attempt was made to bring them into **prominence** by comparative observations.

Contents

1. Growth and age; participation of age groups in migration

In connection with our observations dealt with further below, knowledge of both growth and age frequently is essential. For that reason, we present that part of our investigations first.

For determination of growth, we have used, above all, the frequency distribution of squid sizes and, in particular, of the length of the ventral mantle. Age-marks—like scale and otolith marks of fishes—were not found despite repeated attempts in that directions.

In the frequency curves, we have assigned the measured lengths to classes or groups constructed in the following fashion: 10.5 to 11.4 cm to the 11-cm group; 11.5 to 12.4 cm to the 12-cm group; etc.

The overall period of observation was divided into four periods ("up to 20 May," "21 May to 20 June," "21 June to 20 July," and "after 20 July"), which periods, as such, should be regarded each as one month. The specimens measured before 21 April, thus, are included in the first period, and those measured after 20 Agust are included in the last period, but the majority of the other measurements was carried out during the second half of the first period and during the first half of the last period, respectively, so that the average values found may, after all, be regarded as monthly values.

In order to assess the growth of the males, we first give consideration to Figure 1, in which the measurements made during all the years of observation are summarized. The frequency curves exhibit the following peaks:

Up to 20 May	13 - 14 cm	20 - 22 cm
21 May to 20 June	15 cm	23 cm
21 June to 20 July	15 - 18 cm	23 - 27 cm
after 20 July	17 - 18 cm	?

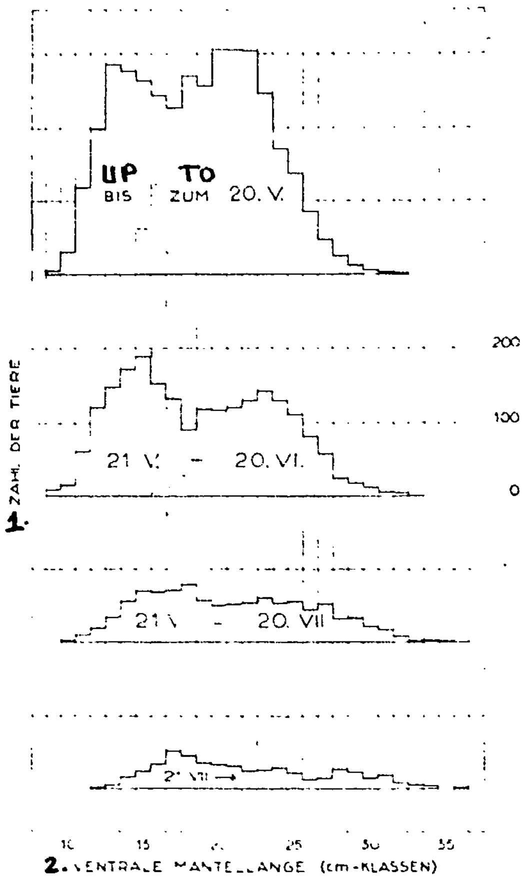

Figure 1 - Length-frequency curves for all males (with the exception of one male measuring 42 cm, 21 May - 20 June, and one male measuring 39 cm, 21 july to the end of the period of observation). Key: 1, Number of animals; 2, Ventral mantle length (in cm-classes). V, May; VI, June, VII, July.

We may see two year groups in these peaks; however, if we follow these peaks in the curves for the individual years (Figure 2), we find a great number of irregularities and, thus, no convincing pattern. It would then be possible that the bimodal appearance of the curve shown in Figure 1 arose purely by chance, and would disappear once the years were fitted differently. However, that the latter is not the case is indicated in Figure 3, in which the curves for several combinations of that kind are plotted: Again, the two peaks are in evidence rather distinctly. The irregularities of the curves for the individual years, thus, are probably attributable to the small size of our specimen material.

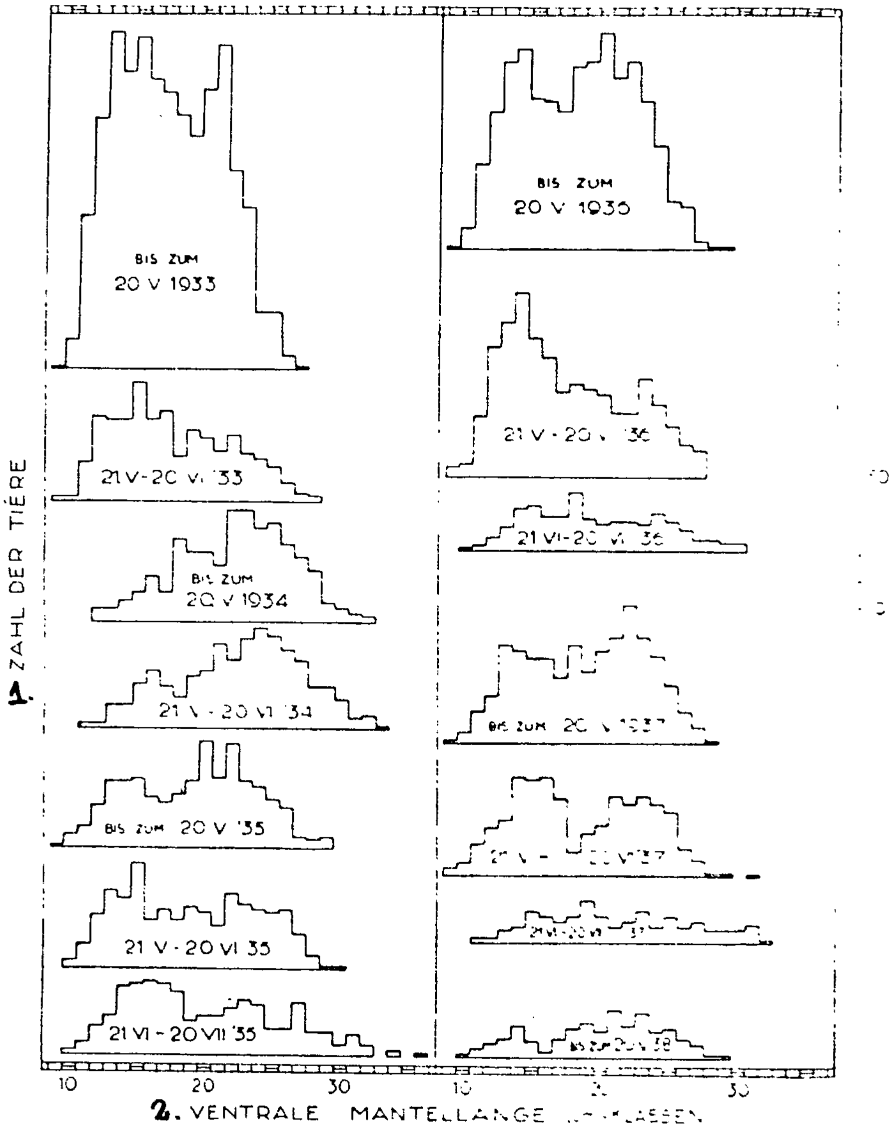

Figure 2 - Length-frequency curves for males. Data obtained in the individual years. Several very small catches are not shown. Key: Bis zum, Up to; 1, Number of animals; 2, Ventral mantle length (in cm-classes).

We then assume for the time being that two consecutive year groups of males participate in the breeding migration. On the basis of their ventral 215 mantle length during the period up to 20 May, we will refer to these year groups as the "13-cm group" and the "21-cm group."

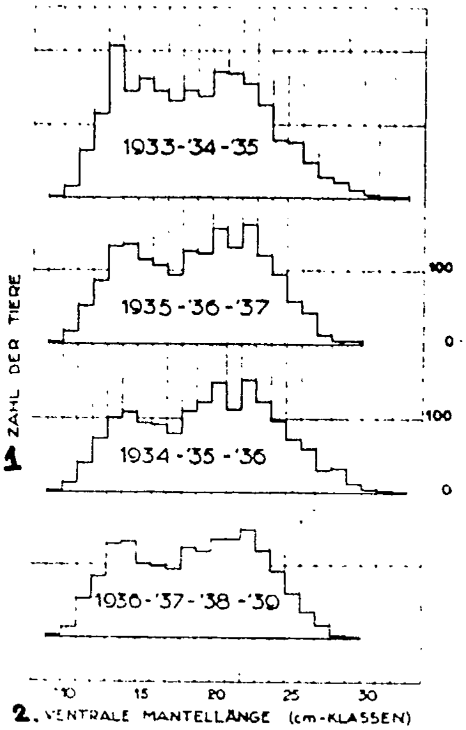

Figure 3 - Length-frequency curves for males. Period up to 20 May. Combinations of different years. Cf in the text for details. Key: 1, Number of animals; 2, Ventral mantle length (in cm-classes).

The extent to which our assumption is justified can be demonstrated, in the first instance, by the course of growth. Between the first measurement period and the last one, i.e. on average from about 5 May to 5 August, growth of the individuals belonging to the 13-cm group amounted to four cm according to the table presented further above. Let us suppose that the water temperature determines the gain, and we are able to estimate that the growth during the next three months (*viz.* during the period between 5 August and 5 November) amounts to a little less than four cm or, let us say, to approximately 3.5 cm. In that connection, we have taken into consideration the fact that the annual temperature maximum is attained in the sea a little later than on land, and is reached in the coastal sea around the end of July or early in August. The specimens belonging to the 13-cm group, thus, would exhibit a peak at 21 cm during the period between 21 October and 20 November, and should—if they actually corresponded to the 21-cm group of the following year—not grow during the period between 5 November and 5 May. Due to the absence of squid from the region of observation, no data are available for that season; however, we have available observations made in young squid just hatched, and 217 these observations indicate that, in their case, growth actually is practically arrested during the winter months. The gain of the squid hatched during the summer actually amounts—as will become evident further below—to about 8.5 cm between June (July) and early October (length at hatching: 0.5 cm); to about 3 cm between early October and early December; and to only about 1.5 cm between early December and early May. These considerations have convinced us that the 13-cm group is identical with the 21-cm group of the following year.

The relative frequencies of these two groups in the different years could also provide evidence for the mutual relations. For example, the 13-cm group was relatively frequent in 1933, and the 21-cm group was relatively frequent in 1934—a finding suggesting that these two groups are identical. However, additional arguments either for or against our view really cannot be derived from our material.

The question now arises regarding the age of the 13-cm group. Unfortunately, only few data are avialble to us regarding the early juvenile phases. The squid individuals hatching rather frequently in the aquarium of our station during June and July measure about 0.5 cm in length. Three juvenile specimens caught along the Belgian coast (Ostende) on 4 September 1934 exhibited ventral mantle lengths of 2.6, 3.5, and 4.0 cm according to the kind communication of Dr. Adam (1941 quoted in the literature). In six males

caught between 28 September and 24 October 1934 near Den Helder, the ventral mantle length amounted to 6.0, 7.9, 9.4, 9.8, 10.3, and 10.4 cm. Finally, 19 males were caught between 24 November and 18 December 1939 exhibiting an av- 218
erage length of 12.1 cm, with the following frequency distribution:

9	10	11	12	13	14	15	16 cm
4	2	2	3	2	2	3	1 individual(s)

A male, measuring 12.3 cm in length, mentioned by Hertling (1929), December 1928, from Haaks light ship, belongs to the same size group.

It is then clear that the latter group must be identical with the 13-cm group of the following spring. If we assume furthermore that the individuals are about half a year old, we are able to fit the afore-mentioned specimens to a continuous growth curve. The latter, in fact, does not represent by itself evidence for the correctness of our assumption that the afore-mentioned autumn and winter animals belong to the 13-cm group of the following spring. However, that assumption is supported by Raja's (1935) measurements of post-embryonal growth in a large body of specimens.

Miss Raja has reported numerous weight values for juvenile <u>Loligo</u> <u>vulgaris</u> caught near Naples. These specimens were also measured; unfortunately, however, the length values have not been reported. Since we were unable to communicate with Miss Raja, we were forced to convert the reported weight values into length values with the aid of the ratio $\frac{\text{ventral mantle length}}{\text{weight}}$ found in The Netherlands. That conversion yielded the following result:

July:	ventral	mantle	length	1 - 4 cm,	average 1 cm
August:	"	"	"	1 - 6 cm,	average 3 cm
September:	"	"	"	1 - 7 cm,	average 4 cm
Oct., Nov.:	"	"	"	4 - 10 cm,	average 7 cm
Dec., Jan.:	"	"	"	9 - 16 cm,	average 12.5 cm

The growth occurring there, thus, is identical with the growth we have assumed for Den Helder.

Lo Bianco (1909) has reported a far more rapid gain, and this also for the vicinity of Naples. According to that autjor, specimens hatched during May would measure 20 cm in length already during December. Since that author, however, reported his observations only in summary fashion, we are unable to establish whether an arror may have occurred.

In this connection, we are interested also in the great numbers of juvenile specimens investigated by Adam (1942 quoted in the literature), which were collected during November of 1935 and November of 1936 along the coast of West Africa [Pulpito Baie, Villa Cisneros, and Angra de Cintra (Rio de Oro)]:

2	3	4	5	6	7 cm
1	4	2	11	12	4 individuals

Just like the Neapolitan specimens, these juveniles were somewhat smaller than the Dutch November squid, i.e. they either had grown more slowly or had hatched later.

Figure 4 illustrates in diagrammatical fashion our observations regarding 219 the growth of the males. It is based on Figure 1. The curves presented in that Figure have been interpreted by us in a way that the two peaks represent the two year groups playing a role in the breeding migration. The frequency curves of each one of these two year groups are plotted in Figure 1 on the basis of estimations, with the assumption that the distribution of the 13-cm group is symmetrical—which, of course, does not have to be so, but appears to us to be permitted for our purposes. The individual curves obtained in that way are plotted in Figure 4 in a more simplified form. This procedure yields a clear overview of the growth up to completion of the second year of

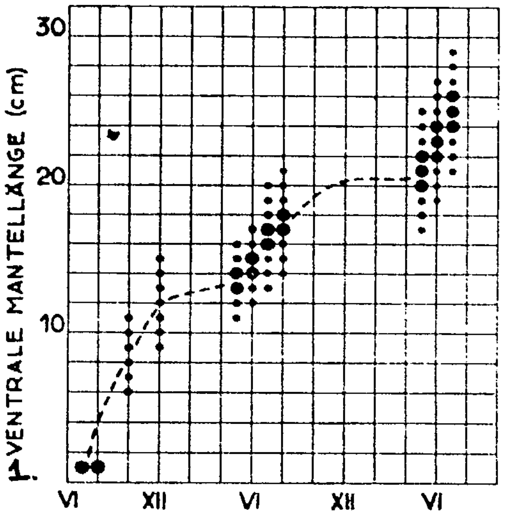

Figure 4 - Diagrammatical representation of growth of males. Key: 1, Ventral mantle length (cm); VI, June; XII, December.

life. The peak of the individuals about 24 months old, according to Figure 1, is located at a length of 24 to 26 cm; the largest ones of these individuals measure 30 to 36 cm in length. Single, larger individuals probably belong to an older, i.e. the third, year group. That appeared to us to be the case, above all, in two specimens: Male, 38.7 cm (21 July 1933), and male, 42.4 cm (3 June 1939).

It then appears that only two age groups play a significant role in the breeding migration.

We have noted that the two-year-old individuals, on average, are more fre-
quent than the one-year-old ones, while one would normally expect that the 220
older year group is smaller due to mortality. However, we have been measuring
only individuals participating in the breeding migration. It would then ap-
pear that a smaller percentage of one-year-old individuals participates in this
migration than of the two-year-old ones. This disproportion between one-year-
old and two-year-old individuals is most marked during the period up to 20 May.

That finding indicates that the two-year-old individuals migrate relatively earlier than the one-year-old ones.

It appears that the growth of the females from hatching to the first winter does not deviate from that of the males. For example, eight October females exhibited no great difference to the above-described males of that month, in that their lengths amounted to 6.0, 7.3, 7.4, 7.5, 8.0, 8.5, 8.8, and 9.0 cm. While 19 males caught during November and December of 1939 measured, on average, 12.1 cm (page 218), 14 females caught during the same period exhibited an average ventral mantle length of 11.7 cm.

The length-frequency curves found during the summer half-year, however, reveal an entirely different pattern than those obtained in the males. In Figure 5 we see that pattern as narrow symmetrical curves with the following peaks:

Up to 20.V.	14–15 cm,
21.V.–20.VI.	14–15 cm,
21.VI.–20.VII.	15–16 cm,
After 20.VII.	15–17 cm.

During the first period, the peak is about one cm higher than in the one-year-old males; however, subsequently, the female peak remained well below the male one.

Seeing these symmetrical curves with a single peak, one might be tempted to conclude that the females encompass only one single year group. However, we could also imagine that there exist several year groups, which, due to partial overlapping yield an "illusory" common curve. Which one of the two possibilities would be applicable cannot be determined on the basis of the overall curves. For that purpose we require curves for individual years, which are largely presented in Figure 6, and the peaks of which, in addition are summarized in the following table.

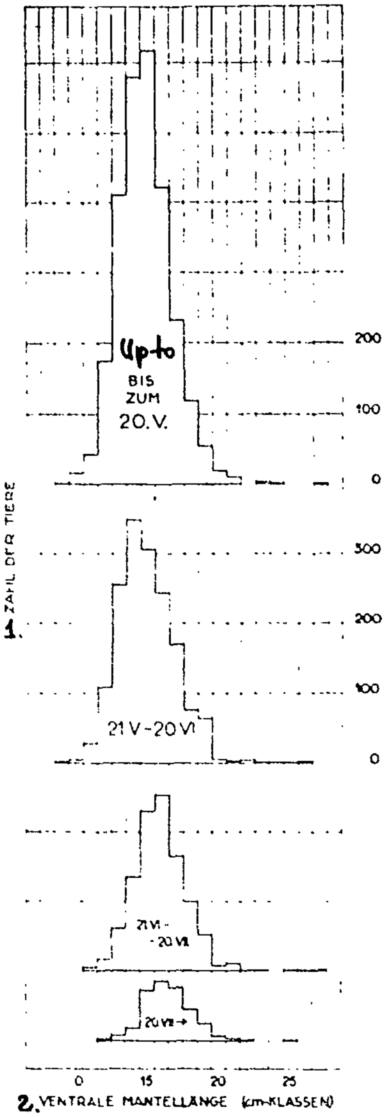

Figure 5 - Length-frequency curves for all females. Key: 1, Number of animals; 2, Ventral mantle length (in cm-classes); V, May; VI, June; VII, July.

	1933	1934	1935	1936	1937	
Up to 20. V.	14–15	17–18	14–15	14–15	14–15	cm
21. V.–20. VI.	13–15	17–19	<15	14	14	cm
21. VI.–20. VII.	16	16–19	15–16	15	16	cm
After 20. VII.	17	?	16	15–16	17	cm

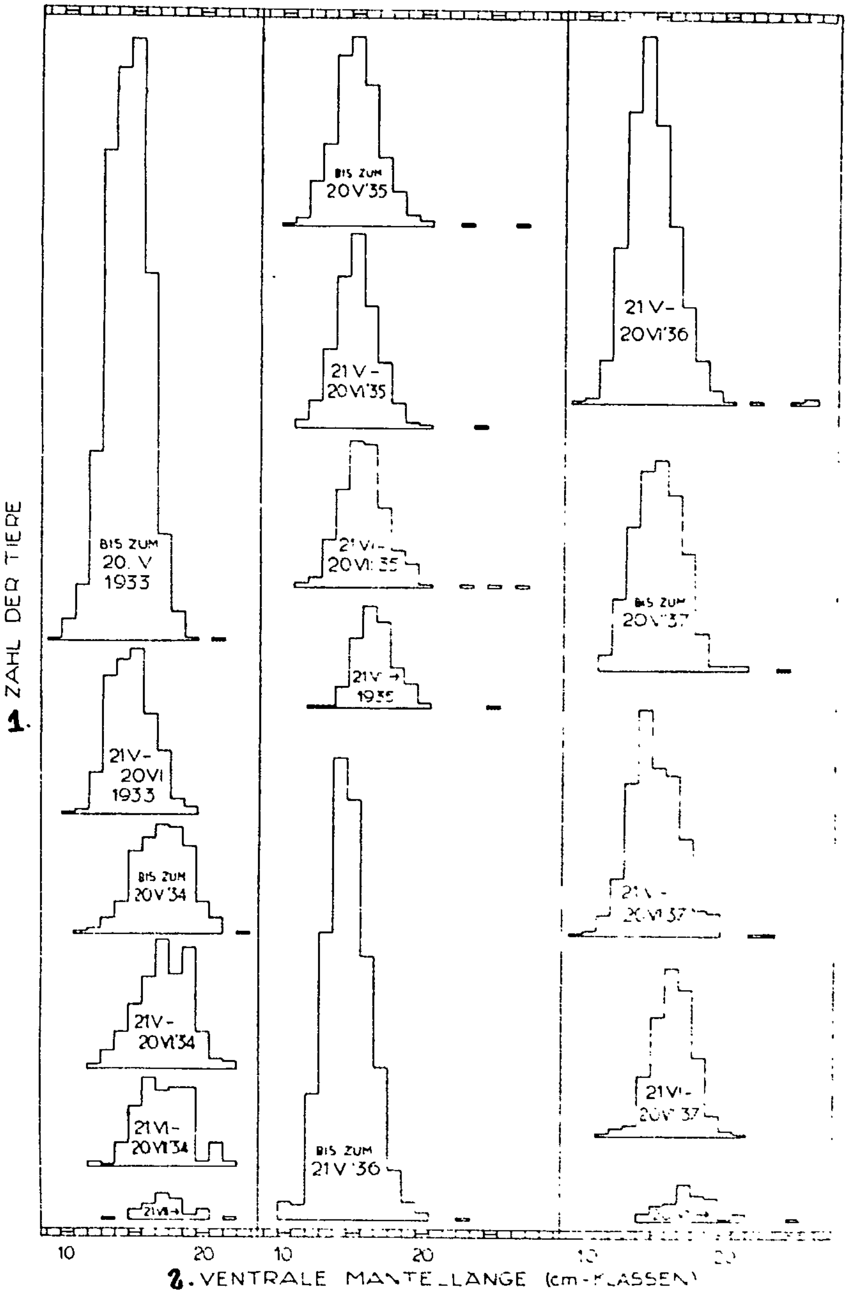

Figure 6 - Length-frequency curves for the females. Several very small monthly catches have been omitted. Key: Bis zum, Up to; 1, Number of animals; 2, Ventral mantle length (in cm-classes).

221 In the individual years, we find that the peaks are located at approximately the same mantle length; only in the year 1934, the peaks were shifted to a considerable extent to the right. Supposing that the females represented only a single year group, growth during the late summer of 1933 or during the winter of 1933 - 1934 would have been about 20 per cent greater than usually. If we now consult the diagrams of the males for the purpose of comparison, we find in the individuals of that sex that, in the year 1934, the peaks exceeded the average one by significantly less than 20 per cent, i.e. by about 10 per cent in the case of the one-year-old individuals, and by five per cent in that of the two-year-old ones. The actual findings were:

	One-year-old individuals	Two-year-old individuals
Up to 20 May 1934:	16	22 - 23 cm
on average:	13 - 14	21 cm
21 May - 20 June 1934:	16	23 - 25 cm
on average:	14 - 15	22 - 24 cm

223 For these reasons, it is not probable that the deviating position of the female peak observed in the year 1934 is due solely to greater growth during the year 1933. We have seen already on page 217 that, in 1934, the one-year-old males were relatively very infrequent, which finding, however, does not permit us to conclude that the brood fared poorly during the year 1933. It is not probable that that situation (had it, in fact, existed) would have affected only the males and not also the females. The unusually large length values found in the year 1934 in the females must be interpreted, in our view, in the following way: Not only did the individuals grow rapidly during the preceding year, but the percentage of the one-year-old individuals was also unusually small.

Poor success of the brood and good growth of the individuals, in general, are not incompatible, since the success of the brood may depend on other factors than does the growth of the juveniles. For example, the extremely warm fall of 1933 may have greatly promoted the growth of the juveniles, while the brood would not have been affected by that factor.

Let us then suppose that the females, like the males, consist of individuals belonging to two year groups, the length-frequency curves of which together form a one-peak diagram. We have estimated that the position of the peaks of the individual year groups are located in the month of May at 13 to 14 cm in the case of the one-year-old individuals, and at 17 cm in that of the two-year-old ones. We have selected the former value, because the females, according to page 220, grow during the year of hatching approximately as rapidly as the males, the peak of which exhibits the value just mentioned for yearling females. The latter value of 17 cm is based on observations made during the year 1934. In this connection we have assumed that, in that year, the peak observed (17 - 18 cm) does not differ much from that of the tw-year-old individuals, because of the small number of one-year-old ones. However, we have demonstrated furthermore that the length values of the two-year-old males were about five per cent higher in the year 1934 than in the average year. For that reason, we have estimated that the normal peak of the two-year-old females amounts to approximately 17 cm.

According to that view, growth of the females between the month of May of the first year of life and May of the seconf year of life would amount to about three cm, i.e. not even half the corresponding length gain seen in the males, which we had estimated (cf. page 215) to amount to seven to eight cm. That estimated value agrees well with direct observations of growth made during the summer months: The lengths of the one-year-old males increased during the period between 5 May and 5 August by four cm (Figure 1), and those of all females, by only barely two cm (Figure 5). It is then clear that the one-year- 224 old females gain less than two cm in length during the period between 5 May and 5 August, i.e.—as in the above-presented estimation of annual length gain—less than half the gain exhibited by the males. The summer observations, thus, support the assumption of the existence of two year groups of females. Despite the large differences in the frequency curves of the males and the females, respectively, we must then assume that one-year-old and two-year-old individuals occur also in the case of the females.

Perhaps there exist also females exhibiting higher ages. Occasionally, one finds individual specimens measuring 23 to 27 cm in length, where it is not possible to determine whether they are well developed two-year-old individuals or normal-sized three-year-old ones (cf. Figure 6). In the meantime, we assume that the latter is the case.

Finally it must be stressed that the larger females, like the older males, arrive somewhat earlier in the coastal water than do the smaller ones. On average, the length of the females decreases somewhat between the first and the second month of observation (Figure 5), while one would expect an increase of length or, at least, an arrest of growth, if the composition of the population remained constant. We must the conclude that a relative increase of the younger individuals takes place.

Let us now give second consideration to several of our results. We have seen that the males after one year attain an average length of 13 to 14 cm, and one year later, one of 21 cm. In the females, the corresponding numerical values were about 13 to 14 cm, and approximately 17 cm, i.e. after the first year of their life, the females grow significantly more slowly than the males. The suggestion arises of associating that slower growth with the great amount of energy required by the females in connection with egg production. The latter activity starts in our species between December and April of the first year of life.

Unfortunately, not much is known about the growth of *Loligo vulgaris* in other regions, and we are unable to make comparisons. Reliable data are available in only a few other cephalopod species.

The North-American squid, *Loligo pealii* LES., grows at approximately the same rate as *Loligo vulgaris*, the common squid of the eastern Atlantic. In *L. pealii*, too, the female exhibits slower growth after the first year of life than does the male. Verrill (1882) has reported that individuals of that species hatched during June attain a ventral mantle length of eight cm during November. During May and June of the following year, the lengths of the one-year-old squid varied between six and 18 cm; those of the two-year-old males, 225
between 20 and 27.5 cm; and those of the two-year-old females, between 17.5 and 22.5 cm. Older individuals occur in small numbers; that species then resembles our species also in that respect.

On the other hand, *Sepia officinalis* L., the common cuttlefish, attains a higher age along the Dutch coast. According to our findings, individuals three years old may be found rather frequently; probably, even older ones do occur. As in the case of *Loligo vulgaris*, the females of *Sepia officinalis* grow less rapidly than the males during the second year of their life.

The males as well as the females of *Loligo vulgaris* migrate earlier into the coastal sea during the second year of life than during the first one. A sequence of the age groups of that nature has been observed in many animal species migrating to their breeding ranges.

We wish to present several examples, but our enumeration does not claim to be complete.

Earlier migration of the older individuals has been observed among the cephalopods in *Sepia officinalis* L. (our own observations); among the fishes, in *Clupea harengus* L.[1], *Oncorhynchus tschwawaytscha* [*tshawytscha*] (WALBAUM), *Salmo salar* L., *Salmo trutta* L., *Fundulus heteroclitus* (L.), *Pleurogrammus monopterygius* (PALLAS), *Merluccius vulgaris* FLEM.(Scheuring, 1929; 1930), and among the birds, "repeatedly in larger species" (Stresemann, 1927; 1934) [for example, in *Ardea cinerea* L. (Verwey, 1930), *Ciconia ciconia* L. (Schuez, 1940), *Phalacrocorax carbo sinensis* (SHAW and NODDER) (Kortlandt, 1942), and furthermore in *Sturnus vulgaris* L. (Kluyver, 1935; Van Dobben and Moerzer Bruyns, 1939), and *Melospiza melodia* (WILSON) (Nice, 1937). It appears that the sequence is reversed in the pike (*Esox lucius* L.) (Scheuring, 1929; 1930). No difference in the dates of appearance has been found in the individual age groups of the skylark, *Alauda arvensis* L. (Van Dobben and Moerzer Bruyns, 1939).

In the majority of these species, it then appears, as in *Loligo vulgaris*, that the older individuals migrate earlier to the breeding grounds than the younger ones.

In birds, sexual maturation frequently takes place in similar fashion. For example, in the cases of the afore-mentioned species *Sturnus vulgaris* and *Melospiza melodia*, Kluyver (1935) and Nice (1937) have established that the clutches of the one-year-old females, on average, appear later than those of the females more than one year old. That finding reflects the close relation existing between the migratory drive and sexual maturity, which misled earlier

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[1] According to Hodgson (1934), however, the order of arrival is reversed in the southern parts of the North Sea.

authors to assume that sexual maturity represented the factor causing awakening of the migratory drive (cf. page 247).

On the basis of this situation existing in birds, we might expect also in Loligo vulgaris that the one-year-old individuals mature later than the older ones [what the author probably means here by maturing is 'getting into the mating condition'—an annual process; Transl.]. We have been unable to elucidate that particular aspect, since the number of specimens caught during the period of maturation was too small (cf. Section 3). According to our own observations, this is actually the case of Sepia officinalis.

2. Ratio of sexes, and sequence of sexes during migration

In all, we have received 7484 males and 5657 females, i.e. 57.0 per cent males, or 132 males per 100 females. The sex ratio may exhibit considerable variations in different years. For example, in 1933, 58 per cent males were 226 caught; in 1934, 61%; in 1935, 60%; in 1936, 53%; and in 1937, 53%. In each one of these years, more than 1500 individuals were examined.

The value of these numerical data is rather uncertain. For example, there exists the possibility that the males are more easily caught than the females. In addition, interpretation of results is not simple in a migrant species like our one. The unequal sex ratio could be based on a greater number of migrating males, but also on a longer time of residence per male individual on the grounds. Finally, we must give consideration to the possibility that we are permitted to draw conclusions only regarding the ratio of the sexes of the individuals participating in the breeding migration into the Dutch coastal sea, and that these conclusions may not, without reservation, be applied in general fashion to the entire species.

Less risky is the interpretation of the change of the sex ratio in the course of the year. That change permits us to draw conclusions regarding the sequence of the appearance of the sexes during migration; these sequences are already known in very different migratory animals, and permit comparisons.

Figure 7 provides numerical values regarding this aspect on the basis of our overall results. It is clear that the males and females arrive almost simultaneously in the coastal sea, with the females, however, being observed, on average, a little later in the year than the males. However, more detailed consideration of the catch numbers gives the impression that the males arrive relatively a little earlier than the females, since their relative frequency decreases gradually, and amounts to 61 per cent in April; 58% in May; 53% in June; and to 53% in July and August. If we give separate consideration to the catches made during the first week of April, during which squid are frequent, we find an even greater number of males, viz. 62 per cent. All these numbers appear to be rather unequivocal; however, if we compare the results obtained in the individual years, it appears that this sequence of the sexes, 227 after all, does not occur every year. Figure 8 illustrates the corresponding data. In the years 1933 and 1934, the two sexes appeared at about the same time; in 1935, the females appeared relatively earlier; and in 1936 and 1937, finally, the males appeared earlier.

We wish to compare that result with several data available in literature for other animal species.

We are informed best regarding the situation existing in birds. Table 1 contains a number of different examples. It appears that the three possibilities imaginable (viz. males before the females; females before the males; and males and females at the same time) are all given in nature. For us it

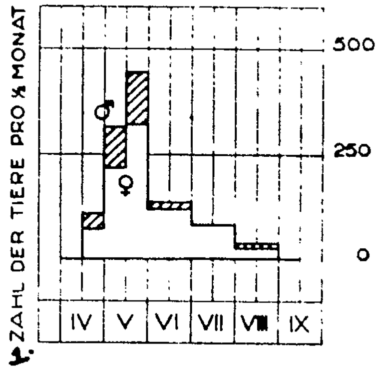


Figure 7 - Occurrences of males and females. Average values for 1932 to 1940. Numbers of males and females to be counted from the baseline. Key: 1, Numbers of animals per half month.

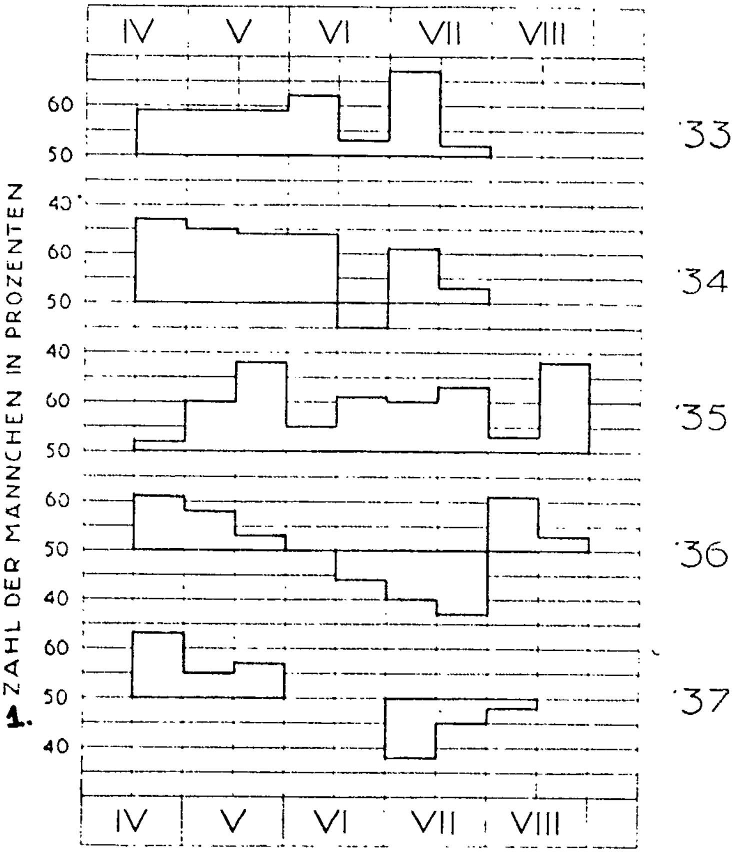
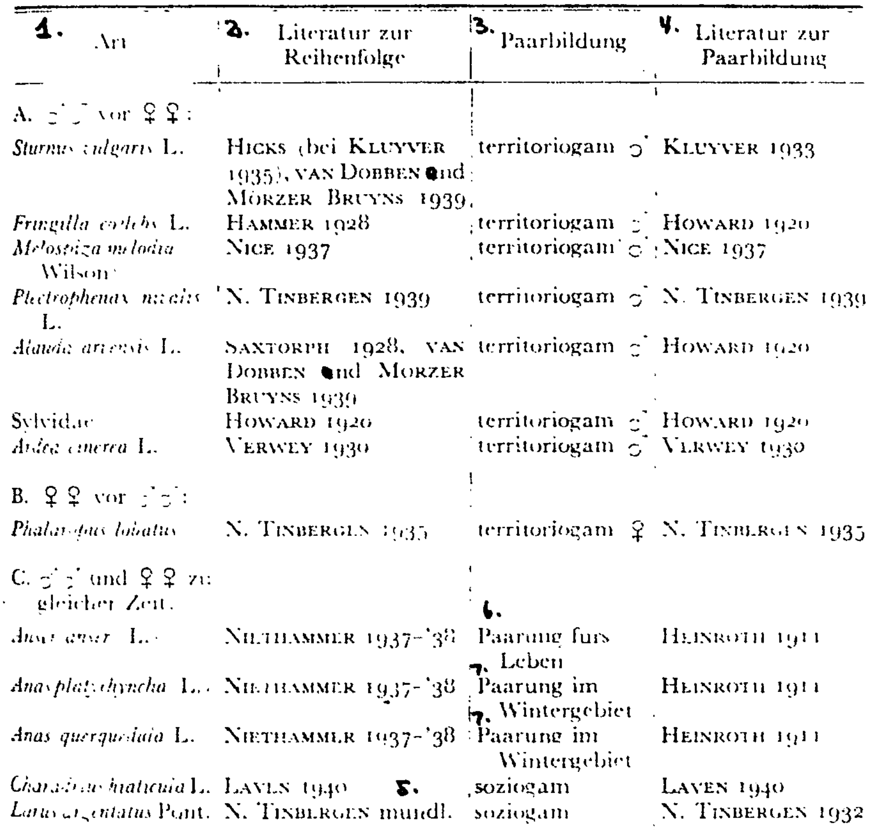


Figure 8 - Sex ratios observed during individual years. Key: 1, Number of males in per cent.

<u>Table 1</u> - Order of appearance of the sexes during the spring migration of various bird species, with data on pair formation. N.B. The symbol (♂ or ♀) appearing after "territoriogam[ous]" indicates the sex of the owner of the territory. <u>Key:</u> -gam, -gamous; A, Males before the females; B, Females before the males; C, Males and females together. 1, Species; 2, Literature on the order of appearance; 3, Pair formation; 4, Literature on pair formation; 5, . . ., personal communication; 6, Pairing for life; 7, Pairing on the winter range.



1. Art	2. Literatur zur Reihenfolge	3. Paarbildung	4. Literatur zur Paarbildung
A. ♂♂ vor ♀♀:			
Sturnus vulgaris L.	Hicks (bei Kluyver 1935), van Dobben und Mörzer Bruyns 1939.	territoriogam ♂	Kluyver 1933
Fringilla coelebs L.	Hammer 1928	territoriogam ♂	Howard 1920
Melospiza melodia Wilson	Nice 1937	territoriogam ♂	Nice 1937
Plectrophenax nivalis L.	N. Tinbergen 1939	territoriogam ♂	N. Tinbergen 1939
Alauda arvensis L.	Saxtorph 1928, van Dobben und Morzer Bruyns 1939	territoriogam ♂	Howard 1920
Sylvidae	Howard 1920	territoriogam ♂	Howard 1920
Ardea cinerea L.	Verwey 1930	territoriogam ♂	Verwey 1930
B. ♀♀ vor ♂♂:			
Phalaropus lobatus	N. Tinbergen 1935	territoriogam ♀	N. Tinbergen 1935
C. ♂♂ und ♀♀ zu gleicher Zeit.			
Anser anser L.	Niethammer 1937–'38	6. Paarung fürs Leben	Heinroth 1911
Anas platyrhyncha L.	Niethammer 1937–'38	7. Paarung im Wintergebiet	Heinroth 1911
Anas querquedula L.	Niethammer 1937–'38	7. Paarung im Wintergebiet	Heinroth 1911
Charadrius hiaticula L.	Laven 1940	soziogam	Laven 1940
Larus argentatus Pont.	N. Tinbergen 5. mundl.	soziogam	N. Tinbergen 1932

is furthermore of interest that the sequence of arrival of the sexes shows relations to breeding biology. For that reason, we have included in Table 1 also data on that aspect. We then arrive at the following rules: 228

In species forming pair bonds on the winter range or having only one sexual partner during life, respectively, the two sexes appear together on the breeding range. On the other hand, species mating only on the breeding range exhibit varying behavior. Their behavior depends on the manner of pair formation.

For describing these differences, we may employ best the division into "territoriogamous" and "sociogamous" species established by Makkink (1942). Makkink speaks of territoriogamy, where pair formation is consummated by means of occupation of a territory, and of sociogamy, where pair formation takes place within a group of conspecifics and prior to occupation of a territory. Territoriogamy proceeds in accordance with the following scheme: One of the sexes (the male one in most species) occupies a well defined site and there performs courtship activities, the function of which is the defence of that territory against conspecifics of the same sex, and attraction of individuals of the opposite sex. The individuals of the latter sex roam about rather freely, and become attached to a certain site only during pair formation. This "territorial system" is very common among birds (as well as in other animal groups). Territoriality was discovered by B. Altum, and subjected to detailed discussion for the first time by H.E. Howard; for additional details, we refer the reader to the corresponding ornithological literature.

In the case of the territoriogamous species, the sex occupying the territory, as a rule, appears on the breeding range earlier than the other sex. The lapwing [Vanellus vanellus], which, without doubt, is territoriogamus, represents an exception, in that, according to Rinkel (1940), the two sexes migrate at the same time. According to the same author, the sex occupying the territory (i.e. the ♂) nevertheless appears somewhat earlier in the breeding biotope. so that the analogy with the other species is again evident.

As already mentioned, the role of the territorial owner is played in most territoriogamous species by the male. We know only a few species, in which the female performs that function. In the single case documented (Phalaropus lobatus), the females actually appear earlier on the breeding range than the males (cf. Table 1).

In contrast to the species mentioned above, the sociogamous species in all probability are characterized in that the two sexes appear at the same time on the breeding range. This behavioral aspect, however, is known to us only in two cases, viz. Charadrius hiaticula and Larus argentatus. Other species have not been investigated. (It may be added in this connection that Larus argentatus is no characteristic migrant, but does cover a certain distance during the spring between the feeding area and the breeding area.)

It then appears in the birds that the separation of the sexes during spring migration is associated with territoriogamy. The connexion is so close that we are forced to assume that the earlier appearance of the territory-occupying sex is necessary or, at least, advantageous for the species concerned.

Howard (1920, page 43) has suggested that the biological significance of this phenomenon is that the later arriving females encounter a uniformly distributed population of males. However, he did not explain how that situation would promote the success of reproduction. It does not appear to us that Howard's interpretation is a convincing one. However, we are not able to replace his interpretation by a more satisfactory one, and, for that reason, 229
can only conclude that the significance of the earlier appearance of the territory-occupying sex is as yet unclear.

The phenomenon of the established sequence may have two causes: Either the two sexes start spring migration at the same time, but migrate at different speeds, or the sex appearing first leaves the winter range earlier. In that respect, we can only say that the latter possibility is probably applicable in Sturnus vulgaris, since the sequence can be demonstrated already at a short distance away from the winter range. In the case of that species, it then appears that the sexes exhibit different thresholds for the stimulus eliciting migration.

The mammalian group contains several species, which, like migratory birds, 230 migrate every year to their breeding grounds. Hilzheimer's (1929) monograph demonstrates that these migrations in the cases of the southern elephant seal [*Mirounga leonina* (L.)], the sea lion (*Eumetopias* sp.) and the northern fur seal [*Arctocephalus* (actually, *Callorhinus*; Transl.) *ursinus* (L.)] are performed earlier by the males than by the females. In this connection, we are interested in certain biological features of these species also outlined by Hilzheimer (1914; 1929). The males of the elephant seal and of the fur seal (no details are reported regarding the sea lion) occupy certain sites along the beach at the onset of the breeding season, which sites they defend in order to await the arrival of the mass of females. Even if their behavior does not correspond in every respect to that exhibited by the birds described further above, it appears to us that the analogy to the territorial system is so convincing that we venture to speak also in the case of these mammalian species of territoriogamy. As in the birds, we see also in this instance that the separation of the sexes in time during the breeding migration is associated with territoriogamy.

In the case of certain bats, the females, toward the end of the winter, migrate to the summer range someehat earlier than the males, where the females then give birth to their young (Eisentraut, 1937). In their case, the situation then is entirely different—a finding, perhaps, attributable to the fact that these animals do not mate following arrival on the summer range, but mated already during the preceding fall. A similar situation has been observed in none of the species hitherto treated.

In the fishes, too, the sexes frequently exhibit separate migrations to the spawning grounds. Scheuring's (1929; 1930) monograph, for example lists:

♂♂ before ♀♀	♀♀ before ♂♂	♂♂ and ♀♀ together
Clupea harengus L.	Callionymus lyra L.	Oncorhynchus gorbuscha (WALBAUM)
Alosa vulgaris (L.)		Oncorhynchus keta (WALBAUM)
Oncorhynchus nerka (WALBAUM)		
Fundulus heteroclitus (L.)		
Pleurogrammus monopterygius (PALLAS)		
Alosa sapidissima (WILSON)		

Salmo salar appears to behave differently in the different parts of its biotope. Connexions with the breeding biology are not known in the case of fishes.

When we now return to the cephalopods after these discussions, we must, in the first instance, note that the behavior of *Sepia officinalis* differs from that of *Loligo vulgaris*. In *Sepia*, the males, on average, appear distinctly earlier than the females, so that the males during the first two weeks of *Sepia* arrival represent 73 per cent of the total catch *versus* only 58 per cent during the following months. There then arose the question whether there existed also differences in pair formation. We know the latter behavioral element in *Sepia* from aquarium observations (L. Tinbergen, 1939). This species exhibits a certain similarity to territoriogamous bird species. For example, the 231 males have the habit of fighting with each other prior to pair formation, and this without that the females are present during fighting. They do not occupy territories in the aquarium; it is not known whether they do that in their natural habitat. The courtship and nuptial ethology of *Loligo vulgaris*, unfortunately, is entirely unknown. Details regarding our species would be highly welcome specifically for the purpose of comparison with the relationships described further above, and this, in particular, since we know that *Loligo* occurs to a greater extent in shoals than does *Sepia*. Today we then know only that the inclusion of these aspects in future treatment of the reproduction of *Loligo vulgaris* will be rewarding.

3. The Gonadal Cycle and its Relation to the Migrations (231)

Regular observation of the gonadal state is important for two reasons: Firstly, the annual cycle of the sexual organs of the cephalopods is not well known. Secondly, these observations may show to what extent reproduction and migrating behavior are associated with each other. This association exists in many migratory animals.

The observations of the gonadal cycle of the males will first be shown. The stages described hereinafter are illustrated schematically in Fig. 9.

The previously described October and December young animals (page 217, German text) were already surprisingly well developed. Six 24 October, 1934, ♂♂ had slightly swollen testes; microscopic examination showed that the testes contained large numbers of spermatozoa. The spermatophore organ (as designated by DREW, 1919), and the spermatophore sac were visible macroscopically, but they contained no spermatophores as yet. In 19 ♂♂, which were collected between 24 November and 18 December, 1939, the development was a good deal more advanced. The testes were almost as swollen as those of the spawning migrants in the spring. In smears, large numbers of spermatozoa were found. In 14 of these animals, the spermatophore sacs already contained low numbers of, though small, spermatophores; those of the other 5 were empty.

Thus, although in early winter, only young animals with maturing gonads were obtained, in the autumn of their year of birth, not all the animals are developed that far, for even the following summer, still quite (233) immature yearlings appear, as will be seen later.

From the period January to March, only very few animals are available. Their condition points to the fact that the gonads gradually develop all through winter, or at least, that their development does not recede:

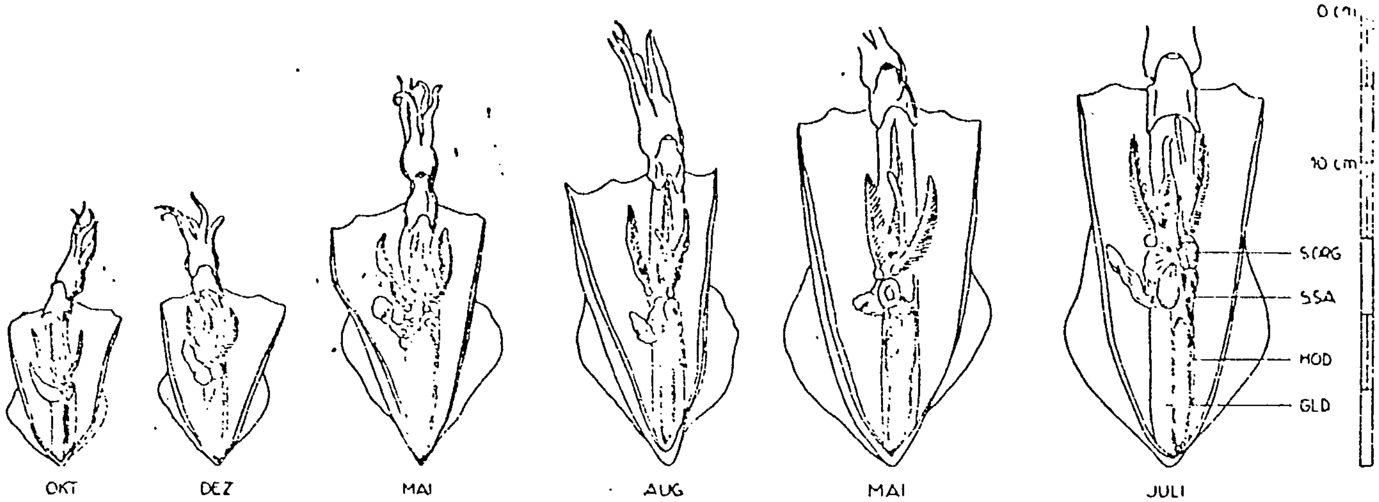


Abb. 9. Gonadenzyklus der ♂♂ von Oktober des Geburtsjahres bis zum Ende des 2. Lebensjahres. Gld. = Gladius, Hod. = Hoden, S. org. = Spermatophorenorgan, S. sa. = Spermatophorensack. Füllungsgrad der Spermatophorensäcke: Mai (1. Jahr) „voll", Aug. (1. Jahr) „halbvoll", Mai (2. Jahr) „voll", Juli (2. Jahr) „viertelvoll".

Fig. 9. Gonadal cycle of the ♂♂, from October of their year of birth to the end of their second year of life. (232)
GlD. = Gladius; Hod. = testis; S.org. = spermatophore organ; S.sa. = spermatophore sac.
Filling degree of spermatophore sacs: May (1st year) "full", August (1st year) "half-full", May (2nd year) "full", July (2nd year) "filled one fourth".

21 January, 1937, 12.0 cm ♂, testis fully developed (5.3 x 1.3 cm). (233)
The spermatophore sac contains a small number of spermatophores.

12 March, 1936, 9.0 cm ♂, testis fully developed, spermatophore sac as above.

13 March, 1936, 7.6 cm ♂, undeveloped, testis undetectable, no spermatophores, hectocotylus distinct.

In April, when the 3/4-year-old animals appear in large numbers in the coastal area, most of them have strongly swollen testes which, even in relation to the length of the animals, are larger than the previous autumn. In smear preparations, large amounts of spermatozoa are found.

In the course of the summer, most of the yearlings have well developed testes. Only in a very small number of animals this organ is undeveloped. Thus, among 4511 mature ♂♂ examined from April to August, only 16 animals were "immature".

In 3 of these animals, the testes were undetectable; in 10 animals they were hardly visible, and in 2, they were somewhat larger, yet scarcely swollen (in a 13.5 cm animal, for example, it was 2.3 x 0.3 cm, that is, about the same size as in a 6-9 cm young animal. 15 of these 16 animals were caught in July and August; hence, they were considerably later than their mature equals in age. Their ventral mantle length varied between 10.1 and 16.0 cm, and was, on an average, 12.6 cm, that is, substantially less than that of the other yearlings which, according to page 214 (German text), at this time, is 15-18 cm. Thus, they were late-born or physically retarded animals.

As seen above, part of the yearlings do not arrive here. They may spawn elsewhere; they may not even take part in the spawning migration. Should this latter be the case, it is quite possible that a much higher number among them are immature than among the investigated yearlings.

In July and August, the testes undergo involution; yet, this manifests itself only by a lesser size of the organ, mainly by decreased width (cp. Fig. 9). The extent of this involution cannot be determined, since winter observations of the 1 1/4 to 1 1/2-year-old animals are lacking completely. From observations of young animals, one may presume that during the second winter, the testes maintain a rather high developmental stage. (234) Nevertheless, it is obvious that the testicular development is subject to an unmistakable periodicity, and reaches its peak during the months of April to June.

During the summer months, the two-year-old squid undergo a similar development as the yearlings dealt with here. Even their testes are large at the arrival, and decrease in late summer (Fig. 9). No undeveloped animals occur among them.

Like the testes, also the other sexual organs of the summer animals are well developed. The vas deferens is fully swollen, and has a milky aspect. In the spermatophore organ, a few half-developed spermatophores usually are found. The spermatophore sac, generally, is fully grown and contains a considerably larger amount of spermatophores than that of winter animals. Thus, they formed between December and April. Only in the isolated immature animals, this formation does not take place; in these animals, all the above mentioned organs are undeveloped and empty.

During the summer months, the filling degree of the spermatophore sacs of about 4500 animals was recorded. It was determined by estimation; the following classification was made: "full", "half-full", "filled one fourth", "almost empty", and "empty", These designations do not relate to the absolute amount of the content, but rather, to the relative amount, that is, they take the size of the animal into account. Some of these studies are shown in Fig. 9.

It resulted, first of all, that the spermatophore sacs of the yearlings, at their arrival, on an average, and in relative terms, are less filled than those of the two-year-old animals. This may best be seen from the following values which relate to animals caught between 23 April and 20 May, 1937.

Animals:	Sizes: 10-17 cm	 18-30 cm
49 "full"	24 %	76 %
69 "half-full"	25 %	75 %
186 "filled one fourth"	39 %	61 %
41 "almost empty"	66 %	34 %
4 "empty"	(100 %)	(0 %)

The 10-17 cm and 18-30 cm ranges were so chosen that the former comprise the majority of the yearlings, the latter the majority of the two-year-old animals.

This may also be formulated in the following manner: (235)

Out of 138 10-17 cm animals:	Out of 231 18-30 cm animals:	
9 %	16 %	were "full"
16 %	29 %	"half-full"
53 %	49 %	"filled one fourth"
19 %	6 %	"almost empty"
3 %	0 %	"empty"

The fact that the described relationship between animal size and filling degree of the spermatophore sacs is statistically significant, may be seen from the following calculation which relates to the period 23 April to 2 May, 1935. At that time, there were received: 39 "full" animals with an average length of 19.5 cm (standard deviation $\sigma_{\bar{x}} = 0.64$), and 37 "almost empty" animals with an average length of 16.0 cm ($\sigma_{\bar{x}} = 0.71$). The standard deviation of the difference is, according to σ_d, $= \pm\sqrt{\sigma_{\bar{x}}^2 + \sigma_{\bar{y}}^2} = 1.0$ cm, and less than one third of the difference, which therefore is statistically significant.

Hence, in early summer, the spermatophore sacs of the two-year-old animals are fuller than those of the yearlings. In other respects, the two age groups behave similarly; thus, hereinafter, they will be dealt with in common, the more so as one cannot determine the age of each animal.

It has already been seen that at the arrival of the animals, their spermatophore sacs are more or less filled. Soon afterwards, the number of animals with less filled sacs increases. Fig. 10 shows that this increase goes on from April until at least the second half of June. In August, there are some discrepancies which may be due to the low number of investigated animals.

Two factors are responsible for these changes: Firstly, the relative increase in the number of yearlings in the course of the year (page 225, German text). As said before, their sacs are less filled than those of the two-year-old animals. Hence, the change in the population composition must bring about a lower average filling degree.

However, this change is too small to explain the whole decrease. Thus, the second important cause are the matings which take place all through summer, and which will be further dealt with in connection with the ♀♀.

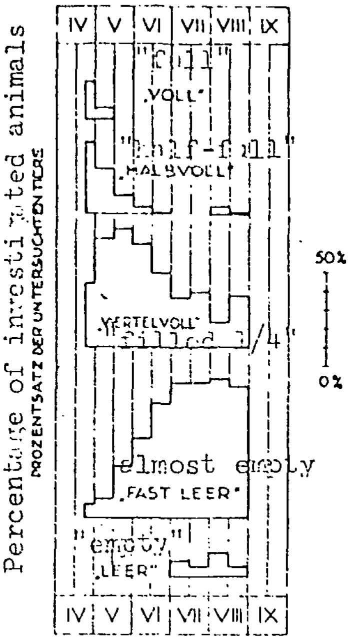


Abb. 10. Füllungsgrad des Spermatophorensackes im Laufe der Zeit, 1934-1940.

Fig. 10. Filling degree of spermatophore sacs during the investigation period, 1934-1940.

(235)

The diagram of the filling degree of the spermatophore sacs therefore shows that before the arrival of the animals, the spermatophore production exceeds the consumption; afterwards, consumption exceeds production. This might imply that during summer, no spermatophores are produced, and that the animals use up a reserve they stored up at the beginning of the reproductive period. However, this is definitely not the case; all through summer, developing spermatophores may be found in the different sections of the spermatophore organ, as established already on page 6.

In Loligo pealii it is similar, as may be seen from DREWS's (1919) fine report on the formation of spermatophores by this species.

As mentioned before, the above said relates to one and two-year-old animals together. Of both age groups therefore, the animals arrive with more or less filled spermatophore sacs which gradually empty during the summer. One cannot say for certain whether the yearlings that have finished spawning will mature again the following spring, or whether the mature two-year-old ♂♂ are those animals which, the first year, may not have been mature, and did not migrate to the spawning area (cp. page 4). However, in either case, it is obvious that the sexual activity is bound to a determined season of the year; this will be dealt with later on.

The observations regarding the gonadal cycle of the females will now follow. One is faced here with the same difficulty as in the case of the ♂♂, namely, that adequate numbers of animals remain only a few months in the observation area.

Some of the stages to be described are illustrated semi-diagrammatically in Fig. 11.

The few young autumn and winter animals that were available for observation, were relatively less developed than the ♂♂ caught at the same time. Both the animals received on 24 October, 1934, and in December, 1939, had very small ovaries, the granular structure of which was scarcely visible (237) macroscopically. At microscopic examination, the about 0.2 mm eggs were clearly visible. The nidimental glands (see Fig. 11) had only started maturing (though they were larger in the December animals than in the October animals); the same applies to the accessory glands. The oviduct, of course, contained no mature eggs as yet, and the spermatheca was not visible macroscopically.

Even one of the March animals was hardly more developed; yet, it was very short, which may have accounted for its delayed development, with respect to the majority of its equals in age.

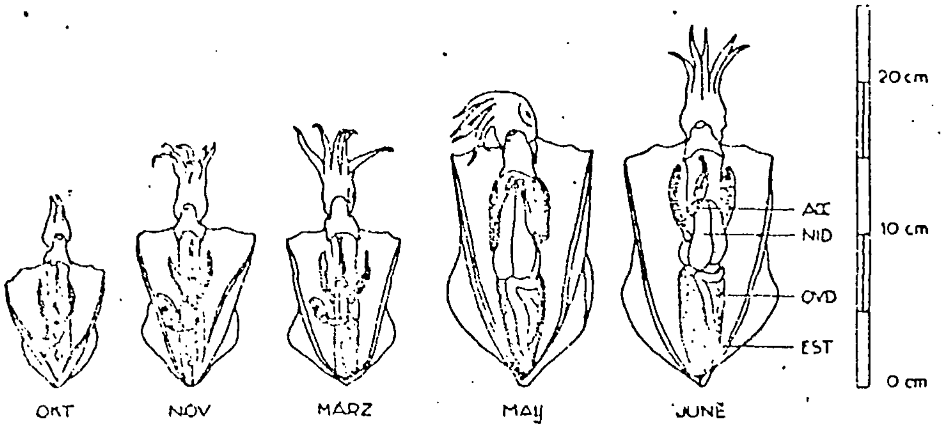


Abb. 11. Gonadenzyklus der ♀♀ vom Oktober des Geburtsjahres bis zum nächtsten Juni. Est = Eierstock, Ovd = Ovidukt, Nid = Nidimentaldrüsen, Acc = Akzessorische Drüsen. Füllungsgrad der Ovidukte: Mai „voll", Juni „mässig".

Fig. 11. Gonadal cycle of ♀♀, from October of the year of birth until the following June.
Est = ovary; Ovd = oviduct; Nid = nidimental glands; Acc = accessory glands.
Filling degree of oviducts: May "full", June "moderate".

In contrast thereto, the ♀♀ appearing in the second half of April - now nine months old - look quite different. The nidimental glands are fully grown and swollen; the same applies to the accessory and oviduct glands. On the mouth membrane, the spermatheca is visible as a small bulge, and the ovary fills part of the abdomen with its 1-2 mm eggs. In front, to the left of this organ, there is the oviduct lying in several loops, with clear, pale-yellow eggs arranged in rows, which help to fill tightly the abdominal cavity.

Until the animals disappear in late summer, the ovary remains fully to moderately developed; a decrease toward the end of this time, as in the case of the testes, was not safely established.

The second or third week of May, a small number of females appear, (239) the eggs of which are not as tightly packed in the ovary as described before, which gives the ovary a strikingly loose, disorderly aspect. This aspect will be dealt with a little later, where it will be seen that these are probably the ♀♀ which have just released their eggs. The appear all through summer.

Also among the ♀♀, there are yearlings with undeveloped gonads. Their ovaries resemble very much those of the winter animals (see above). The same applies to the nidimental and accessory glands.

During 1935-40, the number of these immature ♀♀ was 16 out of 3505 examined animals. In contrast to the immature ♂♂ which, according to the above said, appeared only during the months of July and August, they appeared most frequently during May. Their length was 9.8 - 14.7 cm, on an average 11.5 cm, that is, the same as in the case of the immature ♂♂, considerably less than that of the other yearlings where, according to page 223 (German text), it may, at this time, be estimated at 13-14 cm.

Unfortunately, autumn and winter observations regarding the further development of the ovary are lacking. The following summer, the two-year-old ♀♀, the same as the yearlings, have well developed ovaries at the time of their arrival. Even in these animals, no involution can be detected at the end of summer. Undeveloped individuals do not seem to occur; this is in line with the findings regarding the ♂♂.

The oviduct, which acts as storage organ for the mature eggs, shows considerably varying filling degrees during the course of summer. As in the case of the spermatophore sacs of the ♂♂, the filling degree was recorded for each examined individual, and the following classification was made for the eggs: "many" (= "full"), "moderate", "few", and "none" (= "empty"). Also in this case, to estimate the number of eggs, the size of the animal was taken into account.

As in the case of the spermatophore sacs of the ♂♂, the filling degree is associated with the length of the animal.

Between 20 April and 11 May, 1937, for example, the following animals were examined:

	average length:	
16 ♀♀ "full"	16.2 cm	σ_x = 0.4 cm
78 ♀♀ "moderate"	14.8 cm	
28 ♀♀ "few"	14.7 cm	σ_y = 0.27 cm
9 ♀♀ "empty"	12.4 cm	σ_z = 0.4 cm

The discrepancies in the average lengths between the ♀♀ of the first and the third, the first and the fourth, and the third and the fourth groups are statistically significant, since they exceed 3 x σ_d (calculated according to $\sigma_d = \pm\sqrt{\sigma_x^2 + \sigma_y^2}$). Yet, between the ♀♀ with "moderate" (239) numbers of eggs and those with "few" eggs, there is no essential difference.

According to page 223 (German text), between 20 April and 20 May, the two-year-old ♀♀ are, on an average, about 17 cm long. Among the "full" animals of the above shown Table therefore, there is a higher percentage of two-year-old animals than among the "less filled" ones or, in other words: the two-year-old ♀♀, even when taking their size into account, bear more eggs in the oviduct than the yearlings, as also the two-year-old ♂♂ have relatively fuller spermatophore sacs than the yearlings (page 7).

Also in many fish species, the number of eggs increases with increasing age of the animals (as, for instance, in _Acanthias vulgaris_ Risso, cp. FORD, 1921). Similar findings have been made for some bird species that reproduce for several years during their lifetime. Thus, it is known that the several-year-old ♀♀ of the starling (_Sturnus vulgaris_) (KLUYVER, 1935), the song sparrow (_Melospiza melodia_) (NICE, 1937), and the redstart (_Phoenicurus phoenicurus_) (RUITER, 1941), lay more eggs than the yearlings. However, as to whether the egg production of these three bird species - as well as of _Loligo vulgaris_ - goes on rising with increasing age, is not known; nor can it readily be determined, since their average lifespan, when free, is relatively short. One might expect that the egg production rises at the beginning, to decrease again when the animals get older.

Hereinafter, one and two-year-old ♀♀ will be observed together, as was the case for the ♂♂. A separation may not even be feasible, since the two age groups differ too little in size, and no other characteristics exist to evaluate their ages.

The changes in the filling degrees of the ♀♀ oviducts during the investigation period are graphically illustrated in Fig. 12. The percentages of animals with full to moderately filled oviducts are high at the beginning; however, rather soon after the arrival of the animals, the individuals with less filled oviducts become more frequent. Presumably, analogous to the ♂♂, this is dependent to a lesser degree only on the change in the population composition; rather, the egg-laying may be the main cause. At this time also, the fishermen bring in the first egg clusters (1933: 9 May; 1934: 12 May; 1935: 18 May; 1936: 5 May; 1937: 4 May).

The relative increase in the number of animals with less filled oviducts ceases in the second half of May. One may therefore conclude that before the arrival of the animals, egg production exceeds consumption; then, until the end of May, consumption exceeds production and, eventually, there is equilibrium. Before the appearance of the animals, consumption must be (240) set equal zero, since the eggs are laid only in the coastal waters (where the first ones are found at the beginning of May). From May until about the beginning of August, eggs are constantly being consumed, as seen from the dates of detection of freshly laid eggs (Table 2).

Thus, egg-laying lasts from May to July or August, that is, almost as long as the animals remain in the coastal area, and during all this time, the ovary supplies the oviduct with eggs. (The number of spawning ♀♀ reaches its peak in the second half of May, as will be seen later).

Table 2. Developmental stage of eggs

Month Monat (1933-'37)	[illegible] of Zahl der collected gesammelten Eiertrauben egg clust.	Hiervon untersucht: Examined: undevel. Unentwickelt, frisch fresh	Entwickelt developed	empty and Leer und verfault decayed
IV.	0	—	—	—
V.	30	13	1	0
VI.	37	—	—	—
VII.	37	15	16	0
VIII.	46	4	1	21
IX.	0	—	—	—

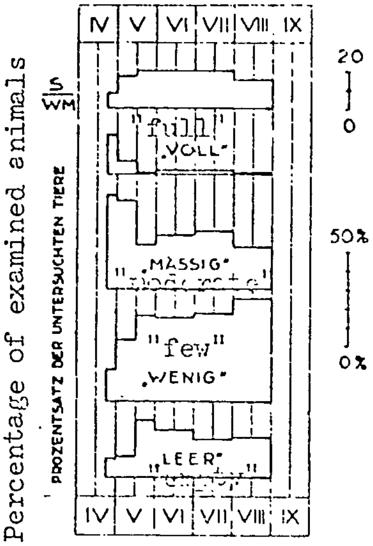


Abb. 12. Verhältniszahl $\frac{S}{WM}$ und Füllungsgrad des Oviduktes im Laufe der Zeit, 1934-1940.

Fig. 12. Ratio $\frac{S}{WM}$ and filling degree of oviduct during the investigation period, 1934-1940.

It has been mentioned before that at the middle of May, females appear, the ovaries of which have a loose and strangely uneven aspect, while their oviducts contain few or no eggs at all. No doubt, these females laid their eggs just recently. Moreover, a rather large percentage thereof have newly deposited spermatophores on the spermatheca mound, which indicates that egg-laying often is followed by copulation. These females with loose ovaries and scarcely filled oviducts, which occur from the middle of (241) May on, and are present all through summer, never are numerous; they always form just a small percentage of all the animals; they may be most frequent in the second half of May, since, undoubtedly, at that moment, a large number of ♀♀ lay their eggs at the same time. Apart from these ♀♀ with slack ovaries, from the middle of May on, a rather large number of other females appear which, likewise, have only few eggs in their oviducts, while their ovaries have normal aspect. These are probably animals the ovaries of which, so to speak, have been regenerated, and the oviducts are filling again. Apparently, the emptying of the oviduct now takes place already when the number of eggs has reached the "moderate" degree, for, after the middle of May, only very few ♀♀ with full oviducts appear. Hence, the animals apparently produce several batches of eggs, the first one being the largest. The number of egg batches cannot be determined.

The oviduct development during autumn and winter is not known. Eggs are definitely not laid during this period. Whether the egg production goes on in winter, or at what time the oviducts start filling in spring, is not known. Nor is it known whether each ♀ reproduces once or twice in its lifetime. It would be possible that the two-year-old animals are the undeveloped yearlings of the previous year. However, in the authors' opinion, this is unlikely.

Finally, the investigation of the female sexual organs also comprised observations regarding the condition of the spermatheca and the presence of freshly deposited spermatophores in its neighborhood. From the reports of LAFONTS (1871), DREWS (1911), and VAN OORDTS (1939), it is known for *Loligo pealii* Les. and *Loligo vulgaris* Lam. that during mating the spermatophores are deposited on the mouth membrane.[1] Here, they are soon emptied; the spermatozoa then reach the spermatheca (= receptaculum seminis), a glandular recess in that membrane. In filled condition, this spermatheca (242) has a milky white aspect. It is then called a "white mouth mound". The empty or half-empty remainders of the spermatophores first adhere to the skin slime of the mouth membrane; then, they disappear, even before the content of the spermatheca is used up.

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[1] Moreover, for *Loligo pealii*, DREW (1911) detected matings where the ♂♂ deposited the spermatophores into the mantle cavity of the ♀. In the ♀♀ of *L. vulgaris* from the surroundings of Den Helder, the authors never found spermatophores in the mantle cavity, despite the fact that several thousand individuals were examined. However, LEBERT and ROBIN (1845) provide an accurate description and illustration of a ♀ of this kind, which carried burst spermatophores at the inner mantle wall. The origin of this animal is not known.

The present observations showed, firstly, that the majority of mature ♀♀ have filled spermathecae. Secondly, they showed how the frequency of matings developed during the investigation period. When few matings take place, many ♀♀ lose the spermatophore remainders. There are then relatively many ♀♀ with filled spermathecae, yet without spermatophore remainders. On the other hand, in times of numerous matings, there are relatively many ♀♀ which bear spermatophore remainders. By determining the ratio between the number of ♀♀ with spermatophore remainders and the number of ♀♀ without spermatophore remainders, yet with so-called white mouth mound, that is, with filled spermatheca, or briefly, $\frac{S}{WM}$ 1), one obtains a more or less accurate measure for the frequency of matings. Fig. 12, top, shows the course of this ratio. At first, it rises rapidly, then more slowly, and descends somewhat in August. One may conclude therefrom that from the arrival on, and close to the departure, the animals mate with undiminished vigor. This conclusion relates to the number of matings per mature female present; the number of totally occurring matings shows a marked maximum in the second half of May, when the number of animals present reaches its peak.

These observations regarding the periodicity of reproduction will be summarized once more. In December, the ovary is still very little developed, and no eggs at all are in the oviduct at that time. Egg-laying takes place only from April to August, with a maximum in the second half of May. Exactly the same periodicity exists for the matings and, thus, the spermatophore consumption. Yet, the testis produces spermatozoa already (24) in October, which are stored already from December on in spermatophores.

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1) The authors used the ratio of $\frac{S}{WM}$, and not $\frac{S}{\text{total of examined ♀♀}}$; otherwise, the presence of immature ♀♀ would have influenced the values.

With regard to this latter point, other periodically maturing animal species behave quite differently. In bird testes, for example, the spermatozoa develop only shortly before the mating period, to disappear again soon afterwards. One might assume that the early maturation of the ♂ squid - long before the mating period - is in association with the capacity to store the sperma in spermatophores. A comparison with other animal species with spermatophores would be interesting.

Finally, it is interesting to compare the reproductive period of these squid with squid from other detection sites, as well as with other cephalopod species. Unfortunately, only few data are available.

LO BIANCO (1909) describes that in the Mediterranean Sea the eggs of *Loligo vulgaris* are caught between November and July, and mainly from March to June. (It should be added that in the Mediterranean this species is present all year round). Hence, the reproduction lasts longer, and starts earlier in the year. Some other cephalopod species show periodic reproduction also in the Mediterranean area. LO BIANCO mentions *Sepia officinalis* L., December to July, seldom in August, October, November; eggs are frequent mainly from March to June; *Octopus vulgaris* Lam., eggs from May to August; *Eledone moschata* Lam., April to July. For *Sepia*, as for *Loligo vulgaris*, the reproductive period in the Mediterranean is considerably longer than in the North Sea where, according to the authors' observations, it lasts only from May to August. *Loligo marmorae* Ver. even spawns all year round in the Mediterranean; according to some authors, this species is identical with *Allotheutis subulata* Lam. from the North-Sea region. This latter does not spawn in winter. It would appear to be an example where the periodicity is very marked in the North, while in the South, it is almost or completely lacking. SASAKI (1921) gives a similar description of the Japanese

Ommastrephes sloani pacificus: In Southern Japan, the mating period is said to go on all year round (although with a maximum in September/October), while in Northern Japan, it would appear to be limited to December. However, this latter conclusion would not seem to be final, since in Northern Japan, during different months, only half-grown animals were investigated.

As with any periodic phenomenon, one may ask on what external factors the reproductive rhythm of *Loligo* is dependent. Apparently, the conditions are different than in many Temperate-Zone birds, the maturation of which is brought about by the increasing length of daylight (ROWAN, 1938). The squid starts its reproduction in the South at decreasing length of daylight, in the North at increasing length of daylight. A periodicity regulation would appear most likely where a determined temperature range is necessary for reproduction, the upper limit of which, in the Mediterranean area, is exceeded between July and November, while the lower limit, in the North-Sea area, is reached only at the end of April. This longer reproductive period (244) in the South, particularly, points in a convincing manner to the effect of temperature. This longer reproductive period in the South is also found in other animals with Southern distribution (which therefore need high temperature for their reproduction), for example, the jellyfish (VERWEY, 1943), and fishes (*Engraulis encrasicholus* (L.), *Clupea pilchardus* Walb.: FAGE, 1920, pages 14 and 42).

As shown above, spawning of *Loligo vulgaris* starts on the arrival of the animals in the coastal area, and goes on until close to the departure of the last individuals. Moreover, it is known that reproduction does not take place, or hardly ever, outside of the coastal area. Hence, arrival and departure roughly coincide with the beginning and the end of reproduction. It is further known that in the spawning area, only very few immature individuals occur. All this would appear to point to a direct relationship between maturity and migration, as has been assumed for years already for birds where, in one case, it was even proved experimentally that both maturity and spring migration are determined by the increasing length of daylight (ROWAN, 1938). Initially, it was assumed that the increasing length of daylight causes sexual maturity which, again, causes the awakening of the migration drive. If so, however, it is not clear how the sexually immature yearlings of many species (Sepia, certain fishes, many wading birds, etc.) are able to take part in the migration. Since PUTZIG (1939) showed that castrated crows take part in the spring migration, this phenomenon must probably be explained to the effect that sexual maturity and migration drive are released by a common cause, namely the increasing length of daylight. In the same way, that is, that maturity and migration drive are released by one and the same cause, also the above mentioned relationships may have to be looked for in the case of Loligo.

Thus, during migration, the animals reach their spawning areas. According to the function therefore, one may speak of spawning migration. However, this does not mean that the migration has merely this significance. This would even be very unlikely, since, generally, several functions are involved. Thus, for instance, the purpose of the known northbound spring migrations of many animal species (birds), for one thing, is to reach the reproduction sites and, for another thing, to make available to them the blossoming reserves of the summer season, while it is likely that also more (245) favourable temperature conditions are found. It may be seen on page 275 (German text) that also for Loligo vulgaris, migration probably serves several functions. The fact that, generally, several functions are involved, makes it impossible to maintain the often used classification of animal migrations according tothe function.

4. Periodicity of Migration

From the diagram showing the numbers of animals caught (Fig. 13), it may be concluded that at Den Helder, from the second half of April to the end of May, immigration generally exceeds emigration, and from the end of May to the end of August, the conditions are reversed, yet without the occurrence of a stationary state, as this is the case for many migratory birds. It may even be assumed that since earliest times, there has also been emigration, and that, likewise, even after the second half of May, there is a constant immigration of new individuals. Obviously, however, the numbers of catches allow only conclusions regarding the difference between immigration and emigration, and not regarding the absolute numbers of animals.

The catch numbers of the separate years, on the whole, provide the same picture, and are not shown here. It is striking that the starting dates of migration over the different years vary only within narrow limits.

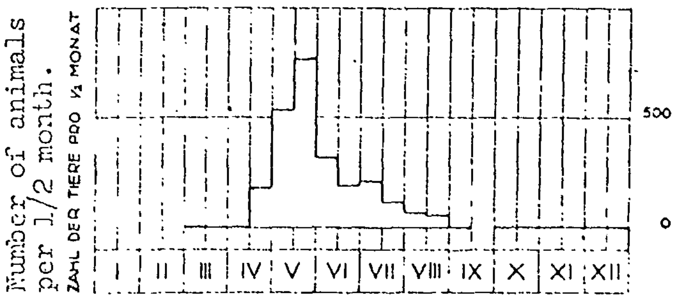


Abb. 13. Fangzahlen von Kalmaren. Durchschnittswerte 1933-1940.

Fig. 13. Number of squid caught. Average values 1933-1940.

It is true that the dates of appearance of the individual animals show considerable differences, as may be seen from Table 3. However, this is not really surprising, since, apart from the presence of the animals, their (245) first capture is largely determined by chance. However, if the dates on which a somewhat more numerous arrival was determined, are put together, for example the days on which, for the first time, 5 or 10 animals each were brought in, there is only a slight difference: in the first case, 13-30 April, in the second, 20-30 April. It may therefore be seen that the beginning of a more numerous arrival is restricted to the second half of April, and that it varies little from year to year. As is known, this latter fact applies to the migration periods of several animal species. The spring and autumn migrations of a number of bird species provide many examples therefor.

Table 3. Arrival dates of Loligo vulgaris

Jahr year	Wenigstens 1 Stück at least 1 anim.	Wenigstens 5 St. at least 5 an.	Wenigstens 10 St. at least 10 an.
1933	13. IV., 20. IV.	20. IV.	20. IV.
1934	21. IV., 23. IV.	25. IV.	25. IV.
1935	20. IV., 23. IV.	23. IV.	23. IV.
1936	3. IV., 13. IV.	28. IV.	28. IV.
1937	2. III., 14. IV.	20. IV.	20. IV.
1938	18. III., 12. IV.	13. IV.	22. IV.
1939	15. II., 6. IV.	22. IV.	29. IV.
1940	27. IV., 30. IV.	30. IV.	30. IV.

The arrival of the bulk of migratory animals, generally, occurs rather suddenly, for in 6 out of 8 investigation years, the dates on which for the first time 5 or 10 animals each were caught, coincide. Only in the years 1938 and 1939, there is about one week between the two dates. In both years, immediately after the capture of the first 5 animals, there was a period of windy weather which lasted several days. Undoubtedly, during these days, the coastal fishery, which provides the researchers with these squid, was interrupted. For this reason, the dates the first 10 squid were caught these years are exceptionally late. Even though the other years, similar occurrences may have affected the arrival dates of the first 5 squid, for the following report, the dates on which, for the first time, 5 animals each were caught, will still be considered as the most reliable measure for the beginning of the main migration.

It is worth searching for relationships between migration starting (247) date and external factors. Table 4 therefore compares temperature and salt content at the Haaks lightship with the beginning of migration.

Table 4. Dates of Appearance and Environmental Factors

	1933	1934	1935	1936	1937	1938	1939	1940
Temp. Haaks 1.-10.III. (°C)	4.8	4.2	6.1	5.6	4.9	5.5	5.8	Kalt. Keine Beobachtungen wegen des Krieges Cold; no observat due to the war
11.-20.III.	6.0	4.5	5.5	5.5	5.5	6.1	6.1	
21.-31.III.	6.1	5.2	6.1	6.4	5.8	6.8	6.0	
1.-10.IV.	7.1	5.0	6.4	6.8	6.5	7.3	6.6	
11.-20.IV.	7.6	5.6	7.2	7.1	7.5	7.4	7.8	
21.-30.IV.	8.2	6.4	8.1	7.4	8.0	7.9	8.5	
Erscheinungsdatum (April) Arrival date	20.	25.	23.	28.	20.	13.	22.	30.
Salin. Haaks 21.-30.IV. (°/₀₀)	34.25	33.30	34.34	34.52	32.94	33.75	33.52	—

It may be seen from this Table that there is no relation to the salt content of the last decade of April. However, there does exist a correlation, though not a very good one, to the temperature, in that the three years in which the last April decade was cold (1934, 1936, and 1940), show the latest arrival dates. However, the temperature is not the only regulating factor. If this were the case, the animals which, in 1934, arrived at 6.4°C, in 1933, would have had to appear already at the end of March, in 1935 at the beginning of April, in 1936 at the end of March, in 1937 at the beginning of April, in 1938 in the middle of March, and in 1939 at the beginning of April, which does not correspond to the facts. Hence, the animals are bound by other factors to the second half of April, and the effect of temperature is only a subordinate factor. From what is known of migratory birds, it is obvious that the length of daylight must account for this binding to the second half of April; this strong influence on the animals was determined by ROWAN et al.

In conformity with the present results are the findings of Mrs. NICE (1937) who thoroughly investigated the phenology of the Song Sparrow (_Melospiza melodia_ (Wilson)), an American migratory bird species. After having shown that in warmer years the animals arrive relatively early, and in colder years later, she shows (page 49) "That time of year is one of the (248) fundamental factors in Song Sparrow migration is shown by the fact that high temperatures in December, January, and early February (that is, considerable time before the arrival of the animals in the last third of February) ... never bring a migration. Migration is conditioned by both increasing length of daylight and temperature." It may be added that it would appear that the rule established by NICE for the Song Sparrow applies also to the migration of many other bird species.

5. Frequency of Spawning Migrant Animals in Different Years.

For a migratory animal species as the present one, apart from the reproductive results of the previous years, the frequency also depends on the percentage of animals taking part in the migration to the investigation area. In the present case, it is not possible to separate the two moments. A further consideration therefore appears to be rather meaningless. However, the authors searched for connections between the number of annually appearing animals and the fluctuations in the "under-water climate". Their calculations were restricted to the months of April and May, since, for technical reasons, the June purchases supplied no reliable data. In Table 5, the number of squid is compared with the salt-content and temperature differences of the observation area. These latter were calculated in the following manner:

For each month, the difference between the monthly reading minus the monthly mean value of many observation years, was determined from the "Marsdiep" and "Haaks" lightship observations (two stations which lie on the inner and outer limits of the Loligo vulgaris distribution area at Den Helder, see Chapter 6a), and then the mean value of these two differing figures was calculated. (249) Finally, the mean value was calculated from the mean values of April and May.

Table 5. Frequency of Squid in Different Years, Temperature and Salt Content.

	1933	1934	1935	1936	1937
Av. fluctuation in salt cont. Durchschn. Salzgehaltsabweichung IV., V. in ‰	+0.7	+0.6	—0.3	0.0	—2.2.
Av. temp. fluctuation Durchschn. Temperaturabweichung IV., V. in °C.	+0.6	—0.1	+0.1	+0.3	+0.5
Zahl der Kalmare IV., V. Number of squid	2734	877	897	2162	1592

It may be seen from the Table that out of the five observation years, the warmer ones had the larger numbers, while no relationship to the salt content was found. Since it may be expected that a southern species requires a relatively high temperature, the explanation that in warm years a larger number of squid migrate as far as this latitude than in cold years, appears increasingly likely. This therefore is the reason for the large catches.

6. Dispersal of Loligo vulgaris at Den Helder

(a) Selection of areas in dependence on environmental factors

In the case of each specimen delivered to the Zoological Station, the fishermen reported both the fishing site and the number of their boat. Since the purchase price of the squid was the same for all fishing sites, the fishermen had no particular reason to cheat with respect to their reports. Nevertheless, the reports were occasionally checked by making additional inquiries; it turned out that the fishing sites, in general, were reported properly.

The area fished by Den Helderian boats is divided into several parts. First, there are the coastal fishing areas, which are identified in Figure 14 by Nos. 1 to 7. All these grounds are influenced more or less by both freshwater and the nearness of the land. Fishing there is carried out with the aid of trawl nets; in Area No. 7 (on the mud flats), fishing is done also with the aid of standing herring nets. The territory of the deep-sea fishermen, in part, overlaps these areas. The deep-sea fishing grounds encompass, in addition to the Haaks light ship and the Diepe Gat (No. 1 in Figure 14), a relatively long stretch of the southern North Sea extending to the Borkum Reef, Klaver Bank, Markhams Hole, and the Breeveertien abreast of Egmond. In all these areas, fishing intensity is lower than in the coastal waters. Fishing in the deep sea is done largely with the aid of trawl nets.

In our subsequent discussions, we will be dealing almost exclusively with the coastal zone, since Loligo vulgaris is strongly bound to that zone during 250 the summer half-year. From that zone, the Zoological Station received during the years 1933 to 1940 more than 12,000 squid, compared to only 180 (approximately 1.5 per cent) from the high sea, i.e. from grounds more seaward than Area No. 1. This disproportion cannot be explained on the basis of the afore-

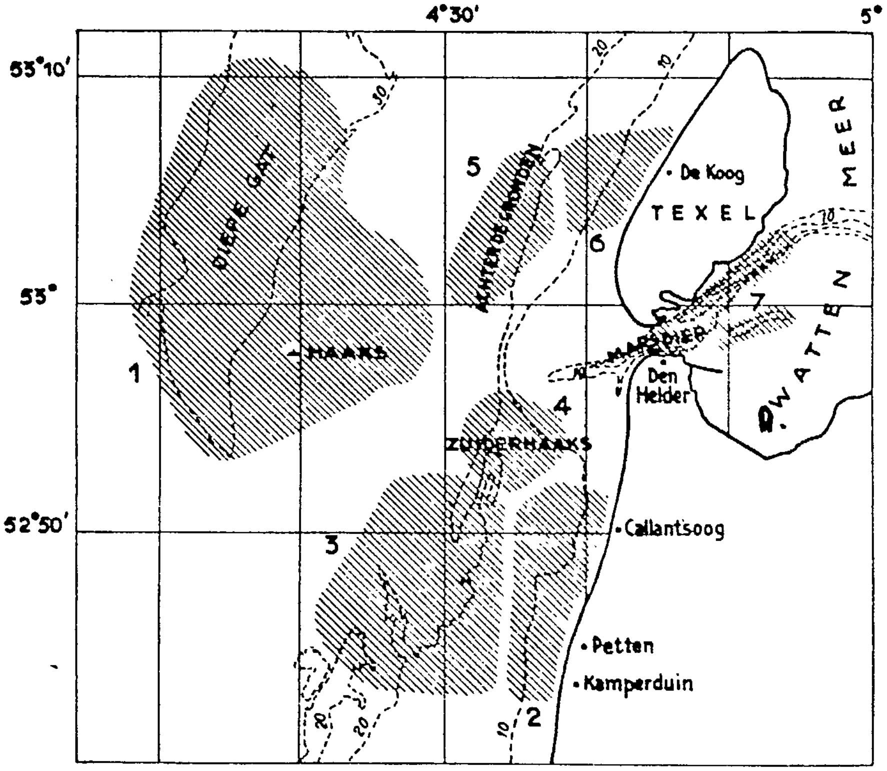


Figure 14 - Map of the coastal area near Den Helder showing the different areas mentioned in the text. Depth in m. Key: A, Mud flats (exposed at low tide).

mentioned lesser intensity of deep-sea fishery, but can be due only to the preference shown by the squid for the coastal zone.

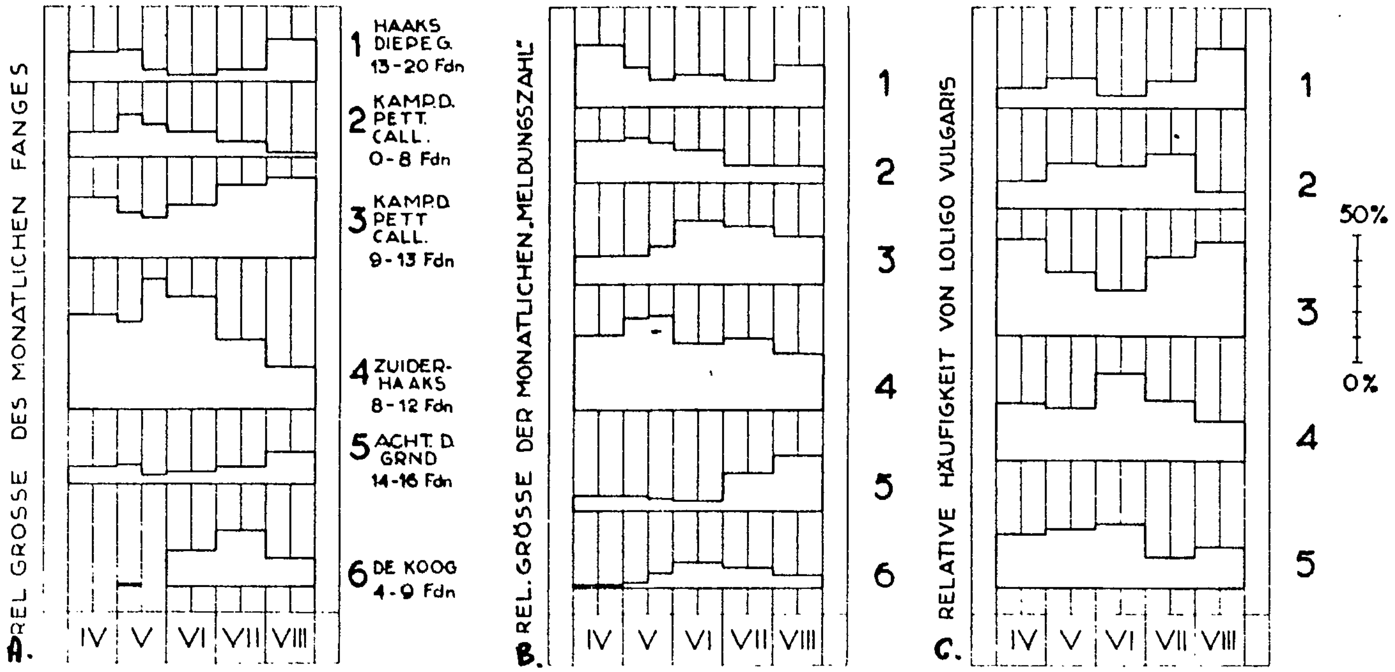
For the purpose of comparison, we are able to make use of the catch numbers of another species, viz. Acanthias vulgaris RISSO [piked dogfish or spur dog]. This scyliorhinid is also purchased on a regular basis by the Zoological Station. During the period between 1 June and 31 December 1938, we received 110 specimens from the coastal zone (Areas No. 1 to No. 7), and 1313 specimens from the outlying fishing grounds, i.e. the catch ratio of this fish was almost the reverse of the one found in the case of Loligo vulgaris.

It is of further interest that even the Loligo vulgaris specimens caught 251 outside of the coastal zone nevertheless were taken not far from land. Only a few winter catches represented exceptions: 24 November 1939, two specimens, Tea Kettle Hole, 20 fathoms; three specimens, 20 miles NNW of Haaks light ship, 15 to 16 fathoms; 18 December 1939, eight specimens, Tea Kettle Hole, 20 fathoms. We will return to these catches further below.

The view that this particular species is rare in the North Sea (Tesch, 1908; Grimpe, 1925) probably can be attributed to this avoidance of the deep sea. Research ships rarely work close to the coast and, for that reason, the marine biologists, who examine the material landed by these ships, never see the squid.

The factors causing this binding to the costal sea will be examined further below. First, we will give more detailed consideration to the occurrence of this species within the coastal waters, and limit ourselves, for the time being, to the summer half-year.

In the first instance, we will ask ourselves where the main mass of the squid may be found during each month. For that purpose, we have calculated, for each summer month, the number of specimens caught per area, and expressed these catches in percent of the monthly total catch. These percentage values are plotted in Figure 15a. However, these particular numerical values would provide a correct impression of the occurrence of the squid only of fishing activities were carried out at the same sites during the entire year. That, however, is not the case, and we must, for that reason, give consideration also to the variations in the fishery intensities. Unfortunately, detailed statistical data are missing, but the records of the Zoological Station do provide some evidence for resolving that question, because the fishermen



a *b* *c*

Figure 15 - (a) Catch numbers; (b) Intensity of fishing activity; (c) Frequency of squid calculated on the basis of (a) and (b). Average values for 1937 to 1940. Cf. in the text for details. Key: Fdn., Fathoms; A, Relative sizes of the monthly catches; B, Relative size of the monthly "Report number;" C, Relative frequency of *Loligo vulgaris*.

also delivered other animal species, apart from the squid. The sites at which these species were caught were also regularly recorded. In order to determine the distribution of fishery activities in both time and space on the basis of these data, we have proceeded as follows: For each fishing site, we calculated the monthly number of reports, and expressed that number in percent of the monthly total number. Figure 15b shows the result of that calculation and, thus, represents the relative intensity of fishery activities at the different fishing sites for each individual summer month. It is evident that that intensity varied considerably.

In order to determine next the relative frequency of the squid, we must calculate the quotient $\frac{\text{Number of squid caught}}{\text{Intensity of fishery (report number)}}$ for each summer month and for each fishing site, and express the value found in percent of the monthly total of these quotients. These percentage values are 253 presented in Figure 15c. They demonstrate that a certain area in the course of the year is at one time more preferred, and at another time less preferred by the squid, but these values do not provide information regarding both the absolute frequency of the squid and squid density. In these calculations, Area No. 6 had to be excluded, since very little fishing was done there at certain times. Area No. 7 also had to be excluded, since fishery is carried out there in a manner entirely different from the fishing done in Areas No. 1 to No. 6.

Our method does not permit us to draw detailed conclusions. Nevertheless, the following aspects are clear. Area No. 3 exhibited maxima at the start of the season and at the end of the season, and a distinct minimum during June. Area No. 1 exhibited a maximum toward the end of the season, but apparently no maximum or no pronounced maximum at the start of the season; it is, thus, uncertain whether Area No. 1, like Area No. 3, exhibits a minimum during June. Area No. 4 exhibited a distinct maximum during June, and a minimum toward the end of the season. Area No. 2 exhibited lower values at the start and, in particular, toward the end of the season than during the middle of the period of squid occurrence. These findings mean: The squid are relatively frequent in Area No. 3 at the start of the season, and least frequent there during June. Since the opposite is true for the neighboring Area No. 2, it appears that a shift of the squid takes place from Area No. 3 to Area No. 2. However, Area No. 4 also exhibits a distinct relative increase and this, in particular, during June. The shift, thus, takes place from Area No. 3 to Area No.2 as well as Area No. 4. The squid then move more or less in the direction of the coast and, at the same time, toward the Marsdiep. The relative decrease in Areas No. 2 and No. 4, and the relative increase in Areas No. 1 and No. 3 during the months of July and August reveals exactly the opposite trend: A shift away from the coast, but also away from the Marsdiep in the seaward direction. Speaking in global terms, water depth increases in regular fashion with increasing distance from the coast (the reader is asked to pay attention, in particular, to the subsurface contous lines shown in Figure 14, and to disregard to some extent the depth data shown in Figure 15a). Since the squid were caught with trawl nets directly at the bottom, we are able to state that they, on average, stay during June in shallower water than at the start of the season and, in particular, at the end of the season. The depth, however, is not the most significant factor in this connection; on the contrary, because the squid pass the months of June in large numbers in Area No. 4, where water depth, in part, is just as great as in Area No. 3. Further below, it will become evident that the squid are guided in the first instance by another factor, viz. the temperature of the water. 254

The squid, thus, apparently perform movements within their summer range that are similar to those known, for example, in the case of plaice. However, while the plaice visits the warmest sites already during May, the squid does that only in June. In connection with these movements, it is then probable that the plaice is guided chiefly by water depth, while the Squid is guided by water temperature.

The few winter squid received by us, on average, came from significantly deeper waters than did the summer squid. We have already mentioned further above that several of these winter squid were caught farther away from the coast than any summer squid (cf. page 251). The distribution of the other winter catches also indicates that the squid live during the winter farther away from the coast and at greater depth than during the summer. Table 6 gives the corresponding data. (These winter squid were specimens four to six months old; cf. page 218.)

Let us next consider the results for the "average year." We will now subject the distribution during the individual years to more detailed investigation. In that connection, we are unable to calculate (as we did on page 251) the frequency of squid, because the intensity of fishery cannot be represented separately for each month in numerical form. For that reason, we content ourselves with the catch numbers. In the Areas No. 1 to No. 7 regularly fished, these numbers exhibited considerable variations. These variations were most pronounced on the mud flats (No. 7), where at one time large numbers of squid were caught, and at another one, almost none at all[1]. It appears that that Area meets the requirements of the squid only under certain conditions. What these conditions actually are could be determined to some degree.

For the purpose of determining these conditions, we investigated first the relationship existing between squid catches, on the one hand, and temper- 255
ature and salinity, on the other one. Figure 16 illustrates the catches made in the mud-flats area (No. 7, Figure 14), expressed in percent of the monthly total catch, as function of the monthly average values of salinity and temperature in the Marsdiep (western boundary of Area No. 7; cf. Figure 14).

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[1] Of course, we have given consideration only to those months, during which fishing was actually carried out on the mud flats, i.e. April, May, and June (with the exception of June of 1938 and June of 1939, when no observations were carried out).

Table 6 - Habitat selection near Den Helder during summer and during winter. Key: 1, Areas far from the coast; 2, Areas close to the coast; 3, Summer animals (April to September); 4, Winter animals (October to March).

	1 küstenferne Gebiete	2. kustennahe Gebiete						
		No. 1	3	5	No. 2	4	6	7
3. Sommertiere (Apr.–Sept.)	180 = 1½%	824	2085	650	1062	4167	661	1677
4. Wintertiere (Okt.–März)	14 = 25%	27	12	—	—	—	—	2

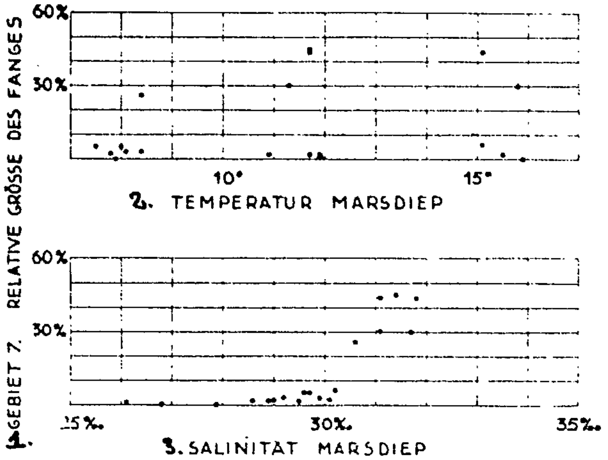


Figure 16 - Relationships between temperature, salinity, and relative catch size on the mud-flats area. Key: 1, Area No. 7: Relative catch size; 2, Temperature . . .; 3, Salinity . . .

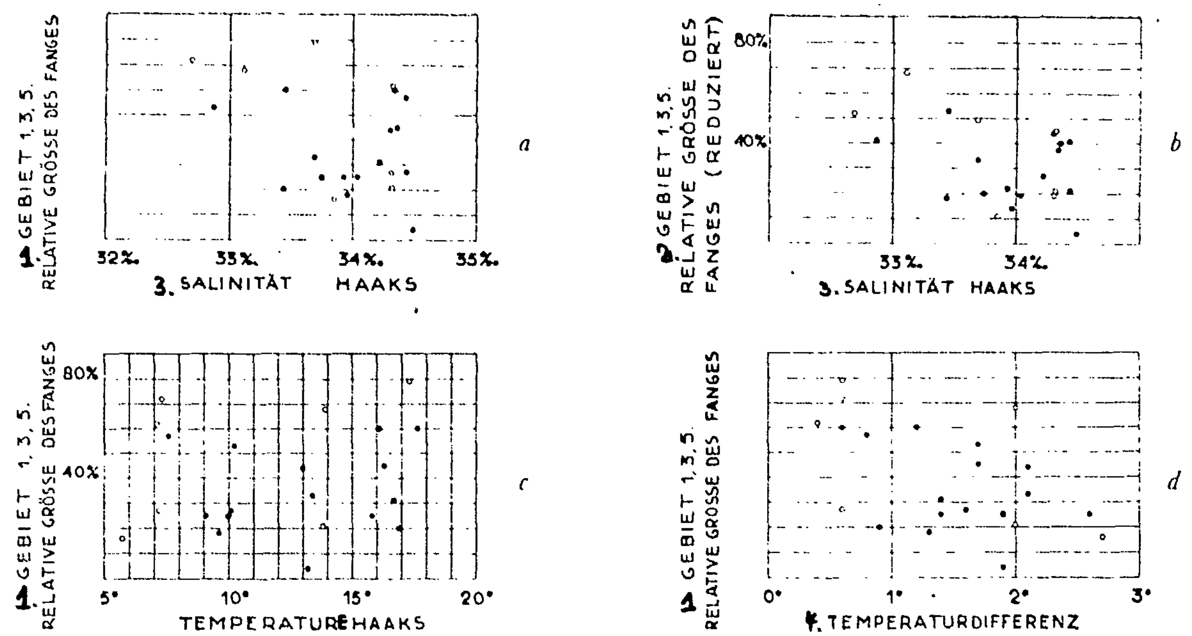
These values have been calculated on the basis of daily surface observations made on the Marsdiep dike (We are indebted to Mr. Ir. F. Liebert, Rijksinstitut voor Visscherijonderzoek, Den Helder, for making these data available to us).

The influence exerted by salinity is very pronounced. Only when the salinity at the dike exceeded about 3.03 per cent did the squid move across the outer borders of the mud-flats sea. Since the water tests were carried out at the seaward entrance to Area No. 7, we are permitted to conclude that a salinity level of 3.03 per cent actually represents approximately the lower threshold for Loligo. It appears that the temperature does not guide the squid at all; at least, the plots representing observations do not indicate the existence of a correlation. That statement, however, is valid only for the temperature range of our observations, and cannot be generalized without reservation.

Scheveningian fishermen told P. Creutzberg in the year 1941 that Loligo vulgaris was caught abreast Scheveningen, in general, more frequently outside of the three-mile zone than near the coast. That report initially surprised us, but can be readily understood on the basis of the aspects just outlined, since the 3.0%-salinity line as well as several of the other isohalines run closer to the shore near Den Helder than near Scheveningen (Atlas, Cons. Int., 1933).

On the basis of this particular correlation between occurrence of squid 256 and salinity, we are, however, not able to draw conclusions regarding the "mechanism" of this interrelationship. It appears to us to be most probable that the squid orient themselves directly toward the salt content (or toward one of its accompanying chemical pgenomena), in that they turn away in phobic fashion from sites exhibiting salinities too low for their requirements. However, we may also imagine that the relationship is an indirect one, and that the squid, for example, are following some prey animal, which, in turn, orients itself toward salinity. Appropriate observations are missing to resolve this particular question; however, we have no evidence suggesting that the latter, more complex mechanism is valid.

The variations in the location of the internal boundary of the area visited by squid, thus, are determined near Den Helder by salinity, i.e. the salt content of the water. There arises the question whether the location of



Figures 17 a - 17d - Relationships between catch size in the deeper parts of the coastal sea (expressed in per cent of the catches made in Areas No. 1 to No. 6) and the "underwater climate." o: Observations made during months where the total catch amounted to 70 to 200 squid. •: Observations made during months where that catch amounted to more than 200 squid. In Figure 17b, we have applied a reduction, which is explained in the text; in Figure 17c, "temperature difference" means $t_{Marsdiep} - t_{Haaks}$. Key: 1, Areas No. 1, No. 3, and No. 5: Relative size of the catch; 2, Areas No. 1, No. 3, and No. 5: Relative size of the catch (reduced); 3, Salinity; 4, Temperature difference.

the outer boundary also exhibits relations to variations in the "underwater climate." For that reason, we have investigated—in the manner outlined further above—the correlation between environmental factors and the occurrence of squid in the areas located farther out in the sea. In that connection, we have compared, for each month of observation, the average salinity and average temperature values recorded at the Haaks ligh ship with the relative sizes of the catch in Areas No. 1, No. 3, and No. 5 (expressed as percent of the total catch in Areas No. 1 to No. 6) (cf. Figure 17).

Salinity exerts a certain influence also in this case (Figure 17a). The squid were most frequent in the more distant areas when salinity at Haaks light ship was relatively low, *viz.* < 3.4 per cent. However, the correlation to salinity was less marked than on the mud flats.

We have seen further above that the squid carry out seasonal migrations within the coastal region. The suggestion arose to determine whether the dependence on salinity was still in evidence or, respectively, more in evidence when the influence of these seasonal migrations is eliminated.

According to the data presented in Figure 15c, the relative frequency of the squid in Areas No. 1, No. 3, and No. 5 amounted to 67% in April, 61% in May, 48% in June, 54% in July, and 77% in August. In order to resolve that particular question, we have multiplied the monthly numerical values (catch numbers in percent of the total catch in Areas No. 1 to No. 6) with $\frac{48}{67}$ for April, $\frac{48}{61}$ for May, $\frac{48}{48}$ for June, $\frac{48}{54}$ for July, and $\frac{48}{77}$ for August, and, 258 in that way, obtained—even if only approximate—"reduction to the June values" in arbitray units. The numerical values obtained by means of this calculation are presented in Figure 17b as function of the salinity recorded at Haaks light ship. The correlation is again in evidence.

This particular correlation may be interpreted in two ways. We may assume that the squid are repelled by water exhibiting salinities > 3.4 per cent. However, it is also possible that the influence of salt content in the distant areas is only an indirect one. For example, we can imagine that the squid, directed by some other factor, attempt to approach the coast until the salinity threshold of about 3.0 per cent is reached. During "less saline" months, when that threshold is located far out in the sea, the squid would be found at a greater distance from the coast than during months associated with higher salinities. The location of the outer boundary of their range would then be determined by the location of their lower salinity threshold, and—in our case—be associated with the salt content of the Marsdiep water. Since the salt content at Haaks light ship, on the whole, exhibits the same course as that in the Marsdiep, we are permitted also on the basis of the latter interpretation to expect greater catches in Areas No. 1, No. 3, and No. 5 when the salinity is low at Haaks light ship, and vice versa.

However, we have evidence suggesting that the second possibility is not valid. During April and June of 1935, there existed, at the same time, high salinity at Haaks light ship and low salinity in the Marsdiep, with catches being low in Areas No. 1, No. 3, and No. 5 as well as in Area 7.

	Relative size of the catch in Areas No. 1, 3, 5	Salinity at Haaks	Salinity in the Marsdiep	Relative size of the catch in Area No. 7
April 1935	27%	3.441%	2.89%	2%
June 1935	4%	3.449%	3.02%	6%

It then appear that the squid are forced in the Marsdiep in the direction of the open sea, but at Haaks light ship toward the coast. There then remained for them only a narrow intermediate zone, which in Aprilof 1935 yielded 71 per cent of all squid landed, and in June of 1935, 90 per cent of all squid landed.

For that reason, we feel that the influence exerted by salinity is a direct one in the more distant areas, and that the squid avoid water exhibit- salinities < 3.4 per cent. 259

Among the other environmental factors, it appears that the absolute value of the temperature does not affect the squid (Figure 17c). That finding, however, does not yet indicate that the temperature of the water exerts no influence at all in this connection. In fact, it appears that there exist interrelations between the occurrence of squid in Areas No. 1, No. 3, and No. 5 and the temperature gradient in the coastal waters. From February to September, the areas far from the coast are colder than the areas near the coast. It appears that the squid are most frequent in the areas far from the coast during the months, where that difference is small. Figure 17d gives the corresponding monthly values as function of the difference $\underline{t}_{Marsdiep} - \underline{t}_{Haaks}$. The correlation is rather evident.

The difference in temperature between areas far from the coast and areas near the coast is subject to distinct seasonal periodicity. During the summer months of interest to us, this difference is most marked during June, and least marked during April and during August. We have seen already on page 253 (Figure 15c) that the local occurrence of squid also exhibits a seasonal periodicity. Table 7 compares the frequency of squid in the areas far from the coast, the size of the temperature gradient, and the salinity level in monthly average values. It turns out that the seasonal migrations are also caused by the temperature gradient, while the salinity exerts no influence in this connection. That is actually true, because, in reality, we have represented in Table 7 the correlation already demonstrated in Figure 17d in a somewhat different form.

We feel that the connexion to the temperature difference is that the squid show a preference for the warmer areas. In our observations, this preferen- 260
ce had to be more marked with increasing difference in temperature between

Table 7 - Occurrences in the areas far from the coast and environmental factors. Key: 1, Month; 2, Relative frequency in the areas far from the coast No. 1, No. 3, and No. 5 (1933 to 1937), after Figure 15c; 3, Difference $t_{Marsdiep} - t_{Haaks}$ (1933 - 1937); 4, Salinity at Haaks (1933 - 1937).

	1. Monat				
	IV. Apr.	V. (May	VI. June	VII. July	VIII. Aug.
2. Relative Haufigkeit in den kustenfernen Gebieten No. 1, 3, 5 (1933-1937). Nach Abb. 15c.	67%	61%	48%	54%	77%
3. Differenz $t_{Marsdiep} - t_{Haaks}$ (1933-'37)	1.0°	1.8°	2.0°	1.3°	0.5°
4. Salinitat Haaks (1933-1937)	33.92	33.81	33.98	33.88	34.06

the coastal water and the Haaks water. It is furthermore evident that that preference binds the squid during the summer to the coastal sea, because it is warmer there than in the high sea, and drives them away from the coast toward the winter (cf. page 254).

A final factor playing a role in the binding of squid to the coastal sea is the depth of the water. We have already seen further above that the squid —at least, during the summer—dwell only at shallow sites. Their occurrence, thus, depends also on the depth of the water. At least in part, that connexion is an indirect one, since both salinity and temperature gradient, which control the occurrence of squid, depend, in turn, on water depth. However, the question arises whether the depth of the water is able to exert also a direct influence independent of both the temperature and the salt content. It appears that an influence of that nature plays no role in our observations. A large number of squid was caught in the Diepe Gat, where the water depth is the same as in areas located twice as far away from the coast, in which areas the species occurs only rarely. All these findings do not exclude the possibility that the depth factor may well exert a direct influence in regions, where the depth differences are considerably greater than in the North Sea.

Let us then summarize the findings made with respect to the influences exerted by several environmental factors on the occurrence of squid. The area preferred by the squid is determined near Den Helder, at the shore-side, by the salt content (salinity) of the water, which cannot drop much below approximately 3.03 per cent. At the sea-side, the threshold shows connexions to both the salt content of the water and the temperature gradient in the coastal sea. On the one hand, it appears that the saline line of about 3.4 per cent represents an outer boundary for the squid; on the other one, the squid prefer the coastal waters because of their greater warmth. The water depth, finally, appears at best to play a subordinate role in the binding of the squid to the coastal zone.

It goes without saying that salinity and temperature gradient are not the only environmental factors affecting the occurrence of the squid. In the vicinity of Den Helder, however, their influences are most marked. In regions having a different character, it is well possible that the effects of this factor or that one are more distinctly in evidence. For example, Lo 261 Bianco (1909) has mentioned the nature of the bottom as an influencing factor: Near Naples, this species reportedly prefers a slimy bottom.

It is clear that the description of correlations presented above can be regarded only as a base for further studies of the orientation of Loligo, and does not permit us to draw conclusions regarding the nature of the responses of this species. Since the behavior of marine animals is not accessible to direct observation, more detailed investigations probably will have to be limited to experimental methods and, for that reason, will be difficult to perform.

(b) Occurrence of males and females separately

In their habitat selection the two sexes exhibited a small difference. Relatively fewer males were caught at the sites far away from the coast than in areas close to the coast. Table 8 provides detailed numerical values.

Table 8 - Sex ratios in different areas. Key: 1, Males per 100 females; 2, Area.

2.	♂♂	♀♀	1. Auf 100 ♀♀ fallen:
Gebietsteil No. 1	448	376	119 ♂♂
No. 6	368	293	126 „
No. 5	355	295	131 „
No. 4	2361	1806	131 „
No. 3	1218	867	140 „
No. 2	642	420	153 „
No. 7	1045	632	165 „

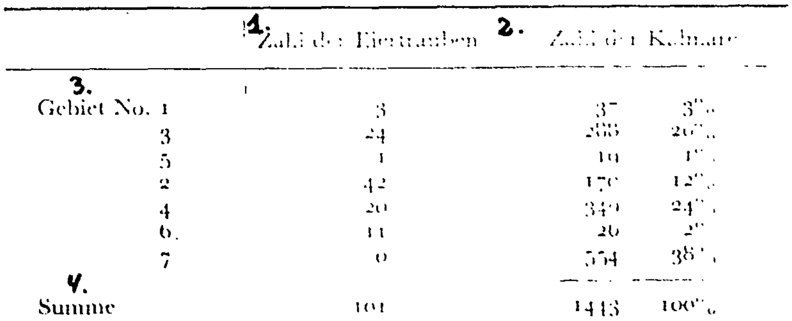
If we inquire once again after the controlling environemtal factors, it appears that a direct influence of water depth can be excluded. Otherwise, the values obtained in Area No. 1 and Area No. 7 would not be that different. Apparently, one of the water properties plays a role in this connection. We could think of the salt content, but also of the temperature. In the former case, the males would prefer a somewhat lower salinity than the females; in the latter one, a somewhat higher temperature. When giving consideration to the differences between Areas No. 2 and No. 3, on the one hand, and Areas No. 5 and No. 6, on the other one, we must remember that the less saline and (during the summer) warmer mud-flats water flows southward when flowing out from the Marsdiep into the North Sea (low tide). For that reason, the sou- 262
thern sites are more influenced by the mud flats than the northern ones, and this, in particular, because the channel located north of the Island of Texel, which channel also drains southward (the Eyerlandse Gat), plays only a

subordinate role in the water balance of the mud flats. The data presently available permit no further analysis of these particular interrelationships.

(c) Occurrence of the eggs

Egg strings were purchased by the Zoological Station only occasionally (above all, during the year 1934); for that reason, we have only relatively few data available on egg finds. Those available pertain only to the coastal region; Table 9 provides an overview of their distribution in the year 1934. For the purpose of comparison, we have listed also the numbers of squid caught.

Table 9 - Occurrences of egg strings and squid near Den Helder during the summer of 1934. Key: 1, Number of egg strings; 2, Number of squid; 3, Area; 4, Totals.



	1. Zahl der Eierfäden	2. Zahl der Kalmare	
3. Gebiet No. 1	3	37	3%
3	24	288	20%
5	1	10	1%
2	42	170	12%
4	20	340	24%
6.	11	26	2%
7	0	554	38%
4. Summe	101	1413	100%

On the basis of this Table, we might conclude that Areas No. 2 and No. 6 are particularly preferred as spawning sites, and that Area No. 7 is avoided for spawning. However, some caution is indicated, since the number of speciemns is rather small. For that reason we do not venture to employ these data for further analysis.

7. Geographical course of the migrations

In this Section, we will make an attempt to reconstruct the course of the migration of *Loligo vulgaris* on the basis of both the data available in literature and our own observations.

The range of dispersal of *Loligo vulgaris* encompasses the littoral zone
of the Mediterranean Sea and of the eastern Atlantic between 21° and 59°N[1]. 263
In the Atlantic region, our species has been found along the coasts of northwestern Africa (Robson, 1926; Boone, 1933; Adam, 1937b; 1941), Portugal (Nobre, 1932), France (Locard, 1886; Dautzenberg and Fischer, 1925; Cuénot, 1927), Great Britain (Plymouth Marine Fauna, 1931; Storrow, 1932; Moore, 1937), Belgium (Adam, 1933), and The Netherlands (Tesch, 1908; the present paper); in the Deutsche Bucht (German Bay), in the Skagerrak, and in the Kattegat (Grimpe, 1925); in the western Baltic Sea (Grimpe, 1925; Kaeckel, 1937); and finally, perhaps, along the coast of Norway (Grieg, 1933). In the Mediterranean Sea, *Loligo vulgaris* has been found, inter alia, along the coasts of France (Vérany, 1853; Locard, 1886), of western Italy (Jatta, 1896; Lo Bianco, 1909), and of Tunesia (Gruvel, 1926).

With regard to the migrations, it appears that the squid does not leave the Mediterranean region during the winter. Vérany (1853) mentioned that this species "habite sédantaire les profondeurs moyens" in the vicinity of Nice. In the commercial market records of Tunesia, "calmars" are reported during the entire year; cf. Table 10; on the basis of Gruvel's (1926) communication we know that we are dealing in that case with our species. In that respect

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[1] Adam (1937a) has mentioned two specimens from the West Indies, but doubted the correctness of that find report.

Table 10 - Landings for the market in Tunesia. Totals for the years 1932 to 1936, after Bulletin Stat. Océan. de Salammbô, Nos. 31, 33, 35, 36, and 37. Key: 1, Month; 2, kg Squid.

1. Monat	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.
2. kg Kalmare	5327	4626	4849	9148	13137	8792	4466	3973	5181	7916	6391	4170

the squid of the Mediterranean region, thus, differ greatly from those of the North Sea, which we know to be marked migrants.

We will next present a detailed description of the migrations in the North-Sea region, i.e. the only region for which data are available in moderately adequate quantity. Grimpe (1925) has already reviewed the data available on the occurrence of squid in that part of the sea; we will supplement his review with our observations.

As we have already seen further above, Loligo vulgaris appears every year 264
in large masses along the Dutch coast, and reaches the vicinity of Den Helder during the second half of April. Their numbers increase up to the second half of May, in order to decrease again rapidly. The last specimens usually disappear between the end of July and early September. Their ages amount to approximately one and approximately two years. In addition, we occasionally find small quantities of squid hatched that year near Den Helder during the late fall. (During the fall, movements of the juveniles, by the way, can be determined only with difficulty, since they, with respect to the mesh size of the usual trawl nets, are still very small.)

In order to determine the direction of migration along the Dutch coast, we made purchases of squid during the spring of 1937 at the same time in Den Helder and in Breskens (Province of Zeeland). At the later place, these purchases were kindly carried out by Mr. C.L. Ter Meulen.

Table 11 - Spring migration along the Dutch coast. Numbers of squid purchased in the year 1937 in Breskens (Province of Zeeland) and in Den Helder. Note: The total period of observation has been divided into periods of 5 days in a two-fold, overlapping fashion, in order to make certain that the results are not tainted by the chance selection of a subdistribution.

	April					May		
Period	6.–10.	11.–15.	16.–20.	21.–25.	26.–30.	1.–5.	6.–10.	11.–15.
Breskens	0	28	19	0	7	5	22	55
Den Helder	0	1	11	46	27	124	75	215
Period	4.–8.	9.–13.	14.–18.	19.–23.	24.–28.	29.–3.	4.–8.	9.–13.
Breskens	0	1	28	18	3	7	5	74
Den Helder	0	0	1	40	17	63	163	101

The squid marketed there came, on the one hand, from the Schelde estuary and, on the other one, from the North Sea off the Islands of Schouwen and Goeree. Table 11 gives the numbers of squid purchased. The squid arrived a little later at Den Helder than at Breskens; the difference probably amounts to five to ten days[1].

Are we permitted to conclude on the basis of that finding that the squid migrate from the south to the north? Strictly speaking, we are not, since we could imagine also, for example, that the squid migrate straight toward the coast from the deep water to the shallow water, and undertake that rise in the north somewhat later than in the south. In that case, however, squid would have to be reported from the deep water prior to their appearance along

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[1] Near Breskens, 27 specimens were caught on 14 and 15 April; near Den Helder, ten specimens on 19 and 20 April, and a little later, considerable quantities. That would give us a difference of about five days. However, near Den Helder, the squid are later in the season far more frequent than near Breskens. If 27 specimens were then caught on 14 and 15 April near Breskens, the squid probably are there relatively more frequent than on 20 April near Den Helder. The difference, thus, probably amounts to more than five days, but it cannot be determined how much more than that. To be on the safe side, we assume that the difference amounts to five to ten days.

the coast. Since the latter is not the case, we assume that the squid migrate northward parallel to the Dutch coast. That conclusion is in agreement with Grimpe's (1925) suggestion to the effect that Loligo vulgaris reaches the southern North Sea from the south.

On the basis of the observations outlined above, we are permitted to conclude that the squid—even if the difference in the dates of appearance cannot be determined exactly—pass by Den Helder at a speed much greater than the velocity of the water, the current of which at that site also exhibits a northeastern direction. If we assume that the distance between Zeeland and Den Helder amounts to 100 nautical miles, the water requires at least 18 to 25 days to cover that distance (cf. Verwey, 1943, pages 440, and 445 and 446), while Loligo covers that distance probably in about five to ten days. However, the northward water movement is the result of one northward current and one southward current. According to unpublished measurements made by the Rijkswaterstaat, the northward dislocation of the water amounts, at the surface near Ijmuiden (four km away from the coast), on average to 10.7 km per tide or 21.4 km per day. The southward dislocation of the water, 0.15 m above the bottom of the sea, amounts there to 3.2 km per tide or 6.4 km per day. The difference between the two movements amounts to 15 km or 8.3 nautical miles per day. If the squid stay in the surface water during high tide, and close to the bottom during low tide, they would cover, on average, 8.3 nautical miles per day. In that case, they would cover the distance of 100 nautical miles—if the current velocity were the same over the entire distance—in about twelve days. If the squid then needed six, instead of twelve, days to cover the distance between Zeeland and Den Helder, they travelled about eight nautical miles per day by means of active propulsion. In any case, we cannot assume that they—as is the case in numerous travelling planktonic organisms in the water and many insects in the air (Fraenkel, 1932)—are transported passively. 265

In apparent contradiction to our assumption of a northern migration through the Strait of Dover is the finding showing that this species is encountered only in isolated instances along the Belgian coast (Adam, 1933; 1942 quoted in the literature[1]), while it is, without any doubt, common along the Dutch 266
coast near Breskens, Scheveningen (cf. page 255), and Den Helder. However, as Mr. Adam has informed us by letter, it is very well possible that this species has been overlooked along the Belgian coast, as was the case also along the Dutch coast until 1931. In any case, we are inclined to assume that the squid reach the North Sea by way of its southern entrance. This species has been found along the Channel coast of France (Locard, 1886), a finding that has subsequently been confirmed by Gallien (1934, quoted in the literature[2]) for Wiméreux (Dept. Pas de Calais). Additional data on numbers and phenology are not available for the western coast of France.

Relatively few specimens are known from the Deutsche Bucht (German Bay). Grimpe listed those known in 1925; by adding the ones listed by Hertling (1934, quoted in the literature), we arrive at the list presented as Table 12. The majority of these squid was mature.

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[1] Mr Adam has kindly informed us that the following specimens have been received by the Bruxelles Museum after the publication of his paper (1933): 1 July 1925, Ostende, eggs; 6 May 1938, Ostende, eggs; 18 May 1927, Ostende, one female; 11 June 1929, Ostende, one female; 4 September 1934, Ostende, three juveniles (cf. page 217 of the present paper). As along the Dutch coast, this species spawns also in the Belgian waters, and juveniles are caught there during the fall.

[2] The numerous personal communications (received by mail) mentioned in the following part of our paper were received in response to an inquiry made by the Zoological Station in 1934. In that connection we mailed questionnaires to institutes of marine biology in western Europe regarding the occurrences of various cephalopod species within the regions covered by these institutes. We are indebted to the directors of these stations for their kind cooperation in replying to our inquiry.

Table 12 - Dates of squid finds in the Deutsche Bucht (German Bay) (53°56' - 55°36' north, 5°17' - 7°51' east). After Grimpe (1925) and Hertling (1934, quoted in literature).

May: 25 May 1920; 28 May 1920; 28 May 1920; three speciemens "probably May 1933."

June: 8 June 1904.

July: 1 July 1908; 11 July 1903.

August: None.

September: None.

October: 2 October 1907.

November: 27 November 1933; 28 November 1932.

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267 On page 251, we have already seen that the literature contains only very few observations from the Dutch coast, although this species, without doubt, is common there. For that reason, we believe that it is well possible that Loligo vulgaris occurs also in the German Bay more frequently than is supposed, but is overlooked due to inadequate observations in the coastal waters. The majority of the specimens mentioned by Grimpe actually has been caught at a rather large distance from the coast, i.e. in a region, where, according to the findings obtained at Den Helder, only a small fraction of the squid present on a given range may be found. On the other hand, however, there exists the possibility that this species inhabits, in the German Bay, a wider zone than near Den Helder, since the 3.4%-salinity line is located in the former region at a far greater distance away from the coast than in the latter one.

Only a few specimens are known from the western coast of Denmark, and those are mostly not dated. We are a little better informed about the Skagerrak and the Kattegat. Loennberg (1891) has described several specimens, which had all been caught along the Swedish coast between the Øre Sund and the Norwegian border. According to Prof. Jaegerskiold's (1937, quoted in the literature) communication and Prof. Bock's (1942, quoted in the literature) communication, neither the Goeteburg Museum nor the Stockholm State Museum of Natural History has received new specimens since the publication of Loennberg's paper. As far as they are known, the finding dates are: 8 July 1860; 3 August 1869; 18 August 1865; 19 August 1872; and 5 September 1872 (Jaegerskioeld). Loennberg, furthermore, has mentioned a communication offered by Hansen, according to which this species has occasionally been caught during the fall near Streomstad. More recently, Dr. Blegvad (1934, quoted in the literature) has stated: "My working district is the Kattegat and the Skagerrak. Loligo vulgaris is not common there."

Only a very few observations are known from the Baltic Sea: 24 September 1872, one male (approx. 30 cm without head tentacles, i.e. probably two years old), Travemuende (Lenz, 1875); fall of 1930, in the Bay of Kiel, numerous cuttlefish measuring four to five cm in length, of which two (caught on 26 November 1930) were identified as Loligo vulgaris (Jaeckel, 1937). (These specimens probably had hatched during that year; cf. page 218 of the present paper.)

It is not certain that Loligo vulgaris reaches the coast of Norway. Grieg (1933) mentioned a doubtful specimen, which he, however, then did not include in his final list. Prof. Brinkmann (1934, quoted in the literature) and Dr. Broch (1934, quoted in the literature) have confirmed that this species has also not been encountered since then near Bergen and Droebak.

Finally, only a few reports are available from the east coast of Great Britain. Older reports cannot be made use of, since they frequently refer to 268 Jeffreys (1869), who did not yet distinguish between Loligo vulgaris and

Loligo forbesi [the northern European squid], describing all squid as Loligo vulgaris LAM. For that reason, we are forced to omit from consideration, for example, McIntosh' (1875) observations in the fauna of St. Andrews (page 89: "Loligo vulgaris LAM. The spawn of this species is frequent"). As sole positive report, we find Storrow's (1932) communication to the effect that Loligo vulgaris was landed regularly during August of 1932 by fishermen from North Shields (Tyne estuary). In addition, we present several negative reports: Stevenson (1935) does not mention this species in The Cephalopods of the Yorkshire Coast; neither did Russell (1922) find it in the waters along the coast of Scotland (Goldseeker material), and Hoyle (1902) was unable to find any specimen in older English museum material.

We then realize that the observations available to us for reconstructing the migrations of Loligo vulgaris in the North Sea region are rather poor. However, one thing is clear: Loligo vulgaris appears later in the season in the more northern areas. We have seen further above that the squid arrive earlier in the Schelde estuary than near Den Helder. Table 13 demonstrates that a similar difference exists between Den Helder and the German Bay as well as between the German Bay and the Scandinavian waters.

The later date of appearance of the Swedish squid was known also to Grimpe (1925). That author was inclined to assume that the Swedish squid belonged to a different subspecies than those of the southern North Sea, and, in 269
connection with that view, interpreted their late arrival in the sense that they reached the North Sea by way of its northern entrance. In fact, Grimpe stated, "above all, it appears impossible that L. vulgaris migrates to the Kattegat diagonally across the North Sea or along its southern and eastern Coasts." Further below we will demonstrate that the racial [or subspecific]

Table 13 - Occurrences of Loligo vulgaris during the course of the year. Key: 1, Month (January to December); 2, Den Helder (average catch numbers per month, 1933 to 1940); 3, German Bay (all catches, cf. Table 12); 4, . . . (all catches).

1. Monat	2. Den Helder (mittlere Fangzahlen pro Monat 1933–'40)	3. Deutsche Bucht (sämtliche Fänge siehe Tab. 12)	4. Skagerrak, Kattegat (sämtliche Fänge)
I.	–	–	–
II.	–	–	–
III.	1	–	–
IV.	181	–	–
V.	1294	3 (+ 3?)	–
VI.	506	1	–
VII.	325	2	1
VIII.	122	–	3
IX.	3	–	2
X.	2	1	-
XI.	1	2	–
XII.	3	-	-

differences assumed by Grimpe to exist between northern and southern squid do, in fact, not exist. If we take into consideration furthermore the absence of Loligo catches in the waters off Norway and off Scotland, we arrive more readily at the conclusion that this species actually reaches the Kattegat and its vicinity along the southern and south-eastern North-Sea coasts. In subsequent contributions it will be demonstrated that there exist also several species among the fishes, which reach the Danish waters chiefly or exclusively by way of the southern North Sea.

How do the squid leave again in the fall? Loligo vulgaris occurs in our waters up to the end of August, and in the Swedish waters up to September. On the basis of these findings, one might be tempted to assume that the Dutch squid migrate during the late summer toward the north. That, however, is hardly probable, since this species occurs in the northern waters far more rarely than in our [Dutch] waters. For that reason, we assume that the squid of the southern North Sea migrate in the fall back through the Strait of Dover.

It is completely uncertain which route the Swedish squid take during the fall: On the one hand, the phenological data available make a southern retreat in the fall somewhat improbable; on the other one, this species has not been found at all in the waters off Norway and off Scotland.

Before we discuss the occurrence of squid on the remaining range of dispersal, we must give more detailed consideration to the subspecies question.

Steenstrup (1856) was the first author to report that specimens caught
in Danish waters have a shorter head than those from the Mediterranean. He
named them *Loligo breviceps*. Grimpe (1925) speaks of *Loligo vulgaris brevi-
ceps* and asserts that the squid of the southern North Sea resemble the Medi-
terranean form. He named the latter *L. vulgaris typica*. Reportedly, the
typica form was bound to the spring, and the *breviceps* form, to the late summer
and fall. Elsewhere in the same paper, Grimpe mentioned, however, the possi-
bility that the differences between the two subspecies under consideration
could be explained "simply as differences in growth or age, respectively"
(page 33). Despite that reservation, Grimpe states on page 34 in connection 270
with his specimen No. 2: "The measurements demonstrate in unequivocal fashion
that we are dealing in the case of this male with a typical specimen of *L.
vulgaris*;" in that of his specimen No. 3: "This male, without doubt, must be
assigned to the 'subspecies' *breviceps*;" in that of his specimen No. 5: "....
belongs....clearly to *L. typica*;" and in that of his specimens No. 6 and No. 7:
"also belong, without doubt, to the typical form."

As criterion in this differentiation, Grimpe employed the ratios $\frac{\text{Ventral mantle length}}{\text{Head length}}$ and $\frac{\text{Ventral mantle length}}{\text{Tentacle length}}$. The latter numerical value appears unreliable to the extent that the non-chitinous tentacles may shrink in non-uniform fashion during fixation. For that reason, we have given

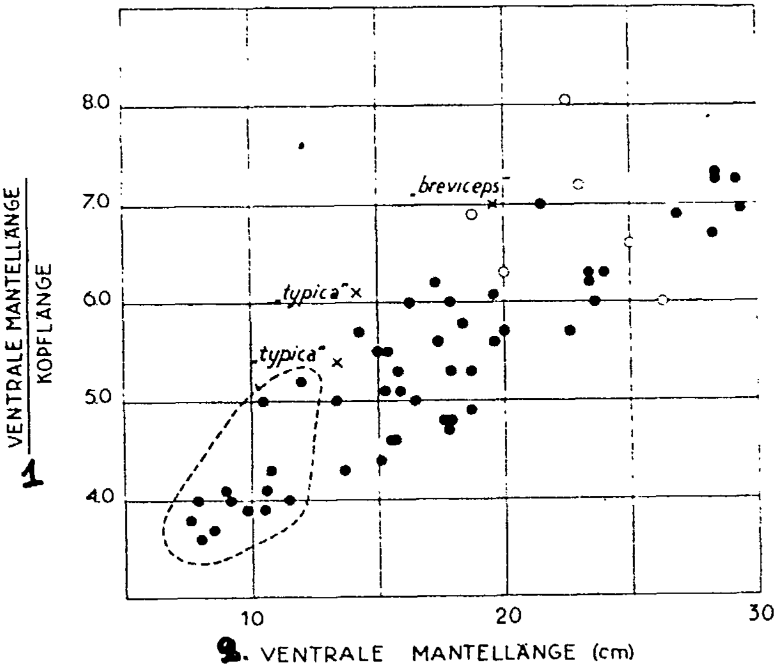

Figure 18 - Relationships between relative head length and ventral mantle length in male squid. ● (not encircled): 15 to 28 August 1936, Den Helder; ● (encircled): March, November, December, Den Helder; o: April to June, Den Helder; x: Grimpe's (1925) measurements. Key: 1, Ventral mantle length/Head length; 2, Ventral mantle length (in cm).

consideration only to the former ratio. In Grimpe, that numerical value is reported as 6.1 and 5.4 for L. vulgaris typica, and as 7.0 for L. v. breviceps. 271
Grimpe did not state where the border separating the two forms lies.

During different months, we have measured the head and mantle lengths of squid caught near Den Helder. These measurements revealed that the numerical value of this particular ratio depends to a large degree on the age of the specimen. For that reason, we have plotted both the proportionality values found by us and those reported by Grimpe as function of mantle length (Figure 18). It is evident that the ratios can be employed only taking into consideration the age (or the ventral mantle length, respectively). It was found furthermore that Grimpe's race characteristics actually are determined by the age of the specimen; according to the diagrammatical representation given in Figure 18, his L. v. breviceps could very well have developed from one of his typica forms.

Finally, our measurements indicate that the Dutch May squid, compared to the August squid, are rather short-headed than long-headed, and otherwise, probably, do not differ from the August specimens. (According to Grimpe's concept, one might expect that the May squid had a longer head; cf. further above.)

On the basis of these findings, it appears to us that we have no reason to divide the Loligo vulgaris of the North Sea into two races—a conclusion, we have already made use of on page 269 in connection with our treatment of the migration routes. Whether there exist morphological differences between the North Sea squid and the Mediterranean squid cannot be established at this time due to lack of adequate material.

Finally we return to the occurrences in the remaining range of dispersal. With respect to the times of occurrence along the Atlantic coast of northwestern Africa, Portugal, and France, and along the Channel coasts of France and England, we have found only Cuénot's (1927) notes and the fishery statistics of Portugal. According to Cuénot, Loligo vulgaris appears between May and October with immature gonads in the Baie of Arcachon. That behavior deviates considerably from that we have found in the North Sea. Immature sexual glands have been found by us in the majority of Loligo forbesi STSTRP. [the northern European squid] caught along the Dutch coast, so that there arises the question whether L. vulgaris has been confused with that species in this particular instance.

The Portuguese fishery statistics (Estatistica etc., 1929 to 1939) are interesting, and we are making use of their data on commercial landings in Lisbon. These reports contain a column headed "lulas." According to both Girard (1889a) and Nobre (1932), that name refers to both *Loligo vulgaris* 272 LAM. and *L. media* L. (= *Alloteuthis subulata* LAM. [a dwarf squid]). On the basis of Girard's discussion, we are able to conclude furthermore that *L. forbesi* ST STRP. is not distinguished from *L. vulgaris* on the Lisbon market; that species, apparently, also is called "lula." Nevertheless, it is clear that the numerical values reported refer, in the first instance, to *L. vulgaris*, since that squid, according to Nobre, is very common on the Lisbon market, while *Alloteuthis subulata*, according to Girard (1889b, page 255), "se montre très rarement sur le marché de Lisbonne," and *L. forbesi* has been described by the same author as "rara especia."

Table 14 gives the average monthly catch numbers for the years 1928 to 1937; in Figure 19, these numerical values are represented in diagrammatical fashion and compared with the numerical values from Tunesia and Den Helder, respectively. The Lisbon landings are subject to a striking periodicity, in that they are much greater during the winter (October to March) than during the summer. That finding could be due to the lower keeping quality of the squid during the summer months; however, if we give consideration to the numerical values reported from the much hotter Tunesia, that suggestion does not appear to be very probable. The latter values exhibited a very prominent peak during the months of April to June, instead of a reduction. For that reason, we assume that the Lisbon summer landings are small because this species occurs there relatively rarely during that period of the year.

Table 14 - Landings for the market in Lisbon. After Estatistica das Pescas maritimas (1929 - 1939). Average catch per month, 1928 - 1938. Key: 1, Month (January to December); 2, Squid (in 1000 kg).

1. Monat	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.
2. Kalmare (in 1000 kg)	9.9	10.2	7.5	3.3	2.7	2.4	1.9	1.6	4.9	8.6	12.6	9.3

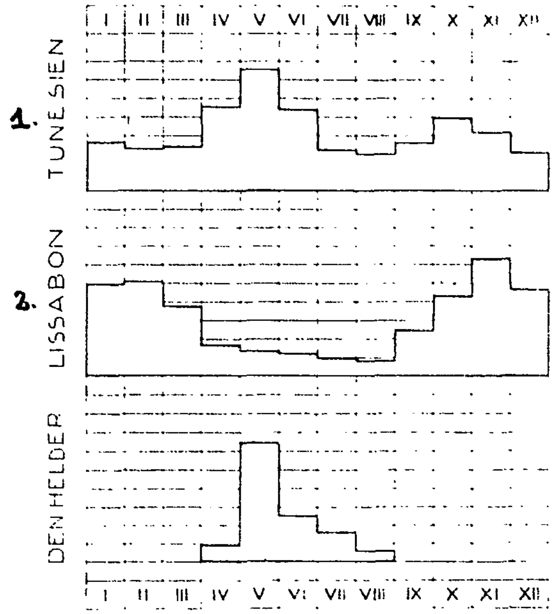

Figure 19 - Average monthly catch numbers for Tunesia (1932 to 1936; cf. Table 10), Lisbon (1928 to 1938; cf. Table 14), and Den Helder (1933 to 1940; cf. Table 13). Scale: Tunesia, one division mark represents 400 kg; Lisbon, one division mark represents 2000 kg; Den Helder, one division mark represents 200 specimens. Key: 1, Tunesia; 2, Lisbon.

The decrease in numbers during the spring, thus, must be caused by migration. Since this species appears in the north only during the summer, it is not improbable that that migration is a northern one. Evidence supporting that suggestion might be found, in the first instance, in the French fishery statistics; unfortunately, however, these statistics do not report squid landings under a separate heading.

We were struck by the finding showing that the maximum of the catches in Tunesia coincides in time with that of the catches in the southern North Sea. That finding, to some extent, taints our interpretation *viz.* that the Lisbon 273 squid migrate during the summer [actually, for the summer] to the north. A part of those squid actually could migrate to Tunesia, and, in fact, we are unable to exclude the latter possibility; however, we believe that that southward migration is highly improbable.

A number of data from the extreme western parts of Europe are furthermore of interest. According to Massy (1909; 1928), this species has not been found in the Irish waters. However, several reports worthy of note are available from the western coast of Great Britain. H.B. Moore (1937) provided the following note regarding Port-Erin (Isle of Man): "Taken frequently in seine nets in Port-Erin Bay and according to local fishermen said to be even more common off shore," to which he added the following footnote: "This record requires verification" (page 195). The same worker has informed us (1934, quoted in the literature): "These squid are present all the year round, showing no apparent seasonal fluctuation, . . . All the above data are obtained from the men, but I myself verified the identity of the species." Unfortunately, more exact details are, thus, missing. Nevertheless, these findings are of 274 interest to us in connection with our subsequent discussions (cf. page 276).

This concludes the presentation of our material. We are forced to concede that our insight into the course of the migrations of *Loligo vulgaris* is still rather incomplete. Above all, exact phenological observations from different parts of the range of dispersal are required to round out the migratory pattern. Systematic purchasing from fishermen probably represents the simplest method leading to that goal. Marine-biological stations usually are able to make such purchases without great expenditures of money and energy.

Despite the limitation of our knowledge, comparative discussion of several of our results is rewarding.

We have seen further above that Loligo vulgaris does not leave the Mediterranean during the winter, but certainly does leave the North Sea.

Sepia officinalis L. behaves is similar fashion. In the Mediterranean, that species is found all year round (Vérany, 1853; Jatta, 1896); in the North Sea, however, it is bound strongly to the early summer according to our observations[1].

Several bird species exhibit a similar difference in their migratory behavior. In these species, the populations of northern Europe behave differently than those of southern Europe; in addition, the populations of Central and eastern Europe differ from those of maritime western Europe. We are then able to state that there exists a connexion between the severity of the winter at a given site and the readiness of the birds to migrate south during the fall. We will briefly discuss several bird species as examples:

Fringilla coelebs L. (chaffinch). The Scandinavian, eastern Baltic, and Central German breeding birds are chiefly migrants; the Italian (Arrigoni Degli Oddi, 1929) and Sardinian (Tschi, 1939) breeding birds are residents. — In the eastern Baltic region and in Central Germany, migrants predominate; in The Netherlands, chiefly resident; in England and Ireland, resident (Witherby, 1938; for additional chaffinch literature, cf. Tinbergen, 1941).

Sturnus vulgaris L. (starling). In Scandinavia, in the eastern Baltic region, and in south-eastern Germany more or less migratory (Schuez and Weigold, 1931). In northern and Central Italy, resident (Toschi, 1939). —

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[1] In contrast, Loligo forbesi STSTRP. is a migrant in the Mediterranean region as well as in the North-Sea region.

In the eastern Baltic region and in south-eastern Germany, in part, migratory; in England and Ireland, resident (Witherby, 1938).

Among the additional species, which migrate in the northern part of their range of dispersal, but do not migrate in Italy, we may mention: *Alauda arvensis* L., *Lullula arborea* (L.), *Regulus regulus* (L.), *Phylloscopus collybita* (VIEILL.), *Sylvia atricapilla* (L.), *Erithacus rubecula* (L.), *Accipiter nisus* (L.), (Arrigoni Degli Oddi, 1929; Toschi, 1939). 275

Additional species migrating in the continental part of their range of dispersal, but not in the maritime part are: *Accipiter nisus* (L.), in Germany frequently migratory (Niethammer, 1937; 1938), in The Netherlands rarely migratory (Eykman, c.s., 1937, ringing records of the Leiden Museum), in England resident (Witherby, 1938); *Sitta europaea* L. and *Troglodytes troglodytes* (L.), both species are residents in The Netherlands (Eykman, c.s., 1937), but frequently migrate from Central Russia (Grote, 1940); *Certhia familiaris* L., in England resident (Witherby, 1938), in Central Russie at least in part migratory (Grote, 1940). Finally, Grote's descriptions leave the impression that the *Parus* species in Central Russia participate in migration in relatively greater numbers than, for example, in western Europe.

There exist, furthermore, several bird species, which migrate in the north (or in the east, respectively) as well as in the Mediterranean region (or in the west, respectively). However, we know no examples of species, that pass the winter in the north, and migrate from the Mediterranean region.

With respect to this difference in migratory behavior, we are permitted to conclude that either, in the south, the stimulus eliciting spring migration is missing in the afore-mentioned species or that the birds residing there do not respond to that stimulus. Which one of these two possibilities is applicable in the case of the fall migration cannot be established by us. However, if we give consideration to the northward migration during the following spring, it is clear that the migration-eliciting stimuli are present in the south (or in the martime part of the ranges of dispersal, respectively), but that the resident birds do not respond to them: The northern forms of several of the above-mentioned species pass the winter on the breeding range of the southern races. When spring arives, the former migrate to the north, while the latter remain where they are.

The effect of that phenomenon is already well known: There, where the winter is severe, the birds disappear; where it is mild, they remain. The individuals having migrated away from the north pass the winter, without exception, at sites, where the winter is milder than on their breeding range. We are then permitted to assume that this migration is actually required, because the birds simply would not survive the winter on their breeding range. However, we are unable to provide any evidence in this connection; as evidence, we require estimations of mortality suffered by these birds if they never left the north during the winter—a complex undertaking. However, on the basis of the facts mentioned further above, we are able to conclude only that the species in question are able to maintain themselves in the south without migration.

Let us now return to Loligo vulgaris. We had found that the northern individuals of this species migrate, while the Mediterranean individuals do not. We are able to state that the Mediterranean individuals either are insensitive to the migration-eliciting stimuli or are not exposed to these stimuli. However, it is not possible to determine which one of these two possibilities is applicable, since the stimuli may be different for the individuals in the Mediterranean than for those from the north, which—as we have seen 276 on page 272—pass the winter probably along the south-western Atlantic coast of Europe.

We have seen further above that the squid from the region of the North Sea, in all probability, pass the winter—like the migratory birds—in warmer regions.

The migrations then have the effect that Loligo is not exposed to winter coldness and its associates phenomena. However, it is not possible to establish the extent to which the latter effect is essential (we saw already that an other function of migration is to get to the spawning grounds; cf. page 244).

We have stated that there exist bird species, which do not leave the maritime western European regions (apparently because of the milder climate), but do leave the more eastern, continental regions. The behavior of squid in the Irish Sea, which behavior we know on the basis of Moore's observations (cf. page 274), is of interest in this particular connexion. According to Moore, the squid are present there during the summer and during the winter. Actually, the winter in the Irish Sea is somewhat milder than in the North Sea, as is indicated by Bruce's (1928) communications. To be sure, the minimum of the annual curve is only 1.5°C higher in Port-Erin than at Haaks light ship in the North Sea; however, Bruce's observations were made at a point close inshore in one or two fathoms of water. The actual difference between the North Sea at Haaks and the Irish Sea near Port-Erin, thus, will be somewhat greater, since deeper stations in the latter region, no doubt, would exhibit higher winter temperatures. —— It would be important to obtain more detailed data on the occurrence of Loligo vulgaris near Port-Erin.

All that remains is to compare the course of the migration of Loligo vulgaris with that of other cephalopods. Let us first consider several species from the North Sea regions.

Sepia officinalis exhibits extensive correspondence with Loligo vulgaris; it is, however, treated in a separate contribution.

The migrations of Alloteuthis subulata have been described in detail by Grimpe (1925). According to that author, these dwarf squid appear early in March in the northern North Sea and, from there, disperse southward in order to reach, for example, the German Bay early in May. However, Adam (1933) has demonstrated that these squid occur already in April off the Belgian coast, and he, furthermore, has mentioned one February catch near Cape Gris-Nez. It then appears that this species appears at about the same time in the south and in the north of the North Sea. On the basis of Massy's (1909) observations, Grimpe assumed that the North-Sea individuals migrate westward during 277 October, and pass the winter at about the same latitude as the summer. Whether that is true also in the case of the individuals migrating north during the spring through the Strait of Dover cannot yet be established. It is, however, clear that the situation in Alloteuthis subulata differs entirely from that in Loligo vulgaris, which, as we know, appears in the north only late in the season.

Even if additional details are still required, we are able to state that that situation reminds one of that encountered in several Central-European bird species. For example, the eastern Baltic starlings (Sturnus vulgaris L.) and the north-west-German rooks (Corvus frugilegus L.) migrate westward during the fall and pass the winter in England and Ireland, while the Russian populations of the latter species also migrate in a strongly western direction (cf., for example, Niethammer, 1938). Like the winter quarters of Alloteuthis subulata (i.e. the ones suggested by Grimpe) owe the relatively high winter temperatures to the influence of the Gulf Stream in addition to their depth, the mild climate on the winter ranges of the afore-mentioned bird species must also be attributed to the Gulf-Stream factor.

Like *Sepia officinalis*, *Loligo forbesi* will be treated in a separate contribution. The migrations of that species, like those of the other North-Sea cephalopods, have not yet been described in literature.

Several data about related species occurring in other regions may be discussed.

The agreement in the migrations of *Loligo vulgaris* and *Loligo pealii* is striking. The studies published by Verrill and Bigelow provide information on that North-American squid, representing the common squid of the East-American coast between Cape Hatteras and Cape Cod. During the summer, that squid is bound to the littoral zone. In the Gulf of Maine, it appears during the spring, spawns during the entire summer at depths between zero and about 50 m, and disappears during the autumn. It appears later in the north and disappears earlier than in the south. Since catches are missing from deeper waters according to Bigelow, we venture to assume that this species migrates northward along the coast.

The morphological differences between *L. pealii* and *L. vulgaris* are rather minor. Since the biologies of these two species—as far as they are known—also correspond in certain respects, the question arises whether these forms should not be regarded as two races of one and the same species.

Migration from the south to the north have, furthermore, been described by Sasaki (1921) in the case of *Ommastrephes pacificus sloani* [the Japanese cuttlefish], which during the spring follows the Japanese coast in a northeastern direction.

We then know several examples of cephalopod species, which, like the migratory birds, migrate during the spring in approximately northern direction toward the temperate zones. However, it appears that additional migra- 278 tory types occur.

8. Summary

1. The present report, which deals with a number of separate questions, relates to the research of the biology of Loligo vulgaris Lam.. It is based on the investigation of about 12000 squid caught in the neighborhood of Den Helder. This species is generally present in this area from April to August, and as isolated individuals during the other months; it reproduces regularly in this area.

2. Growth was determined by the analysis of ventral mantle lengths frequency curves.

3. At the beginning of May, the length-frequency curves of the nearly one-year-old ♂♂ show a peak at 13-14 cm, and those of the almost two-year-old ♂♂, at 21 cm, while three-year-old animals probably are seldom. A schematic growth curve of the ♂♂ is shown in Fig. 4.

4. The ♀♀ grow about equally fast as the ♂♂, until they reach a length of about 12 cm (that is, until they are about 1/2 - 3/4 years old). The second year of their lives, they grow much more slowly than the ♂♂; thus, their frequency curves, in the month of May, show peaks at about 13-14 cm and about 17 cm. Slow growth during the second year of their lives has also been found in the ♀♀ of Loligo pealii Les. and Sepia officinalis L.. Three-year-old ♀♀ of L. vulgaris would seem to be seldom.

5. The yearlings, on an average, appear later in the spring than the two-year-old animals. Similar findings exist for many fishes and birds that migrate to their mating areas.

6. The sexual ratio of the spawning migrant animals is unequal; among the total of animals caught, 57 % were ♂♂. Initially, the percentage of ♂♂, on an average, is somewhat higher than later on in summer; however,

this does not apply to each separate year. The sequence of the sexes during the migration to the spawning area is discussed comparatively, and the relationships to the mating biology are dealt with.

7. Spawning lasts as long as the animals frequent the area in large numbers, that is, from April to August. It reaches its peak in the second half of May, when the majority of the animals are present.

8. The testes of the ♂♂ born the same year contain spermatozoa (279)
already in October. Testicular growth goes on during the winter, and reaches its peak in May to July, to decrease again in August. It was not possible to determine to what extent it recedes again during the second winter. All that can be said about the two-year-old animals is that their testes are strongly developed in spring and early summer, and that in August, they undergo involution.

9. The spermatophore sacs of the ♂♂ born the same year contain spermatophores already in December. Until they appear in April, the spermatophore production of the yearlings (as well as of the two-year-old ♂♂) exceeds consumption (which might then be set equal to zero). Yet, as soon as the animals arrive, consumption exceeds production which, however, does not cease. As a result thereof, the spermatophore sacs get steadily emptier.

10. The ♀♀ born the same year have no eggs in the oviduct in December, while in the ovary the eggs still are very small. Accessory, nidimental, and oviduct glands still are in the initial stage of development. Between December and April, the ovary develops considerably; no decrease in the growth was determined at the end of summer.

11. Before the animals arrive in the spawning area, the eggs increase in the oviduct, while none are deposited as yet. Thus, the oviducts are filled more or less. Shortly after arrival, more eggs are laid than the

oviduct supplies, and the number of animals with empty or scarcely filled oviducts increases. However, after the end of May, consumption and supply, on an average, are in equilibrium. Probably, the eggs are not laid on a continuous basis, but rather in batches.

12. At Den Helder, the ♂♂ of Loligo vulgaris deposit their spermatophores exclusively on the mouth membrane of the ♀, where the spermatheca (= receptaculum seminis) is found. In the large majority of summer females, this organ is filled with sperma. From the occurrence of freshly deposited spermatophores, one may conclude that the ♀♀ are fertilized all through summer, yet somewhat less at the beginning and at the end of the mating period than in the middle.

13. Two-year-old squid, in relation to their size, have fuller spermatophore sacs or more eggs in the oviduct than yearlings, which gives (280) rise to comparisons with other animal groups. Among the birds, older females often lay more eggs than younger ones.

14. Various cephalopod species, such as Loligo vulgaris, reproduce periodically. For some species, the spawning period lasts longer in the Mediterranean than in the North Sea region, which might point to the influence of temperature.

15. The reproduction of Loligo vulgaris, in the North Sea, starts with the lengthening of daylight, in the Mediterranean (according to LO BIANCO's statements), with the shortening of daylight; this does not speak in favour of a marked influence of this factor which is so important in relation to the periodicity of bird reproduction. On the other hand, a common cause for the periodicity of reproduction and migration is not unlikely; under point 18, it will be seen that the latter, probably, is influenced by the length of daylight.

16. One of the migratory functions is the reaching of the spawning areas. A classification of the migratory types according to functions is unsuitable, since, generally, several functions are involved.

17. The periodicity of migration results from Fig. 13. Immigration is followed immediately by emigration, without a stationary state in between.

18. The immigration starting dates differ only slightly from year to year, which shows a relationship to the water temperature. In cold years, the animals arrive later than in warm years. The influence of temperature is only a subordinate factor; far more important is the factor "time of year" (NICE), that is, probably the length of daylight. The same discovery was made for migratory birds.

19. The number of squid varies each year. Out of five comparative years, the warmer ones provided larger catches. L. vulgaris, a migrant of southern origin, probably requires high temperatures, which prevents the species from migrating as far north in cold years as in warm years.

20. L. vulgaris is strongly bound to coastal waters. At Den Helder, it is seldom caught more than 20 miles offshore. Its occurrence within the coastal zone will be subjected to further analysis.

21. In June, the bulk of the squid is found closer to the coast than (281) in April and May, or July and August. Some winter catches, on an average, originate from deeper waters than the summer catches: These seasonal migrations probably are caused by the preference for higher temperatures, as will be mentioned under 23.

22. The shallow coastal waters (area 7 of Fig. 14 (German text)) are frequented by the squid only when the salt content at the western inlet rises above about 3.03 % (Fig. 15, German text), while the temperature would appear to have no influence.

23. The coastal-water areas further offshore (areas 1, 3, and 5 of Fig. 14) are frequented mainly when the salt content is low (at the Haaks lightship below 3.4 %), and the temperature gradient between the Haaks lightship and the western limit of area 7 is low. The animals seem to dislike the unmixed, salty North Sea water, and to prefer the warmer areas. Both properties bind them to the coastal waters where the salt content is lower and (in spring and summer) the temperature higher than farther offshore.

24. For the binding of the squid to the coastal waters, the water depth plays hardly more than a subordinate part.

25. The ♂♂ are relatively more numerous in areas strongly influenced by land than in other areas (Table 8, page 261, German text). They probably require a lower salt content or a higher temperature than the ♀♀.

26. The location of preferred spawning areas is described, yet without giving rise to further conclusions.

27. The range of distribution of L. vulgaris extends over the Mediterranean and East-Atlantic coasts, between 21° and 59°N.

28. In the Mediterranean, L. vulgaris does not disappear in winter, which gives rise to comparisons and discussion. The same applies to the Portuguese coast: there, however, the species is much more frequent in winter than in summer, which may be due to immigration.

29. Along the Dutch coast, L. vulgaris migrates in spring from South to North. Its migratory speed is higher than the speed of the resultant of the water movement; hence, the change of location takes place in an active manner.

30. Most probably, L. vulgaris reaches the North Sea through the (282)
Strait of Dover, from where it migrates along the Belgian, Dutch, Northwest-German and Danish coasts as far as the Kattegat and Skagerrak; here, the species appears only in late summer.

31. It is uncertain how the North Sea animals depart in autumn; also the location of their winter quarters is not clear.

32. In the Portuguese waters, animals ~~hibernate~~ pass the winter, that probably pass the summer in Northern regions.

33. The occurrence on the Eastern coast of England is not clear.

34. The differences between GRIMPE's species, *L. vulgaris breviceps* and *L. v. typica*, are dependent on growth, and are not ~~essential~~ significant.

35. According to MOORE (1937), in the Irish Sea (as in the Mediterranean and on the Southwest coast of Europe, see above), *L. vulgaris* does not seem to leave during the winter, which gives rise to comparisons with bird migration.

36. The migrations of *L. vulgaris* are briefly compared with those of other cephalopods, as well as with those of other animal species.

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