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PERIODIC FLUCTUATIONS IN THE SIZE OF VARIOUS STOCKS OF FISH AND THEIR CAUSES

BY

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1. Introduction.

A. Object and Delimitation of the Investigation.

The stock of any species of fish in some marine area will generally alternate from year to year in number and composition according to size groups.

Especially since the systematical fishery investigations were started under the auspices of the Conseil permanent international pour l'exploration de la mer a great work has been done in order to explain the causes of these alternations in the stocks of fish. This work intends to make it possible to give prognoses of the yield of the fisheries.

The investigations have shown that we may state the following causes of fluctuations from year to year within each stock of fish:

1. Interference on the part of man.
2. Hydrographical (terrestrial-cosmic) causes.
3. Purely biological (physiological) causes.

All of them may directly change the stock of fish or indirectly cause a change, the fish because of its physiologically conditioned demands reacting upon changes in the surroundings.

It is often difficult or impossible to decide which changes in the stock of fish are direct effects and which are due to the reactions of the fish, for any change in the biocoenosis of a stock of fish will involve more or less perceptible changes in the stock.

1. Interference on the part of man may be either removal of part of the stock by the fishery or the transplanting of eggs, fry, or older fish.

It has been proved by marking experiments in the scientific fishery investigations that the interference of the fishery with the stock of fish may often directly cause a considerable change in the size of the stock.

There is a slight possibility that the quantity of fish removed by the capture is determined partially by the fact that the fish gradually may learn to avoid the fishing gear (H. M. Kyle, 1926, p. 324).

Many cases are known of changes in the biocoenosis produced by the fishing causing considerable changes in the stock of fish. It has been shown, especially, that a virgin, accumulated, and slowly growing stock of plaice may be changed into a fast growing "current stock" when it is made the object of fishing, because of the decreased competition for food. A specially characteristic instance of this is the plaice stock of the Belt Sea as shown by C. G. Joh. Petersen, 1920.

2. A change of the current may be one of the hydrographical causes producing direct changes in the distribution of the fish in that it changes the distribution of the fry. That this factor plays a prominent part in

the fluctuations of the stock of plaice in the Horns Reef Area will appear from what follows. Transport by the current may also be of great importance for the distribution of fish with a small locomotive power. A. C. JOHANSEN, 1927, has pointed out the possibility of the current directly influencing the occurrence of the herring after spawning time.

Changes on account of the physiological reactions of the fish on the alternations in the hydrographical conditions are of considerable importance, especially because of the influence of the hydrographical conditions on the survival of eggs and fry. The classical investigation into the importance of the alternating frequency of the year classes for the stocks of fish is JOHAN HJORT: Fluctuations in the Great Fisheries of Northern Europe, 1914. Changes in the hydrographical conditions are an important cause of migrations of the fish, and by these changes from year to year changes take place in the stocks of fish, too.

Here, too, the differences in biocoenosis arisen by the changes are often of great importance.

3. Purely biological causes may, on a parity with all extrinsic conditions, produce changes in the stock of fish.

Thus we see that differences in the frequency of each year class once arisen may produce continued changes in the stock of fish both direct by the life-cycle of the fish (reproduction — growth — propagation — death) and by the migrations conditional on the life-cycle of the fish according to the physiological demands changing with the age and the stage of maturity.

As mentioned above, any change in the biocoenosis of the fish produces new changes in the stock of fish.

The importance for the fish not only of the quantity of food animals but also of enemies has been pointed out by various authors. Thus UMBERTO D'ANCONA, 1926, has treated the biocoenosis among sharks and various other species of fish, H. BLEGVAD, 1928, the dependence of *Zoarces viviparus* and *Gobius niger* on the stock of cod, and the present writer, 1929, the dependence of the herring on the stock of cod. VOLTERRA, 1928, has given a theoretical treatment of these purely biological variations.

The variations may be periodic[1] or non-periodic. In the course of time a large number of theories on the existence of several years' periodic variations of the physical and biological phenomena have been put forth, but in very few cases this existence has been proved with absolute certainty.

As to the stocks of fish in the sea the following theories on several years' periodic variations have been put forth:

1. Hydrographic (terrestrial-cosmic) causes.

a. Supposed periods of insolation with a length of 2.25, 2.67, and about 6.5 years.

W. B. SCHOSTAKOWITCH, 1929, 2, supposes that such periods are the cause of periodic variations in the following stocks of fish and fisheries (length of period in brackets): the plaice fishery in the Belt Sea (2.50, 5.90), the herring fishery at Bohuslän (2.70, 5.54), the sardel (i. e. anchovy) fishery in the Zuyderzee (2.82, 5.20), the cod fishery at the Lofoten (2.85, 5.33), the quantity of cod liver at the Lofoten (2.85), the sturgeon fishery in Kura (3.10, 6.30).

b. The solar spot period of about 11 years.

B. HELLAND-HANSEN and NANSEN, 1909, would find this to be the explanation of an 11 years' period in the quantity of liver and spawn of the cod at the Lofoten. JOHAN HJORT, 1914, pointed out that this cannot be correct. W. B. SCHOSTAKOWITSCH, 1929, 2, supposes that it is the cause of periodic variations in the sardel (i. e. anchovy) fishery of the Zuyderzee (10.00 years), the plaice fishery of the Belt Sea (10.33 years), the sturgeon fishery in Kura (11 years), and the quantity of cod liver at the Lofoten (11 years).

c. Insolation periods of $55\frac{1}{2}$ and 222 years.

[1] Everywhere in this paper a "periodic variation" means a cyclic-like periodic variation.

A. V. Ljungman, 1879, thought this to be the cause of a periodic variation of 111 years in the herring fishery at Bohuslän.

d. Periods of $18^1/_2$ and 111 years in the tide-effecting forces.

B. Storrow, 1922, assumes periods of about 9 (in the herring fisheries) and $18^1/_2$ years in the yield of various fisheries as a consequence of a period of $18^1/_2$ years in the hydrographical conditions.

Otto Pettersson, 1922, supposes that periods of c. 18 and 111 years in the yield of the fisheries correspond to periods of the same length in the tide-effecting forces. The variations in the herring fishery at Bohuslän he takes to be due to the period of 111 years.

Ed. le Danois, 1925, assumes the existence of periods of $4^1/_2$, 9, $18^1/_2$ and 111 years in the yield of the fisheries.

2. Purely physiological causes.

a. Effect of the quantity of spawning fish on the stock of the following years.

J. P. Jacobsen and A. C. Johansen, 1921, have pointed out the probability of a periodic variation of 5 or 6 years in the salmon fishery of the Gudenaa now nearly ceased.

The present writer (Aage J. C. Jensen, 1927) has been able to ascertain the existence of a period of 3.7 years in the herring fishery at Bornholm and has ascribed this to the same cause.

b. Effect of the competition for food.

Theoretical investigations by V. Volterra, 1928, have shown that there is a possibility of periodic variations in the stocks of fish because of the competition for food among various species of fish living in biocoenosis.

3. Unknown causes.

E. Neupart, 1925, assumes periods of 8 and 80 years in the tunny fishery at South Portugal.

The present writer (l. c. 1927) has found the probable existence of a periodic variation of about 11 years in the herring fishery at Bornholm.

Theories on periodic variations arisen in direct consequence of interference on the part of man have not been put forth. Because of the irregular variations in the commercial fishery it must be considered a matter of doubt whether such an interference should in any case play a material part as the cause of periodic variations in the stocks of fish.

Practically all previous investigations of several years' periods in the stocks of fish or in the fishery as also in the biological phenomena on the whole, have, in order to ascertain the existence of such periods, been based on mere inspection or on a counting of the number of cases in which the phenomenon in question coincides with the supposed periodic fluctuation, and the number of cases in which they do not coincide.

An objective decision of the question whether the periods may be regarded as realities is possible by the application of the theory of errors as an objective criterion.

In the following, therefore, various stocks of fish and fisheries have been examined in order to ascertain whether periodic fluctuations within a period length of several years' duration may be demonstrated in them. By the choice of stocks and fisheries I have endeavoured to provide a material comprising different stocks of fish so as to give an impression of the generality of these fluctuations, and to contribute to the decision of the question which different fluctuations can be found in the stocks of fish.

Such an objective inquiry into the question whether cyclic-like periods of several years are factors to be taken into consideration in fishery-biological investigations of the variations from year to year in the stocks of fish, has hitherto been made only in the above mentioned investigation of periodic variations in the herring fishery at Bornholm (Aage J. C. Jensen, 1927).

Because of the extent of the investigation; for it requires a great many calculations, it has proved necessary to confine it to four different stocks of fish, in the first place two stocks of plaice belonging to two different races and living under rather different biological conditions, viz. in the southern part of the North Sea and in the Belt Sea, in the second place the stock of mackerel that is worked in the eastern Skagerak and the adjacent parts of the Kattegat, and finally the stock of herring at Bornholm.

The investigation is naturally delimited by its object: by means of an objective criterion to demonstrate cyclic-like periodic variations of several years' duration in the stocks of fish, and then to inquire into their causes.

B. Associated Variations.

In connexion with the above survey of the different possibilities of the occurrence of periodic variations in the stocks of fish or in the fisheries we should mention the fact that a periodic variation in the stock of fish or in the yield of the fisheries may be associated with secondary periodic variations.

Let us suppose that the number of fish in one population in any year is determined by a physical factor, e. g. the temperature of a certain season falling a certain number of years before (which for brevity's sake is called the "determining year" in what follows) and that this factor varies according to a cyclic-like periodic curve, where all the "waves" are uniform, e. g. a sine curve. If the length of the period of this curve is a whole number of years, the size of the population determined by the physical factor will be variable according to a cyclic-like periodic curve with the same length of periods and with oscillations repeated periodically with the same values. If the length of the period of the physical factor is no whole number of years, this factor will not be repeated periodically with the same values, the situation of the determining year in proportion to the wave of the cyclic-like period shifting somewhat in the course of time. The size of the shifting within one year, measured in lengths of periods, is equal to the reciprocal values of the length of the period.

Only in case the dependence of the number of individuals (S) within the stock of fish on the physical factor (y) is linear, i. e. when $S = cy$, where c is a constant, the number of fish will vary in a curve conformable with the one described by the physical factor. If on the other hand the dependence is not linear, if e. g. $S = c \cdot y^n$, where c and n are constants, or if it follows VAN'T HOFF's law, the curve, according to which the number of individuals varies, of course will not be repeated period by period with the same amplitude. After some (A) years the annual shifting of the determining year will accumulate to a whole number of periods — exact or approximate. After that the determining factor is repeated with the same or approximately the same values as in the first A years. In the size of the population will consequently arise a new periodic variation with a length of period of A years. I have called such a periodic variation an associated variation.

Conditions will be quite the same if the number of individuals in any year is not determined by the physical factor in one year a certain number of years before, but by this factor in a certain period (a "determining period") a certain number of years before the casually considered year. The case is of course the same, if it is not the number of individuals but another quality of the stock, e. g. its growth, which is considered.

Beside the importance of the fact that a complex periodic variation in the stock of fish can arise as a consequence of one cyclic-like periodic variation of the determining factor, it is worth noting that the presence of associated variations in a population of fish determined by a factor the curve of which varies in a rhythmic periodic way, can thus in some cases give information on the question whether the dependence of the stock of fish on the said factor may be considered linear or no.

Some examples will show the multiplicity of the associated variations.

1. In the case of a length of period of 2.4 years the annual shifting is 0.417 of the period and thus we get the following shiftings:

In years	0	1	2	3	4	5	6	7	8	9	10	11	12 etc.
Shifting (lengths of periods)	0	0.42	0.83	1.25	1.67	2.08	2.50	2.90	3.33	3.75	4.17	4.58	5.00 etc.

As will be seen the associated period of the first order is 12 years, but the difference from a whole number of periods after 5 or 7 years is rather slight. This variation must appear as a combination of a period of 4 and one of 6 years.

2. When the length of the period is 2.7 years the annual shifting will be 0.370 of the period and thus we get the shifting given in the following table:

In years	0	1	2	3	4	5	6	7	8	9	10	11	12 etc.
Shifting (lengths of periods)	0	0.37	0.74	1.11	1.48	1.85	2.22	2.59	2.96	3.33	3.70	4.07	4.44 etc.

It will be seen that the determining series of years after 27 years will be repeated with exactly the same values, but that maxima and minima of different order arise in the associated variations during this period, the difference of the shifting from a whole number of periods being variable.

At two points of time, viz. after 8 and after 19 years, the differences from a whole number are very small, viz. 0.04, and consequently a variation of 8—9—10 years will arise, which will appear as a periodic variation of 9 years.

3. By a length of period of 2.9 years the annual shifting is 0.345 of the period, and the successive shiftings are:

In years	0	1	2	3	4	5	6	7	8	9	10	11	12 etc.
Shifting (lengths of periods)	0	0.34	0.69	1.04	1.38	1.72	2.07	2.42	2.76	3.10	3.45	3.80	4.14 etc.

After 29 years the determining series of years is repeated with exactly the same values, other periods than that of 2.9 years being very inconspicuous.

4. With a length of period of 3.7 years the annual shifting is 0.270 of the period, and the successive shiftings are:

In years	0	1	2	3	4	5	6	7	8	9	10	11	12 etc.
Shifting (lengths of periods)	0	0.27	0.54	0.81	1.08	1.35	1.62	1.89	2.16	2.43	2.70	2.97	3.24 etc.

Only after 37 years the determining series of years is repeated with exactly the same values, but after 11 and 26 years it is repeated with approximately the same values.

With a less distinct approximation it is repeated after 4 and 7 years.

5. With a length of period of 4.5 years the annual shifting is 0.222 of the period, and the successive values are:

In years	0	1	2	3	4	5	6	7	8	9	10	11	12 etc.
Shifting (lengths of periods)	0	0.22	0.44	0.67	0.89	1.11	1.33	1.56	1.78	2.00	2.22	2.44	2.67 etc.

After 9 years the determining series of years is repeated with exactly the same values. Further it appears that, with the exception of this period, there are no associated periods, the deviations from a whole number only reaching a secondary minimum after 4 and 5 years (the original periodic variation).

A calculation of the influence of such an associated variation on the size of the stock of fish is, however, complicated by the fact that the hydrographical factor in the different years of the determining series of years influences the population of a later year in a different way. As a rule, one or some few of the years of the series are of special importance. Further a calculation is rendered difficult by the proportionality between the physical factor and the population determined by it being in no case known sufficiently, so that hypothetical values must be taken into consideration.

Quite corresponding considerations may be made if the variations from year to year in the number of individuals or composition of a population of fish is dependent on another factor varying periodically from year to year, e. g. the amount of spawning fish.

C. Material of the Investigation.

The material for the investigations of the biology of the fish is provided by quantitative and qualitative determinations of the stocks of fish and by an examination of simultaneous conditions of nourishment and hydrographical conditions. This material falls into two groups. In the first place quantitative fishing experiments, marking experiments, analyses of representative samples of fish, made in order to determine composition according to age groups, sex, maturity, etc., and determinations of race are made in the scientific marine investigations, in the second place statistics of the yield of the fisheries have been used. As yet it has been possible to a small extent only to make direct investigations in aquaria of the physiological demands of the fish and their reactions on changes in the physical conditions of the environments.

The material available in the fishery statistics has been used to a considerably smaller extent by the scientific fishery investigations than the rest of the material. The former material constitutes the principal basis of the present investigation.

At first we must subject the material offered by the fishery statistics to a closer inspection.

In many cases the fishery statistics gives information on variations in the quantity of the stock of fish in the area investigated.

This will especially be the case when the annual quantity caught constitutes a considerable part of the total stock of the species in question, and the percentage of re-capture in marking experiments proves that this occurs very frequently. For a limited area it is possible from the quantity of commercial fish re-captured within one year combined with the statement of the fishery statistics as to the quantity caught, to make a direct calculation of the number of fish above a certain size and age, as has been pointed out especially by A. C. Johansen (1906, pp. 79—80) and Heincke. It is of great importance that the marked fish should be representative of the stock of fish sought by the fishermen during the marking experiments, and that due regard is paid to various sources of errors (loss of marks, etc.).

In the case of the fish marked the percentage of re-capture during the first year shows a highly differing quantity in the various cases, but it has turned out in all cases of successful marking experiments that so large a quantity is re-captured that the stock of fish may be considered limited in proportion to the annual quantity caught by the fishery.

When a species, worked by the fishery within a limited area, every year shows somewhat the same distribution, the variations from year to year in the average yield of the fishery per fishing unit, i. e. per unity gear per time unit, will give the size of the stock of fish fairly well. When the fishing intensity is not subject to great variations from year to year, the total yield of the fishery will also be indicative of the variations from year to year in the size of the stock.

Against this view H. M. Kyle (1928, p. 24) has raised various objections; he has especially objected that with a fluctuating fishing intensity the yield per fishing unit, the stock being the same, will be inversely proportional to the fishing intensity.

E. S. Russell (1931, p. 16 ff.), who in a very thorough investigation discusses Kyle's objections, in this connexion draws attention to the fact that what the yield per fishing unit of the fishery is indicative of, is the stock left after the fishery has taken a certain portion.

It should be kept in mind that the fishing intensity practically always shows a smooth variation from year to year, whereas the size of the stock is subject to considerable and irregular fluctuations (see e. g. Kyle, 1926, p. 323). Hence, it must not be overlooked that also the variations from year to year in the size of the stock after the fishery has taken its part depends chiefly on the natural oscillations within the stock, and not on the variations of the fishing intensity.

Further it should be noted that a principal cause of the fluctuations in the fishing intensity are fluctuations in the size of the stock, the intensity often varying proportionally to the latter (Aage J. C. Jensen, 1931, 2), so that against Kyle's assertion there is in most cases a positive correlation between fishing intensity and yield per fishing unit. Consequently the catch per time unit in practice often shows a variation from year to year proportional to both the total of the catch and the size of the average stock.

Beside the determination of the relative amount of the stock by quantitative fishing experiments this is the only method by which to obtain information on the variations from year to year in the quantity of the stock.

The information yielded by the fishery statistics is of course always much less specified than the information that can be given by a scientific research about the stock of fish of an area, as the statistics gives only a measure for the weight or number of the stock.

It should not be overlooked that on this principal point it gives information which is mostly more reliable than the determinations of the quantity of the stock that can be made by quantitative fishing experiments to such an extent as is generally possible. There will always, and more especially in the case of shoal fish, be so great local variations in the distribution of a species within a certain area that a determination of the average density of the stock by fishing experiments (i. e. of its total) will in practice involve a great mean error.

As mentioned above this paper will discuss the fluctuations from year to year in the stocks of fish. The fluctuations in the yield of fisheries are chiefly a consequence of the different recruiting of the stock of commercial fish of the different years, whereas the population worked may consist mainly of an "accumulated" stock of several older year classes (cp. E. S. Russell, 1931, p. 5).

D. Methods of the Investigation.

In the yield of the fisheries there are often variations where an individual cycle extends over series of years of nearly the same or a greater length than the series of years from which statistic information about the yield of the fishery is available. The cause may be changes in the fishing intensity during the years, or changes in the numbers of individuals or in the composition of the stocks of fish. As far as possible both kinds of variation will be eliminated before the investigation is made.

The effect of the fishing intensity is eliminated in the values for the yield per unity gear and time unit.

However, it is often impossible from the data of the fishery statistics to find an exact expression to the yield per unity gear and time unit, as the fishing intensity is difficult to measure. In order to eliminate to a certain degree the above mentioned variations extending over a longer series of years I have in this paper calculated approximate values for alternations in the yield as deviations from average values ("normal values") determined by a normal graph for the fishery found by a graphic smoothing for a certain succession of years. How much can be eliminated by a calculation of these deviations and the degree of elimination, is in some cases a matter of estimate only.

In case the fishing intensity cannot be exactly determined, we may proceed in two ways.

The method generally used at the treatment of variations in the yield of the fisheries is the drawing of a rough normal curve for the yield of the fishery. This curve is drawn with as uniform a course as possible, and as the basis of the drawing is generally used an approximate smoothing, mostly for a succession of less than 10 years. It follows from the way in which the normal curve is constructed that a certain subjectivity is inevitable.

Further the so-called Cock-Blanford's method can be applied, by which we can eliminate any few years variation by using as normal values such values for the catch as are found by an ordinary arithmetical smoothing for a succession of years, as many years being smoothed as the approximate length of the period in question is supposed to comprise. In these normal values determined by an ordinary smoothing the effect of the said periodic variation in the fishery is eliminated more or less. The deviations of the catch values from the normal values resulting from these smoothings will show approximately the period sought for (if such a period exists), all other variations being eliminated to a considerable extent by the calculation of the deviations[1]. Thus it is possible by this method to give a direct determination of the question which

[1] See e. g. Yule, 1911, p. 200.

integer is nearest to the length of the period, and by graphic interpolation to give a closer determination of the length of the period.

In the curve showing the variations that are found as the difference between the original values and those determined by the ordinary arithmetical smoothing, the amplitude has become smaller than is actually the case.

This problem was discussed by PAUL SCHREIBER, 1896. He points out that the error in amplitude may be corrected more or less by introducing the following reduction factor:

$$\varepsilon = \frac{N \sin \frac{T}{2}}{\sin N \frac{T}{2}}$$

where N denotes the number of years used in the arithmetical smoothing and $\frac{2\pi}{T}$ denotes the length of the period.

After eliminating from the material variations extending over long series of years we can determine the existence of possible periods, and, in case they prove real, with an approximation dependent on the dominance of one of the periods in question for the variations in the yield of the fisheries, we can determine its constants by comparing it with a sine curve and calculating the correlation coefficients[1] between the catch values and values found by means of the sine curve, i. e. the function: $y = A \cos (nT - \varphi)$, A being the amplitude, T as above, φ the phase from a certain year (Y), and n the distance from Y of the year considered.

It cannot be concluded *a priori* that a periodicity in the stock of fish and the fisheries varies according to a sine function, and if this is not the case, a sine curve determined as the one the values of which give the highest correlation coefficient with the catch values, will rarely give the same phase and amplitude as a correlation calculation with values determined by the curve which the periodic variation in the fisheries tends to follow. The length of the period must be very nearly the same in both cases.

The length of the period is, however, in this investigation the most important of the constants for the periodic variation in the fishery, and values for phase and amplitude determined by a somewhat less exactness must be considered sufficient.

The material cannot be considered sufficiently exact for a determination of the question which periodic function is followed by the variation in the stock. Consequently, no attempt at such a determination has been made in this paper. We should more probably be able to decide the question by an examination of the causes of the period.

The reason why the values of the sine function have been chosen for comparison is that they are so easily determinable and that, provided the same constants, they are intermediates between the values of all theoretically possible periodic variation curves.

By calculating the correlation coefficient between the anomalies for the series of observations (the catches) and a sine function we get an exact means of deciding the question how large is the probability, that a periodic variation in the series of observations may be considered a reality.

[1] In the calculation was used PEARSON's formula:

$$r = \frac{\Sigma p \alpha_x \alpha_y}{\sqrt{\Sigma p' \alpha_x^2 \cdot \Sigma p'' \alpha_y^2}} = \frac{\Sigma ab - \frac{\Sigma a \cdot \Sigma b}{n}}{\sqrt{\left(\Sigma a^2 - \frac{(\Sigma a)^2}{n}\right)\left(\Sigma b^2 - \frac{(\Sigma b)^2}{n}\right)}},$$ and as test for the significance $t = \frac{r\sqrt{n-2}}{\sqrt{1-r^2}}$, and

P from Table IV, p. 139, in R. A. FISHER, 1930, where instead of n we should use $n - 2$. $P < 0.05$ is applied as a criterion whether the correlation is "significant" (l. cit. p. 45). a and b are paired deviations from an approximate mean, n number of paired variates.

2. The Stock of Plaice in the Eastern Part of the North Sea.

A. The Yield of the Fishery as a Representative of the Stock.

Up to the war the principal working field of the Danish plaice fishery in the North Sea was the stock of plaice of the eastern part of the North Sea as far as about 6° E. L., and the bulk of the catches were made in the Horns Reef Area and were landed at Esbjerg (cp. Fig. 1 and 2). That the fishing was intense is proved by the percentage of re-capture during the first year after the marking, this being about 50 per cent. in the area A 3 and about 30 per cent. in the area B 4, (i. e. the Horns Reef Area between depths of 10 and 20 metres, and of 20 and 40 metres, respectively) in the Danish and German marking experiments carried out in February—April (see A. C. Johansen, 1910, p. 131, and 1915, p. 21 ff.), and it may therefore be taken for granted that the fishery was representative of the size of the stock.

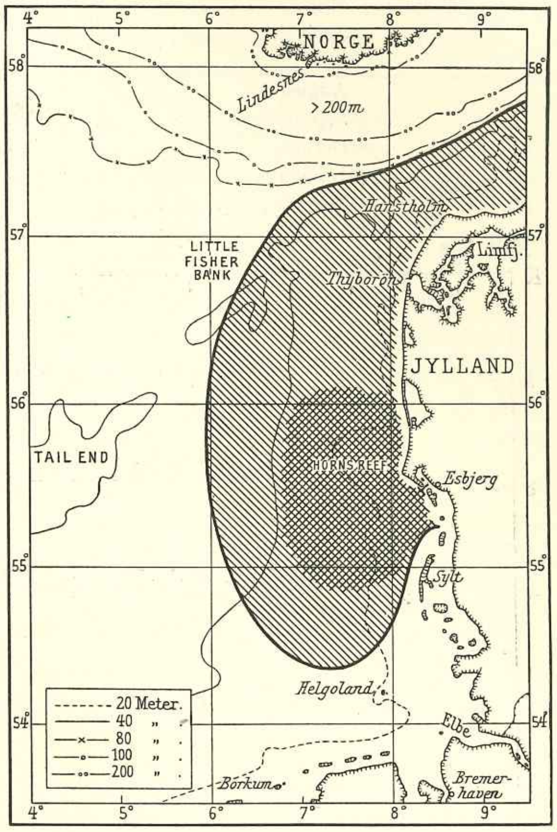

Fig. 1. Fishing grounds of the Danish plaice fishery in the North Sea during the first 10 years of this century (according to A. C. Johansen, 1910, and Dansk Fiskeritidende).
Hatching indicates extent of fishing areas.
Cross hatching most intensive worked areas.

During the war the conditions for the fishery in the North Sea were completely changed because of the mine barrier, etc., and the change in the market which was abnormal during the war and also during the first four years after the war. After the war a considerable part of the yield of the plaice fishery was taken from more remote grounds of the North Sea (Aage J. C. Jensen, 1931, 2, Fig. 7, p. 18).

From 1916 the haddock fishery has played a considerable part by the side of the plaice fishery and has employed a part of the cutters which has been changing from year to year (cp. Aage J. C. Jensen, 1931, 2, p. 17).

Thus, if only because of the uncontrollable alternation of the fishing intensity, the yield of the plaice fishery during and after the war is very difficult to reduce in a way so as to give an adequate expression to the size of the stock of each year (cp. Aage J. C. Jensen, 1931, 2, p. 23).

By the inquiry into the variations of the yield of the fishery we shall therefore in the first place confine ourselves to examine the yield of the plaice fishery up to the war.

The Danish plaice fishery in the North Sea is a seasonal fishery, before the war culminating in the months of March—June (cp. Table 1). Therefore the yield of the plaice fishery of 1914 cannot have been much reduced because of the war.

The yield of the Danish plaice fishery in the North Sea during the years 1892—1914 is shown in Fig. 2 and in Table 2. According to F. V. Mortensen and A. C. Strubberg, 1931, the Danish seine fishery from Esbjerg was begun in 1888—89. This caused a large increase in the yield in spite of the fact that the quantity of fish was decreasing (see e. g. Fr. Heincke, 1913). It is very difficult to provide any standard of the fishing intensity. So we must content ourselves with a normal curve the course of which cannot be accounted for in detail by measurable changes in the fishing intensity. In order to exclude too much subjectivity the normal curve has in this case been drawn with a uniform percentage rise. It is constructed in such a way that the sum of the percentage deviations of the catches from the normal curve is zero. The normal catch of 1892 being

Table 1. Monthly Distribution of the Yield of the Plaice Fishery (Sea Fishery) in Tons Landed at Esbjerg during the Years 1910—1914.

	1910	1911	1912	1913	1914
January	0	0	0	0	86
February	0	0	0	145	46
March	364	430	626	530	533
April	910	688	1792	1520	1097
May	1234	1308	1584	1242	1234
June	1005	662	1189	837	517
July	464	479	681	524	325
August	298	330	272	560	45
September	202	402	473	616	189
October	175	465	704	592	340
November	205	20	102	75	103
December	6	0	0	0	0

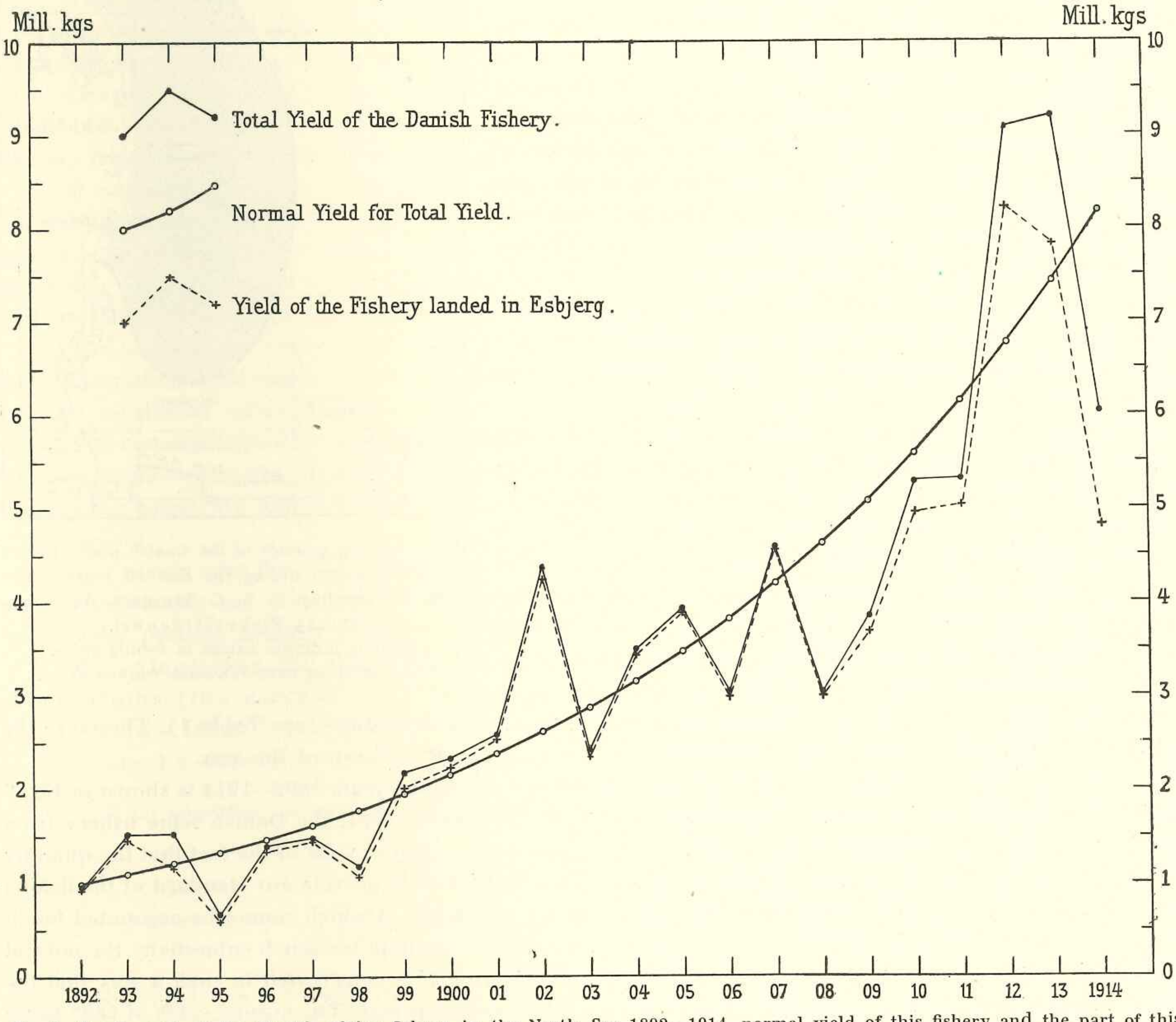

Fig. 2. Total yield of the Danish plaice fishery in the North Sea 1892—1914, normal yield of this fishery and the part of this fishery landed at Esbjerg.

put at 1 million kilogs, the rise of the normal curve will be 9.3 per cent. per annum. This curve in shown in Fig. 2.

By means of this normal curve is also eliminated part of the effect of the changes in the quantity of the stock, thus e. g. the constant decrease in the quantity of the stock which, apart from the fluctuations from year to year to be considered in this treatise, has taken place. This change is due to the intense fishing.

Table 2. Total yield of the Danish plaice fishery in the North Sea in metric tons. "Normal yield" of this fishery and percentage deviation from the normal.

Year	Total Yield	Normal Yield	Percent. Deviation	Year	Total Yield	Normal Yield	Percent. Deviation
1892	964	1000	— 4	1904	3495	3148	11
1893	1515	1100	38	1905	3930	3464	13
1894	1514	1211	25	1906	3021	3811	— 21
1895	679	1332	— 49	1907	4592	4193	10
1896	1412	1466	— 4	1908	3030	4613	— 34
1897	1489	1613	— 8	1909	3856	5076	— 24
1898	1182	1774	— 33	1910	5289	5585	— 5
1899	2170	1952	11	1911	5312	6145	— 13
1900	2316	2148	8	1912	9080	6761	23
1901	2566	2363	9	1913	9206	7439	24
1902	4381	2600	68	1914	6044	8185	— 26
1903	2402	2861	— 16				

B. Periodic Variations in the Yield of the Danish Plaice Fishery in the North Sea.

The deviations in percentage from the normal curve are presented graphically in Fig. 3 (curve A) and in Fig. 6 (continuous curves). The maximum deviation amounts to 68 per cent., the average being about 25 per cent.

Examining the curve of the deviations in percentage we note an apparent variation the length of the periods of which approaches 2.7 years.

We are now able to examine whether the period of 2.7 years may be considered a reality, and to examine the constants of the period by a determination of the constants of the sine curve showing the highest positive correlation coefficient with the curve of the catch anomalies (cp. p. 10).

The length of the period being about 2.7 years, the part of a period traversed during one year will thus be about 133.33°.

In the table are given the correlation coefficients between the percentage catch values and theoretical

Table 3. Correlation coefficients between percentage catch anomalies and values determined by a sine function with a length of period of about 2.7 years and varying phase.

$n = 128°$ 2.81 years		$n = 133°$ 2.71 years		$n = 134°$ 2.69 years		$n = 135°$ 2.67 years		$n = 139°$ 2.59 years	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
160	0.542	210	0.662	215	0.651	225	0.641	275	0.532
165	0.547	215	0.668	220	0.664	230	0.655	280	0.539
170	0.550	220	0.668	225	0.669	235	0.665	285	0.540
175	0.546	225	0.665	230	0.672	240	0.663	290	0.539
180	0.538	230	0.660	235	0.667	245	0.655	295	0.536

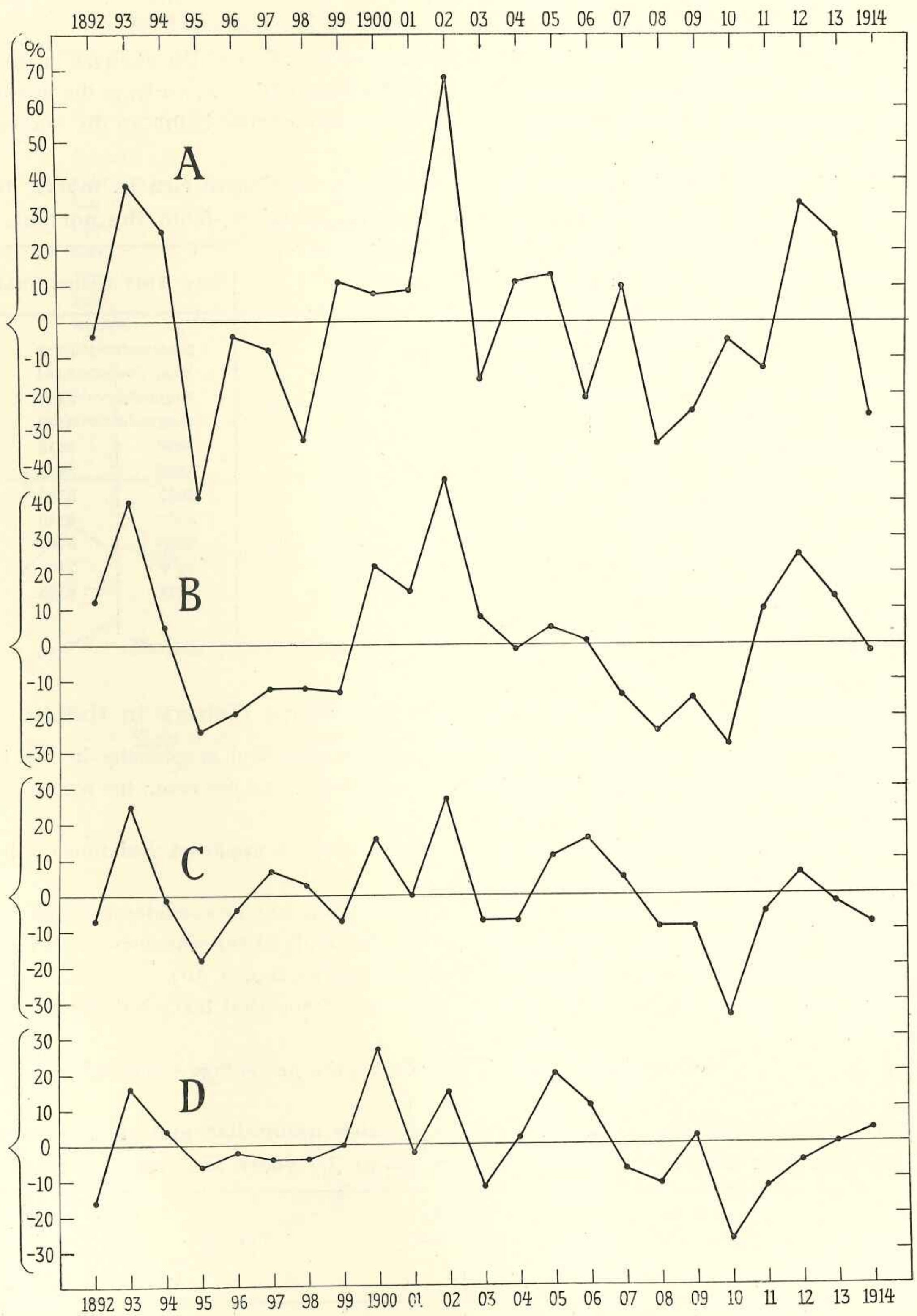

Fig. 3. A: Per cent. anomalies for the Danish plaice fishery in the North Sea.
B: $y = 25 \cdot \cos(134\,T - 230)$ eliminated from catch anomalies.
C: $y = 25 \cdot \cos(134\,T - 230) + 19 \cdot \cos 36\,T$ eliminated from catch anomalies.
D: $y = 25 \cdot \cos(134\,T - 230) + 19 \cdot \cos 36\,T + 12 \cdot \cos(75\,T - 37.5)$ eliminated from catch anomalies.

catch values deduced from sine curves with lengths of periods of about 2.7 years and a varying phase. The values are presented graphically in Fig. 4.

Within each of the series for the various n-values the maximum value for r is determined graphically, and in Fig. 5 these values are presented.

It will be seen that when we confine ourselves to whole degrees, the highest correlation coefficient $r = 0.672$ will be found for the value of $n = 134°$, $\varphi = 230°$. As t in this case is 4.16 and $P < 0.01$, the period is probably a reality. The amplitude A, determined as the regression coefficient (by the method of least squares), is found to be 25 per cent. In Fig. 6 A the values found from this sine function (the broken curve) is given and compared with the catch anomalies.

For all values of $r > 0.413$ the value of P will be less than 0.05, i. e. the correlation is significant. This is the case for all values of n greater than between 124° and 125° (length of period c. 2.9 years), and for

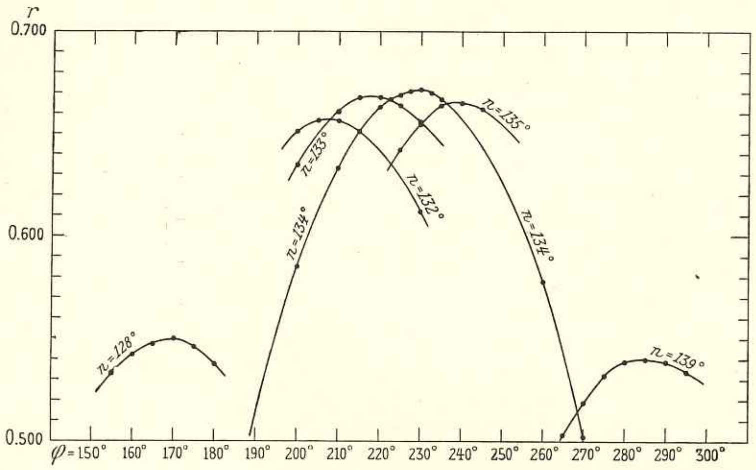

Fig. 4. Correlation coefficients between per cent. catch anomalies and values determined from sine functions with varying length of period and varying phase.

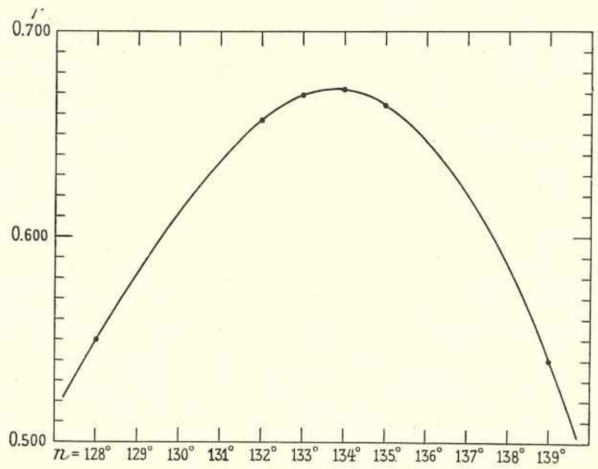

Fig. 5. Maximum values for the correlation coefficient between per cent. catch anomalies and values determined from sine functions with varying length of period.

n less than between 141° and 142° (length of period c. 2.55 years). The greatest correlation found between the catch anomalies and a sine function, where n is 120° (length of period 3.0 years) is $r = 0.22$.

In the curve, Fig. 3, A, showing the percentage catch anomalies, and in Fig. 3, B, showing the latter after the elimination of the values of the sine function found, will be noted a variation which, if periodic, has a length of period of about 10 years (where, consequently, n is about 36°) and a phase of about 0 years.

If we calculate the correlation coefficient between values found from the named sine function with a period of 10 years and catch anomalies where the sine function $n = 134°$, $\varphi = 230°$, $A = 25$ per cent., is eliminated (Fig. 3, Curve B), we get the result: $r = 0.733$, $A = 20$ per cent.; and a calculation of the correlation coefficient between the sine values of the 10 years period and the original percentage catch anomalies gives the result: $r = 0.517$, $A = 19$ per cent. In this case $t = 2.77$ and $0.02 > P > 0.01$, i. e. here, too, the correlation turns out to be significant. Finally, a calculation of the correlation coefficient between the sine values and catch values of the 10 years' period smoothed for each period of 3 successive years, where the 2.7 years' period is practically eliminated, gives the result: $r = 0.831$.

If we suppose the constants of the period of about 10 years to be: $n = 36°$, $\varphi = 0°$, and $A = 19$ per cent., and if we combine values determined from this period with the values determined from the sine function previously found, where $n = 134°$, $\varphi = 230°$, and $A = 25$ per cent., the curve found in this way must show a greater correspondence to the curve showing the percentage catch anomalies than the two sine curves separately, and a calculation of the correlation coefficients between the percentage catch anomalies and the combined sine function does give $r = 0.864$, $\sigma_r = 0.053$. It is shown in Fig. 6, B.

In the curve, Fig. 3, C, where also the 10 years' period is eliminated, is noted a rather characteristic

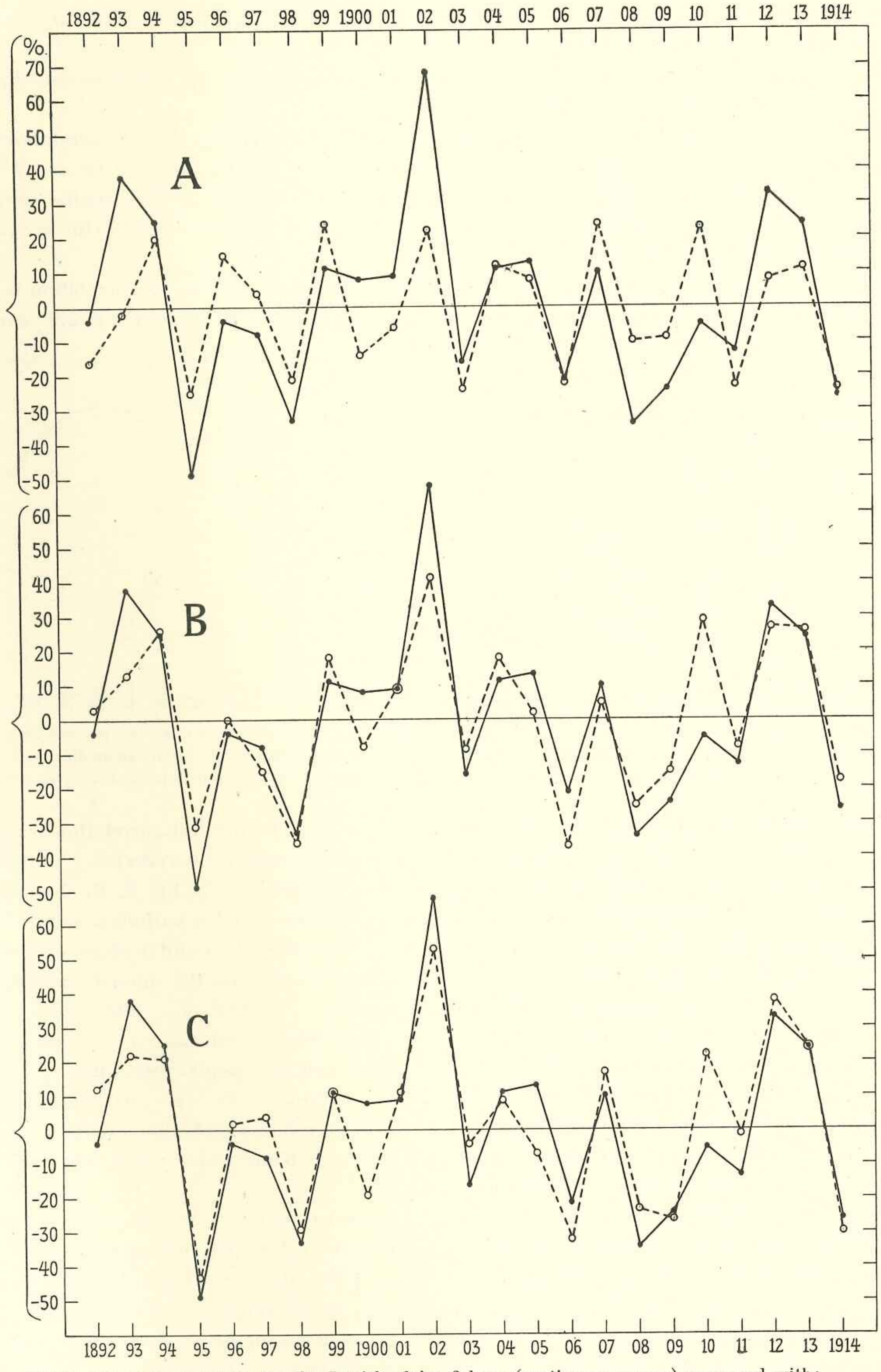

Fig. 6. Per cent. anomalies for the Danish plaice fishery (continuous curves) compared with:
in A: values determined from sine function $y = 25 \cdot \cos(134\,T - 230)$.
in B: values from sine function $y = 25 \cdot \cos(134\,T - 230) + 19 \cdot \cos 36\,T$.
in C: values from sine function $y = 25 \cdot \cos(134\,T - 230) + 19 \cdot \cos 36\,T + 12 \cdot \cos(75\,T - 37.5)$.

periodic variation where during 19 or 20 years can be counted 4 periods, and where consequently the length of the period is about 4.8 to 5 years.

If we determine the correlation coefficient between the "reduced" catch values shown in Fig. 3, C, and values found from sine curves with periods of 4.8 to 5 years, and if we choose the phase in such a way that there seems to be the best possible covariation between the values of the sine curve and the "reduced" catch values, we get e. g.:

for a period of 4.8 years; $n = 75.0°$, $\varphi = 37.5°$; $r = 0.463$; $t = 2.39$; $P = 0.03$
for a period of 5.0 years; $n = 72.0°$, $\varphi = 0.0°$; $r = 0.410$; $t = 2.28$; $P = 0.035$.

Consequently, the results of these calculations show that the correlation must be considered significant.

The reality of the period can be determined by another method of calculation, it being possible to eliminate most of the effect of the other periods without introducing considerable errors.

By a smoothing of the original percentage catch values for each 3 successive years the 2.7 years' period is practically eliminated, so that other periods, among which a possible 5 years' period, would be more dominant. By a smoothing for each 5 successive years a possible 5 years' period is eliminated, but at the same time a considerable part of the effect of the 2.7 years' period as well is eliminated, 5 being nearly a multiple of 2.7.

In the difference between the values of the two smoothed curves, we shall also have eliminated the outcomes of all fluctuations of a longer duration in the yield of the fishery that have appeared during the series of years in question, and thus we shall have disconnected the possible 5 years' period from the other dominant fluctuations.

If we calculate the correlation coefficient between these values, found as differences between the values of the smoothing for the 3 years' and the 5 years' periods, and values obtained from a sine curve with a period of 5 years, i. e., $n = 72°$, and if we put $\varphi = 0°$ (reckoned from 1892) we get $r = 0.498$; $t = 2.64$. And for $n = 75°$; $\varphi = 37.5°$ we get $r = 0.538$; $t = 2.92$. In both cases $0.02 > P > 0.01$.

Thus we may regard the period of about 5 years as a reality.

An attempt at determining the values for the constants n and φ which agree best with the original percentage anomalies in Fig. 3, A or the "reduced" percentage anomalies of Figs. 3, B and 3, C is hardly of interest because of the considerable error involved in a determination of the length of the period.

If we suppose the constants for the period of about 5 years to be $n = 75.0°$, $\varphi = 37.5°$ — the length of the period thus being 4.8 years — a calculation of the correlation between the original percentage anomalies and the sine function with these constants will give $r = 0.313$, and the amplitude 12 per cent.

If the sine curve with these constants is combined with the two sine curves previously determined, where the constants were $n = 134°$; $\varphi = 230°$; $A = 25$ per cent. and $n = 36°$; $\varphi = 0°$, $A = 19$ per cent., respectively, a calculation of the correlation between the values of the combined sine curve and the original percentage anomalies will give the coefficient $r = 0.890$; $\sigma_r = 0.043$ ($t = 8.9$). The values determined from this combined sine function are compared with the percentage catch anomalies in Fig. 3, D.

It should be remembered that the constants of each of the periods found involve some errors; thus the lengths of the periods of about 5 and 10 years were determined arbitrarily.

In Fig. 3, D is made an elimination of the values of the three combined sine functions.

It is seen that we could not determine the whole of the variations from year to year in the yield of the fishery by the sine functions found; nor could this be expected. The normal curve used in the calculation of the percentage catch anomalies was drawn arbitrarily with a uniform percentage rise and no doubt corresponds only roughly to the variations in the yield of the fishery which are due to variations in the fishing intensity, and to the alternations in the quantity of the stock which have taken place in the series of years considered and fall outside the periodic variation dealt with here. Besides, it should be kept in mind that the statistical statements of the size of the catch involve some errors, which veil the periodic variations from year to year in the yield of the fishery, although the greater part of these errors must be considered systematic ones.

How great a part of the fluctuations must be ascribed to the periodic variations appears from the fact that while the standard deviation[1] for the original percentage catch anomalies is 26.4 per cent., it is 12.3 per cent. for the "reduced" catch anomalies shown in Fig. 3 D, and thus we may reckon that abt. 55 per cent. of the fluctuations from year to year in the statistical statements of the yield are due to periodic variations.

By the curves Fig. 3, C, D it is seen that in the reduced catch anomalies there is possibly another periodic variation, these curves showing maxima in 1893, 1899—1902, 1905—09, and about 1914. The interval between the various maxima is thus 6 to 7 years. However, an ascertainment of the reality of the period cannot be based on the material in hand.

In the preceding we have shown that in the yield of the plaice fishery in the North Sea there is a period of 2.7 years and that there are probably two more periods of about 5 and 10 years, respectively. In the following we shall examine whether an explanation of the former period can be given on the basis of our present knowledge of the biology of the plaice, and whether there is a biological probability of the existence of the other periods found.

C. Fluctuations from Year to Year in the Yield of other Plaice Fisheries in the North Sea.

The yield of the plaice fishery of the other countries fishing in the North Sea cannot very well be compared to the Danish plaice fishery. In these countries are landed many small plaice below the Danish minimum, and, on the other hand, catches of large plaice from the open North Sea constitute a considerable part of the yield of the fishery (cp. e. g. Fr. Heincke, 1913). Hence the yield for these countries is more uniform from year to year than the Danish one, and is less influenced by the frequency of the various year classes.

For the years 1903—1913 the changes from year to year in the yield of the plaice fishery have on an average been for the English fishery about 7 per cent., for the German fishery about 10 per cent., and for the Dutch fishery about 9 per cent. above and below normal, the normal yield of the English fishery being put at an amount decreasing from about 14 million kilogs. in 1903 to about 7 million kilogs. in 1913, the yield of the German fishery being constant, and that of the Dutch fishery increasing from about 6 million kilogs. in 1903 to about 11.5 million kilogs. in 1913.

Other conditions influencing the variations from year to year in the yield of the plaice fishery, are therefore in the case of these countries of a comparatively far greater importance.

The Dutch fishery is the one that is most similar to the Danish fishery, 80—90 per cent. of the catch being taken on the nursery grounds (cp. Heincke, 1913, p. 32). It shows maxima in 1904—1905, 1907 and 1911, and minima about 1903, 1906, 1908 and 1912—1913. Thus it would seem possible here also to trace a periodic variation in the yield of the fishery with a length of period of about 3 years.

D. Discussion of the Causes of the Periods Demonstrated.

a. The 2.7 years' period. As mentioned in the survey on pp. 4 and 5 the cause of a periodic variation with a period of several years can be either of a hydrographical (terrestrial-cosmic) or of a purely biological nature. The terrestrial-cosmic causes may influence either the fishing intensity or the stock of fish.

[1] The formula $\sigma = \sqrt{\frac{n \Sigma pa^2 - (\Sigma pa)^2}{n(n-1)}}$ was used. n and a as in footnote p. 10; p number of identical variates.

That the 2.7 years' period found in the yield of the fishery, however, is due to a period in the stock of plaice appears from Fig. 7, where the yield of the Esbjerg fishery per "cutter day", i. e. the average catch per Esbjerg cutter per day in which fishing has been carried on from Esbjerg, is compared with the catch anomalies. As mentioned above (p. 8) we may be sure that the variations from year to year in the yield per fishing unit at any rate in the main are due to variations in the stock of fish.

As a matter of fact it is seen that the curves of the two graphs correspond to a considerable degree. The yield per "cutter day" expresses rather badly the yield of the fishery per fishing unit; far better is the expression per "fishing day", i. e. per cutter per day's fishing. These yields per "fishing day" from the few years for which statistic statements are available (A. C. Johansen, 1910, p. 18), on the basis of about 200

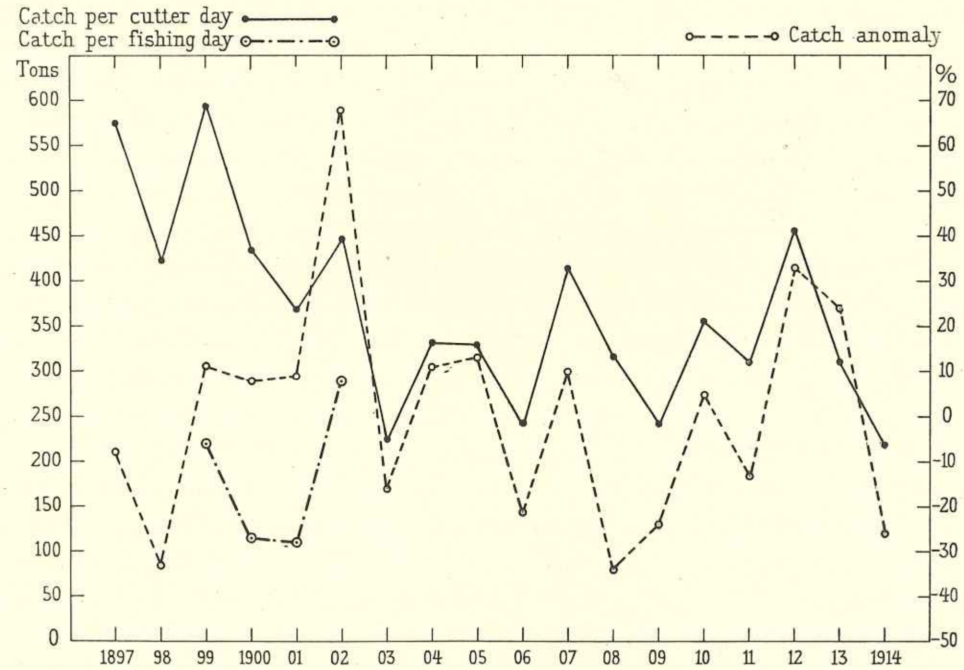

Fig. 7. Per cent. anomalies for the Danish plaice fishery in the North Sea compared with the yield of the Esbjerg plaice fishery per "cutter day" and per "fishing day".

fishing days or more, are also given in Fig. 7, and it is notable that they correspond much better to the percentage anomalies than the catches per "cutter day".

The hydrographical factors that may offer themselves, are temperature, salinity, and current. In order to ascertain whether the temperature, direct or through the quantity of food, influences the quantity of fry decisively during the development of the tiny fry, I have compared the variations in the salinity and temperature of the spawning areas in a certain year with the yield of the fishery some years later, viz., when the fry has grown up to constitute the part of the catch which determines the fluctuations in the yield from year to year.

Owing to the fact that the average age of the plaice which determine the variations from year to year in the yield undoubtedly has changed in the course of the years 1892—1914 (see later on), with the same displacement between the hydrographical factor and the catch, we can expect to find a covariation only for a short series of years.

As for the years considered we have no age analyses of representative samples of plaice landed at Esbjerg, so as to directly ascertain of which age groups the catches of the considered period were composed, we must, in order to obtain information on this point, examine the lengths of the plaice landed, in order to fix their approximate age.

From the period considered here, 1892—1914, we have determinations as to the length of the commercial plaice caught by the cutters in 1904, 1905, and 1906, when the average length was respectively 27.2, 28.1, and 27.4, the largest and the smallest plaice measured in the catches of the cutters being 22 and 45 cms., respectively, but most of the lengths ranging about the mean number between 24 and 30 cms. (A. C. JOHANSEN, 1910, pp. 36—37).

As the bulk of plaice of the III-Group of these years in course of the fishing season attain a length of 24 cms. during the summer growth, and the bulk of the plaice of the IV-Group had attained a length of 29 cms. (A. C. JOHANSEN, 1910, pp. 74—75), we note that the III- and the IV-Groups constituted the bulk of the catches of the cutters. If the yield of the fishery was determined by the production of fry some years before, and this again was influenced by the conditions of temperature and salinity during or immediately after the spawning period, a significant correlation between the catch and the hydrographical factors must be expected.

That possibly temperature is perceptibly influencing the mortality of the eggs is stated by EHRENBAUM, 1910, p. 8. As, however, the very year 1922, which was the richest spawning year after the war, had a very low temperature of water in February—March, it cannot be the principal cause of the variations in the frequency of the year-classes.

Moreover if the surface temperatures at Vyl and Horns Reef Lightships (Nautisk-meteorologisk Aarbog) in January—March are compared with the percentage anomalies of the weight yield of the Danish plaice fishery in the North Sea 3 or 4 years later, we cannot here trace any connexion between the temperature and the weight yield of the fishery, and further there seems to be only a slight tendency to a periodic variation from year to year with a length of period of abt. 2.7 years in the monthly mean temperature.

From the period of 1905—1914 only we have a sufficient number of observations of temperature from the very spawning areas. The most important spawning area of the North Sea is the south-western North Sea, but also the area S.E. of the Dogger Bank is of importance (cp. E. EHRENBAUM, 1910).

In the Table 4 below are shown the average anomalies of temperature in January, February and March, calculated from the anomalies for the various decades given in Bulletin hydrographique. La mer du nord, 1922, a) for Lat. 52°30′ N.—Long. 3°00′ E., which is situated within the most important spawning area, and b) for Lat. 55°00′ N.—Long. 6°00′ E.

Table 4. Average anomalies of temperature of the surface water near the spawning areas in the southern North Sea.

Year	1906	1907	1908	1909	1910	1911
a) at 52°30′ N. Lat. 3°00′ E. Long.						
January	— 0.2	— 0.6	— 0.8	0.5	— 0.1	— 0.2
February	0.2	— 1.8	0.0	— 0.8	0.2	0.1
March	— 0.3	— 1.1	— 0.6	— 1.4	0.4	— 0.2
b) at 55°00′ N. Lat. 6°00′ E. Long.						
January	0.0	— 0.3	0.0	0.1	0.1	0.0
February	0.1	— 0.3	0.4	0.4	— 0.6	0.6
March	— 0.2	— 0.6	— 0.3	— 0.3	— 1.4	0.1

If these anomalies are compared with the percentage anomalies of the weight yield of the Danish plaice fishery three or four years later (Table 2), it is seen that a positive correlation cannot be traced between temperature and catch. Thus this tends to show that if any at all, there is only a very slight causal connexion between the yield of the plaice fishery and the temperature during the period that is most critical to the fry.

The variations from year to year in the salinity at Vyl and Horns Reef Ligth Vessels seem to exhibit a tendency to a periodicity with about the same length of period as that found for the fishery.

A connection between the salinity and the frequency of the year classes most likely should be explained by the fact that the variations from year to year in the salinity are due to variations in the currents.

The currents must be supposed to highly influence the amount of fry as they carry eggs and fry from the spawning places to the nursery grounds.

While the spawning takes place mainly in January—February and culminates in the South-Western Bight of the North Sea during the latter half of January (BUCHANAN-WOLLASTON, 1926), we do not find the bottom stage of the plaice at the coasts of the south-eastern North Sea until the end of March and the beginning of April, and so we consider April, 1st the "birthday" of the plaice.

The currents of the southern North Sea vary highly from year to year.

The idea that the current is the main determining factor in the results of the different spawning years, was advanced by D. E. THURSBY-PELHAM, 1928, 2.

The variations from year to year in the salinity principally express variations of the current, but the error in the determination being so considerable in proportion to the size of the variations from year to year, they do not express the variations in the current very well.

The variations from year to year in the monthly mean salinity at the Vyl and Horns Reef Lightships are only few tenths of one pro mille. The systematic error in the monthly average of salinity may, according to J. P. JACOBSEN, 1908, p. 15 be estimated at 0.17 ± 0.3 pro mille, while the actual error of observation causes an error of only ± 0.05 pro mille in the monthly average. For each lightship the systematic error will generally vary in the course of time.

The direction of the wind no doubt affords a better basis of an estimate of the current, the force and the direction of the wind being the main cause of variations in the current. For the years 1924, 1925, and 1928 A. BÜCKMANN, 1930, p. 78 has compared force and direction of the wind with the frequency of these year-classes. He found that while conditions of the wind were unfavourable in 1924, there were in 1925 and 1928 favourable winds for a transport of the fry to the south-eastern North Sea. BÜCKMANN points to the fact that the principal spawning area in the South-Western Bight of the North Sea according to VAN GOOR and WULFF is situated in the Atlantic water, which is poor in plankton, and that it will therefore be of constitutive importance that the fry is carried to such a place where the water is mixed with the coast-water of the North Sea, which is rich in plankton. But apart from this it would undoubtedly be of no less importance to consider the mere question whether eggs and fry are carried towards the southern and south-eastern coasts of the North Sea or away from them.

It is hardly the right course to use the size and direction of the wind-gradient as an indicator of the current, the effects of the special directions of wind on the current being very different. An investigation of the effects of the wind on the current has been made by I. N. CARRUTHERS, 1926, p. 57, who found that a N.E. wind will hold up the current or will bring about a reversal of the current, while S. and W. winds will quicken the current.

As to the Horns Reef Area we have from the years 1919—1929 reliable information on the frequency of the year-classes. On Fig. 8 they are compared with the percentage frequency of winds partly from N., N.E. and E., partly from abt. S. and S.W. at the Horns Reef Lightship in February and at Yarmouth and Dungesness. A high degree of conformity is noted here.

For Dover Strait the effect of the N.E. winds, which inhibit the current, seems to be more pronounced than the effect of winds about the S.W., which quicken the current. Carruthers writes, "the records which, up to the present exhibits the most pronounced North Easterly movement was not associated with predominant South Westerly winds as might have been expected; in point of fact the actual winds at the time were devoid of any Easterly component" (CARRUTHERS, 1926, p. 61). It looks as if similar conditions hold good of the supply of fry in the Horns Reef Area. However, the observation data in hand will not settle the question.

We do not know the relative significance of the spawning area in the South-Western Bight and the one S.E. of the Dogger Bank for the supply of young plaice in the Horns Reef Area, but most likely the latter area is most important for the Horns Reef Area on account of the smaller distance.

The distance from the spawning area in the South-Western Bight to the western coast of South Jutland is 220—260 nautical miles, and BUCHANAN-WOLLASTON, 1926, found the rate at which the larvae of 1920—21 were drifting, to be between 18 and 37 nautical miles in 12 days or 1.5—3 miles in 24 hours. This nearly corresponds to the results of the measurings of current in this part of the North Sea. On an average we cannot allow for so swift a current off the East Frisian Islands. It appears from the direct current measurements (see FRITZ WENDICKE, 1913) and the English surface drift bottle experiments treated by I. N. CARRUTHERS, 1925, that the average rate at the surface is about 1.5—2 nautical miles in 24 hours between the Southern Bight and the coast of South Jutland and very slow at a depth of 10 metres and more. The time elapsed from the spawning of the eggs to the time when the plaice reach the bottom stage being about 2 or 3 months (cp. E. EHRENBAUM, 1910), they can on an average during this time traverse a distance of 90—180 nautical miles at the said rate, 1.5—2 nautical miles in 24 hours. In ordinary circumstances, therefore, only a very small part of the young plaice from the spawning area in the South-Western Bight will reach the western coast of South Jutland. It is not very likely that any great part of the plaice fry would be able to reach this place after having developed into the bottom stage on the way. But later in the year there is no doubt a certain immigration of the younger age-groups from the south into this area (AAGE J. C. JENSEN, 1928, 1, p. 10). The rapidity of current, however, changes so much from year to year, that we may state that in certain years rather a large quantity of fry can be carried to this place from the South-Western Bight, while in other years, when the current is slower or its direction is perhaps even reverse of that of the normal resultant current, practically no larvae are carried from the South-Western Bight to the western coast of South Jutland.

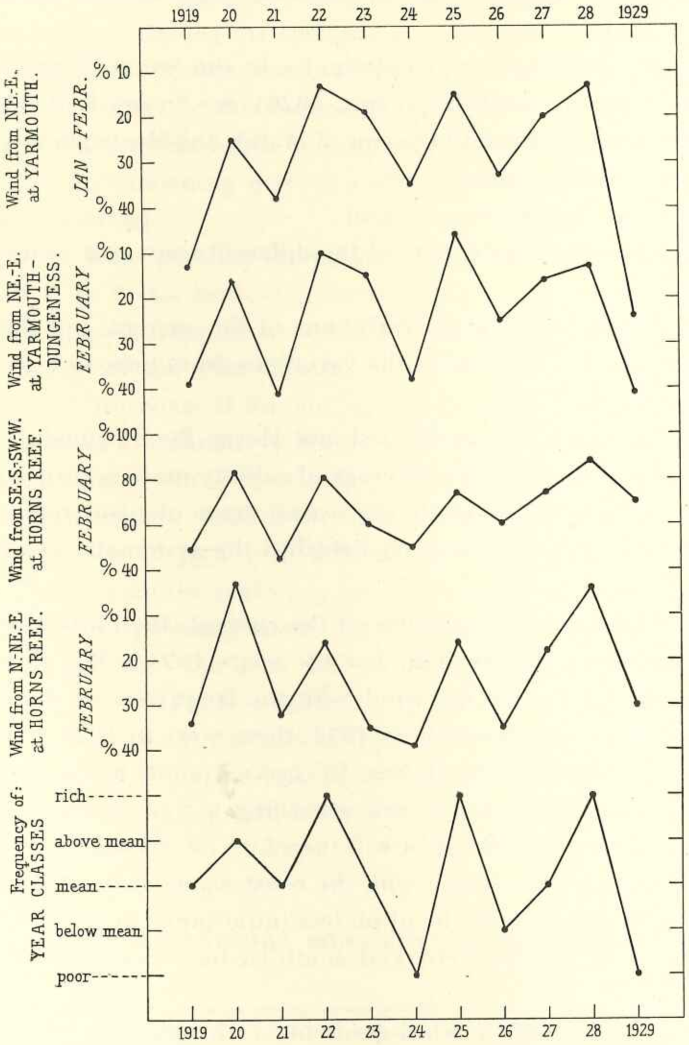

Fig. 8. The frequency of the year classes of the plaice in the Horns Reef Area 1919—1929 compared with the frequency of winds from round N.E. and round S.—S.W. in the southern North Sea in February (and Jan.—Febr.) of the same year.

As to the western part of the nursery grounds of the plaice in the southern and south-eastern North Sea off the East Frisian and the Dutch coasts we must no doubt pay special attention to the winds over the spawning area of the South-Western Bight.

The principal determining factor in the composition according to age-groups of the older plaice in this area is the quantity of fry carried to the Horns Reef Area and not an immigration of plaice older than the 0-Group from other areas. This appears from the fact that the relative frequency of the year-classes in this area seems to be fairly constant throughout the age-groups, at any rate up to the IV-Group, incl. (cp. AAGE

J. C. JENSEN, 1931, 2, p. 10), while there is a great difference between the Horns Reef Area and the other parts of the nursery grounds of the southern and south-eastern North Sea as to the composition in age-groups of the stock of plaice (AAGE J. C. JENSEN, 1928, 1).

The Danish post-war plaice fishery has covered vast areas of the southern North Sea and the yield must therefore to some degree be influenced by the relative frequency of the year-classes also in the western parts of the nursery grounds of the plaice. But in the years down to 1914 so great a part of the Danish plaice fishery in the North Sea took place within the Horns Reef Area (cp. Fig. 1), that the yield of the fishery must have been influenced to a considerable degree by the relative frequency of the year-classes within this special area. That the weight yield of the fishery is greatly influenced by the age-composition of the stock was shown directly by D. E. THURSBY-PELHAM (1930, p. 79) in an investigation of samples of commercial plaice.

Then the question suggests itself: is there in the frequency of the winds from the said directions a periodicity with a length of period similar to the one found in the plaice fishery?

Table 5. Frequency (per cent.) of winds from N., NE., and E. at the Horns Reef in February.

Year	Frequency	Year	Frequency	Year	Frequency	Year	Frequency	Year	Frequency
1880	6	1891	8	1902	23	1913	19	1924	39
1881	47	1892	35	1903	12	1914	3	1925	16
1882	13	1893	22	1904	37	1915	17	1926	35
1883	7	1894	12	1905	20	1916	24	1927	18
1884	17	1895	60[1]	1906	15	1917	13	1928	4
1885	10	1896	12	1907	24	1918	8[1]	1929	30
1886	39	1897	15	1908	18	1919	34[1]	1930	46
1887	20	1898	23	1909	36	1920	3[1]	..	..
1888	54	1899	21	1910	12	1921	32	..	..
1889	27	1900	31	1911	20	1922	16	..	..
1890	6	1901	36	1912	21	1923	35	..	..

[1] Observation from Fanø, Horns Reef failing.

From Fig. 9 and Table 5 where the frequency of winds from the N., N.E., and E. is given for the period 1880—1930, it is seen that during these 51 years we find 18 maxima; consequently the length of the period, if a period be demonstrable, must be about 51 : 18, i. e. about 2.84 years. If we put n at the nearest whole number of degrees, i. e. 126° or the length of the period at 2.86 years, and the phase, reckoned from 1880,

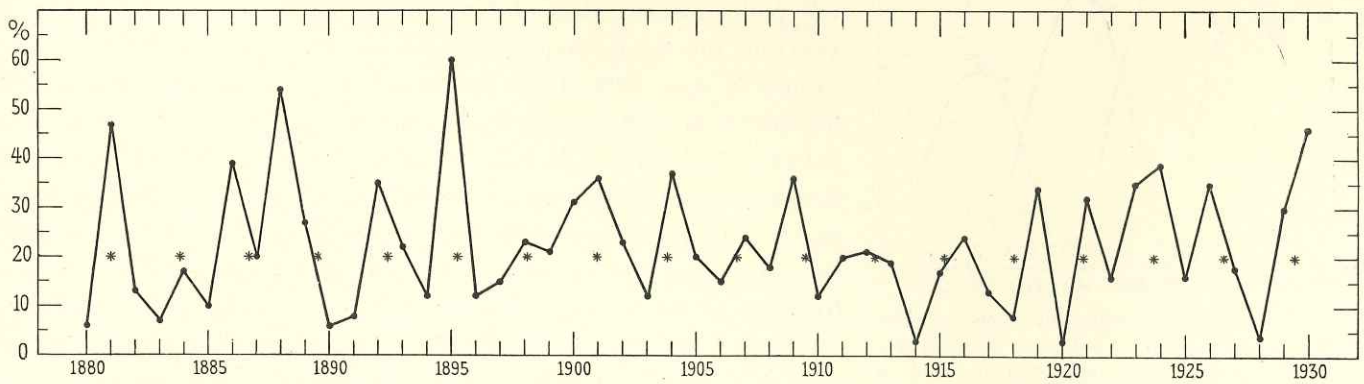

Fig. 9. Per cent. frequency of winds from N., NE., and E. at Horns Reef in February 1880—1930. Stars at intervals of 2.85 years.

at 126° and we correlate the percentage wind frequency and the values of the said sine function, we get the correlation coefficient $r = 0.38$ and $t = 2.85$. P being in this case < 0.01, the period of about 2.85 years in the wind frequency must thus be considered a reality. If we calculate the correlation between the wind frequency and the values of the sine function for the period 1889—1911 alone (a series of years shifted 3 years in proportion to the series for which the fluctuations in the yield of the fishery were examined) we get $r = 0.50$, $t = 2.7$, $0.02 > P > 0.01$, so that here, too, the period must be considered a reality.

This length of period, however, is so different from the one found for the yield of the plaice fishery, that in 23 years (the length of the series of years considered in the investigation) we have 8.0 of the 2.86 years' periods, while we have 8.5 of the 2.7 years' periods. So we see that if the two fluctuations vary by opposites about 1892, they run together about 1914.

The periodicity in the frequency of the various north-eastern winds is not, however, very marked and by examining various series of years we may find somewhat differing values of the length of the period.

The period between 1886 and 1912 is the one where the frequency of the wind may come into consideration as a determining factor for the catch of the period of 1892—1914, as, from our knowledge of the growth conditions of the plaice, we may consider the plaice of two years to be the youngest ones able to play an important part in the fluctuation from year to year of the yield, the oldest ones being plaice of about 6 years.

An examination of the correlation within this period between the frequency of N.E. winds and values determined by sine functions with varying length of period and phase will give the values shown in Table 6 and Fig. 10.

Table 6. Correlation coefficients between frequency of winds from N., N.E., and E. at the Horns Reef in February 1886—1912, and values found from sine curves with varying period and phase (reckoned from 1880).

$n = 110°$		$n = 115°$		$n = 120°$		$n = 125°$	
φ	r	φ	r	φ	r	φ	r
190°	0.436	230°	0.439	300°	0.355	40°	0.371
220°	0.450	260°	0.502	330°	0.466	70°	0.393
250°	0.338	290°	0.471	360°	0.444	100°	0.320

The highest value for the correlation coefficient, $r = 0.502$, where $t = 2.90$ and $P < 0.02$, is found for $n = 115°$. For the years 1886—1912 the period within the frequency of wind thus shows the best congruity with a sine curve with a length of period of 3.13 years.

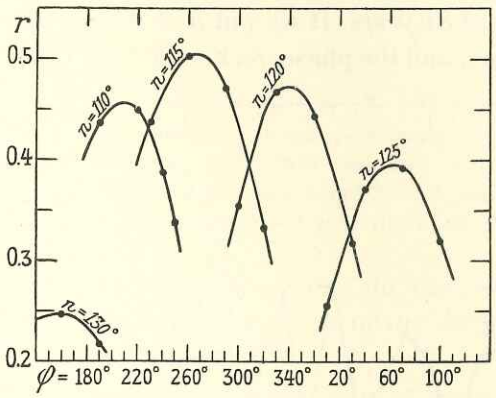

Fig. 10. Correlation coefficients between frequency of winds from N., N.E., and E. in February at Horns Reef and values determined from sine functions with varying length of period and varying phase.

In spite of the great difference between the length of period found in the frequency of wind and the one found in the yield of the plaice fishery it is still probable that in the period of abt. 3 years in the wind frequency we have the cause of the 2.7 years' period in the yield of the plaice fishery. This possibility is due to the fact that there has not always been the same distance of time between the spawning years determining the yield of the catch and the year the catch of which we consider. For the North Sea we have no observation data by which to follow the changes in the composition of the stock in age groups as, e. g., we have been able to do in the case of the Kattegat and the Belt Sea (cp. Aage J. C. Jensen, 1931, 1, p. 35 and foll.). In all areas where the influence of an intense fishing on a stock of plaice could be traced, we have seen that the stock at the same time turned into a fast growing one, and that the commercial plaice are constantly recruited from younger age-groups while the older age-groups become comparatively rare. Similar conditions must have prevailed in the North Sea during the period 1892—1914. We must therefore suppose the distance of time between the catch of 1892 and the spawning years determining the variations from year to year about 1892 to have been somewhat longer than that between the catch of 1914 and the spawning years determining the variations from year to year about 1914.

It must be remembered that the variations from year to year in the catch are mainly determined by the intensity of the recruiting, i. e. indirectly by the frequency of the year classes some years before.

If we make a direct comparison between the variations from year to year in the frequency of the north-eastern winds and the consequent variations of the catch, we must therefore allow for the fact that the shifting of phase between variations in the frequency of winds and catch, during the first part of the period the catch of which we consider, viz., at the beginning of the nineties, was greater than at the end of this period, i. e. the second decennium of this century.

As mentioned above (p. 21) it is possible to directly demonstrate a distinct co-variation between the frequency of N.E. winds and the quantity of fry for the years 1919—1929 for which we have determinations of the relative frequency of the year-classes in the southern Horns Reef Area. It will now be of importance to examine whether the variations from year to year in the yield of the fishery are directly dependent on these variations in the quantity of fry.

The variations from year to year in the yield, which may possibly be due to the variations in the frequency of the year classes, become more distinct if we calculate the deviations between the catch of each year and values determined by a smoothing of the catch for three years.

The catches smoothed for three successive years, with the corresponding catch anomalies are:

Table 7. Catches of plaice landed at Esbjerg from the Danish sea-fishery, in metric tons, smoothed for three years, and with per cent. catch anomalies.

Year	Catch	Catch smoothed for three years	Percentage catch anomalies	
			above normal	below normal
1920	3445	3213	7	..
1921	1333	2435	..	45
1922	2527	2449	3	..
1923	3488	3271	7	..
1924	3798	5460	..	30
1925	9094	7561	20	..
1926	9790	8686	13	..
1927	7175	9882	..	27
1928	12682	11923	6	..
1929	15913	14603	9	..
1930	15214	abt. 16500[1])	..	8

[1]) 13804, according to statistics published later.

The average growth of the plaice in the Horns Reef Area — as in other parts of the North Sea — was considerably slower during the first years after the war than before the war; for according to KIRSTINE SMITH, 1923, p. 27 the various age-groups (in numbers) constituted the following percentages of a sample of commercial plaice taken in the spring of 1922 in the southern Horns Reef Area (at a depth of 28 metres): II: 19, III: 49, IV: 24, V: 7, VI: 1, ?: 1.

Thus, in spite of the change in the rapidity of growth, the III- and the IV-Groups were dominant as regards weight in the recruiting of the stock of commercial plaice.

This has been the case, too, during the years after 1922, which appears from the fact that plaice of about 20—25 cms., i. e. the plaice that recruit the stock of commercial plaice, in the spring made up a principal part of plaice of the III- and IV-Groups (AAGE J. C. JENSEN, 1928, 1, and 1931, 2). The average length in the autumn is but badly representative of the length of the plaice that have been of importance for the fishery, as they only constitute the part left of the stock after the fishery has taken its part.

We may give numerical values to the frequency of the year classes during the years after 1920 by using for the years down to 1925 the degrees of frequency which I was able to find (AAGE J. C. JENSEN, 1928, 1, p. 27), and for the years after 1925 my later determinations of the relative frequency of these year classes (1931, 2, p. 10). It is true that the relative frequency of the year classes as mentioned is different in the different parts of the nursery grounds of plaice fry in the southern North Sea, and the yield of the Danish plaice fishery landed at Esbjerg is to some degree dependent also on the stock of plaice growing up in the other parts of the nursery grounds of the southern North Sea. This Danish plaice fishery has, however, for the most part been carried on within the area the population of which is recruited from the nursery grounds of the southern Horns Reef Area, so that the yield of it must be supposed to have been mainly dependent on the quantity of fry derived from this area.

The relative frequency of the various years then shows the following numerical values:

Year class	Relative frequency	Numerical value	Year class	Relative frequency	Numerical value
1919	mean	3	1925	rich	5
1920	above mean	4	1926	below mean	2
1921	mean	3	1927	mean	3
1922	rich	5	1928	rich	5
1923	mean	3	1929	poor	1
1924	poor	1			

As we have seen above, two year classes constituted the catches of plaice, viz. the III- and the IV-Groups, and it will be necessary, in order to find the relative values for the quantity of fry determining the variations from year to year in the frequency of the year-classes, to calculate mean numbers for the amount of fry for each two successive years.

In doing so and comparing the yield of the plaice fishery with these numerical values for the quantity of fry three or four years before, we find the connexion shown in Fig. 11. It is seen that there is a very distinct connexion between the amount of fry and the catch some years later.

There is, however, a very long way from the wind frequency to the yield of the catch some years later, so that many factors will interfere with an ascertainment of the connexion by means of a correlation calculation. One of the principal interfering factors is the rapidity of growth, which varies from year to year, and which is determined among other things by the competition for food among the plaice.

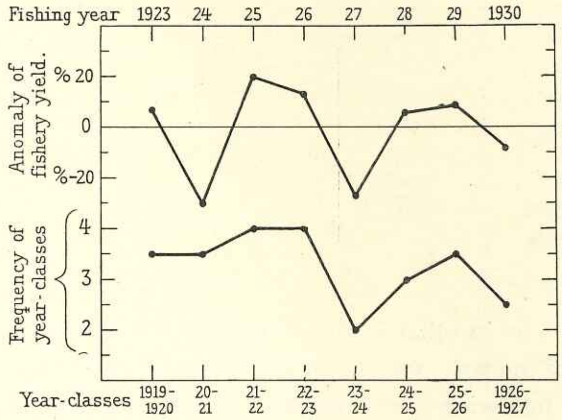

Fig. 11. Anomaly of the yield of the Danish cutter plaice fishery landed at Esbjerg (difference between catch and a 3-years' smoothing) compared with frequency of the year-classes 3—4 years before.

The competition for food among the youngest year classes will tend to emphasize the period of abt. 2.7 years. As pointed out below there is a rather considerable uniformity in the food of the 0-Group and the I-Group, as the principal food of the 0-Group after June—July and of the I-Group beside small *Polychaetes* consists of *Cumaceae, Amphipodes,* and crab larvae. Consequently, by consuming the animals on which the 0-Group was to live a numerous I-Group may render difficult the nutrition conditions of the former group, and accordingly cause that a large number of these plaice perish. On account of their much larger size the plaice of the I-Group consume much more food than the 0-Group. If this is the case, two rich year classes will rarely succeed each other, but on the contrary a specially rich year class is often followed by a specially poor one. In fact, this seems to be the case; thus the year classes 1926 and 1929, which succeeded the rich years of 1925 and 1928, respectively, were comparatively poor. Our knowledge of the relative frequency of the year classes is, however, still covering too few years for the decision of the question whether this be a common feature or not. Of course the competition for food is strongest among plaice of the same age-group, and the inhibition of growth within a dense 0-Group can be directly demonstrated as shown by H. BLEGVAD, 1927, 1, p. 15. Only the year class succeeding the inhibited one will be able to develop at liberty, but, as we have seen above, it depends on the frequency of certain wind directions which of the following will develop strongly. The condition in question will therefore tend to produce a periodic variation in the stock with the length of rather more than two years and will thus emphasize the periodic variation which is due to the period of about three years in the meteorological conditions, but at the same time it will disturb the narrow co-variation between the frequency of winds about the N.E. and the yield of the plaice fishery and thus make the direct demonstration of the connexion difficult.

These conditions of competition do not correspond to the one treated by VOLTERRA, 1928, § 2, where two species prey on the same food, and one is inhibiting the other by having a higher coefficient of increase, and where periodic fluctuations cannot ensue. For in the present case the age-group corresponding to the inhibited species will in one year grow to be inhibiting the next age-group.

These effects of the competition for food on the part of the youngest age-groups on the composition of the population may, however, be considered a special case of the association of two species treated by VOLTERRA, 1928, § 3, one of which feeds on the other. Thus the influence of the I-Group on the 0-Group will be much the same as that of the I-Group living directly on the 0-Group. Matters are, however, somewhat different, as the I-Group does not, like the species living on the other, in the case treated by VOLTERRA, decrease in number, because it has reduced too much the quantity of food (i. e. the other species) available for the species, but because it grows up and changes its food matter.

The series of years for which it is possible to determine the relative frequency of the year classes, i. e. the years after 1919 (AAGE J. C. JENSEN, 1928, 1, p. 24 ff., 1931, 2, p. 7 ff.) is too brief for a direct decision of the question whether in the quantity of fry there is the said periodicity of about 3 years, but as the rich spawning years of the plaice in the southern Horns Reef Area fall in 1920, 1922, 1925, and 1928, and the poorest in 1921, 1924, 1926, and 1929 or 1930, we see that in the quantity of fry, as well as in the frequency of the considered directions of wind during these years, there is a period of nearly 3 years in length. The fact that a similar length of period is found also in the rapidity of growth of the plaice in the Horns Reef Area determined by marking experiments during the years 1903—1912 (AAGE J. C. JENSEN, 1931, 2) is also in favour of this explanation of the 2.7 years period being correct, because the rapidity of growth, as mentioned below, is greatly influenced by the density of the stock, and the latter fluctuates more or less parallelly to the frequency of the year classes.

After the war, too, the period of about 3 years in the frequency of the plaice fry is very distinct in the yield of the fishery, especially in the yield of the sea-fishery which mainly takes place on the nursery grounds, i. e. the cutter fishery the yield of which is landed at Esbjerg. This is shown in Table 7.

In an examination of the question whether we can demonstrate a connexion between the quantity of fry and the yield of this fishery some years later, it should be kept in mind that the yield up to 1922 incl. was very small on account of the slow market. The very rapid increase from 1924 to 1925 and the high yield of the next years are no doubt due to the year classes 1919—1923 being comparatively rich (AAGE J. C. JENSEN, 1928, 1), while the continuous rise in the yield of the fishery of the years 1925 to 1930 must be ascribed mainly to a rise in the fishing intensity stimulated first and foremost by the decreasing working expenses of the fishery, and also by the fact that the stock of fish constantly during this period proved abundant and therefore a profitable working object for the fishery, although, on the whole, the stock of commercial plaice was decreasing during the period (AAGE J. C. JENSEN, 1931, 2).

Table 7 shows that the yield approaches a maximum in 1922—23, the difference between the catch of each of these years and that of 1921 being greater than respectively $^1/_3$ and $^2/_3$ of the difference between the catches of 1924 and 1921. A distinct maximum is found in 1925—26 and in 1928—29, while the year

1930, as compared with 1929, shows a comparatively slight rise. These variations present themselves distinctly in a calculation of the difference between the catch and values determined by a three years' smoothing. The differences, too, are shown in Table 7.

The yield of the haddock fishery from Esbjerg shows the opposite variation in the years after 1923, but this is due to the fact that the cutter fishery is divided between plaice and haddock fishing, although in such a way that the plaice fishery is the principal one. Thus the greater or smaller yield of the plaice fishery is determinative of the intensity of this haddock fishery (cp. AAGE J. C. JENSEN, 1931, 2, p. 17).

b. The period of about 5 years. The determined period in the yield of the plaice fishery can hardly be ascribed to physical causes, as I have not been able to demonstrate any period in the physical conditions of the North Sea of about this length. Further, it is out of the question that it should be associated with the periodicity of about 3 years in the stock of plaice.

So we shall have to examine whether it may be due to purely physiological causes.

It is seen at once that the period is not due to the average age of maternal plaice of each single year class of the plaice (about the same as the average age of mature female plaice, yet approximately only because the older plaice produce comparatively much fry), this being on an average 6—7 years.

As to the 0-Group we may suppose that an inhibition of the growth may result in a comparatively high mortality. But this is hardly ever the case with the I-Group and older groups. We shall, however, examine the question whether changes in growth brought about by variations in the density of the population may produce a periodic variation of about 5 years. We might very well assume the existence of a direct dependence of the yield of the fishery of the following autumn on the rapidity of growth during the summer (cp. A. C. JOHANSEN, 1910, p. 76). This is not the case, however, as appears from a comparison between growth and yield of the fishery (AAGE J. C. JENSEN, 1931, 2, p. 21).

In order to ascertain how far it is possible for an age-group of plaice to influence the growth conditions of the plaice of other age-groups, we must examine in how far plaice of the different age-groups compete for food.

While the first bottom stages from April to July nearly exclusively feed on small *Polychaetes* and *Harpactides* they will already about July begin to eat small bivalves and *Gasteropods, Amphipodes* and *Cumaceae* (*Diastylis*) besides *Polychaetes* (cp. V. FRANZ, 1910, M. V. LEBOUR, 1920, and A. SCOTT, 1922).

As to the I-Group a more considerable part of the food consists of molluscs, the bulk of it, however, being still *Diastylis,* crab larvae, and other small *Crustaceae.* Not until they attain a length of about 20 cms. do the plaice mainly feed on bivalves (V. FRANZ, l. c.). On an average this length is attained as II-Group (AAGE J. C. JENSEN, 1931, 2, p. 25).

The mussels which for the II-Group and older plaice become the chief food matter, are especially *Nucula nitida, Mactra subtruncata, Syndosmya alba,* and *Corbula gibba.* Occasionally they take gasteropods and some few fish, further comparatively large quantities of *Pectinaria* and *Amphiura filiformis.* The larger the plaice grow, the greater is the importance of the molluscs as food matter (R. A. TODD, 1915).

According to FRANZ, l. cit., *Corbula gibba* are mainly consumed by plaice below 20 cms., whereas plaice of 30—40 cms., etc., up to the very large ones, seem to prefer *Mactra subtruncata.* For the plaice of 40 cms. and upwards large crayfish constitute the bulk of the food.

At no definite age or size is there any break in the choice of food matter, and from one age-group to another there is nowhere any essential difference in the kind of animals chosen for food, the less so, as the length of the different age-groups overlap. A rather sudden change, however, takes place after the second year of life, when the food of the plaice changes from being principally small *Crustaceae* to being mainly bivalves, whereas the 0- and the I-Groups to a somewhat higher degree have food animals in common, the 0-Group in the summer beginning to take considerable quantities of *Cumaceae.* This difference in the choice of food of the younger age-groups is the more marked, as these age-groups are overlapping to a slight degree only as regards length.

The chief place of occurrence of the various age-groups changes in an off-shore direction during early summer (May—June), i. e. at a time of the year when the growth is very rapid and the plaice are feeding intensely. As generally an older age-group live in somewhat deeper water than the nearest younger one, a vigorous year class may consume the food on which the following one would have to live, and in this way check its growth considerably. A migration of the plaice towards shallower water does not take place until September or October.

As will appear from the above considerations, the I-Group will presumably to some degree be able to influence the growth of the 0-Group, whereas the II-Group influences the I-Group to a less degree. A vigorous III-Group will possibly influence the growth of the contemporary II-Group, and a vigorous IV-Group may check the growth of the contemporary III-Group and, to a less degree, of the contemporary II-Group, whereas the V-Group only to a slight degree checks the growth of the contemporary IV- and III-Groups because it emigrates from the place. However, the plaice of one year class compete for food among themselves to a still higher degree than they compete with other age-groups.

A comparison between the proportional frequency of two year classes in two successive years, i. e. of the two groups at the same age, and the difference in their mean length has shown that the mean length of the plaice of any year class is to a very great extent determined by the number of individuals within the age-group. (Aage J. C. Jensen, 1928, 1, p. 33, and 1931, 2, p. 12). In other words, an examination of the same age-group of two year classes will show that the plaice of the richer one are of the smallest average length, and, consequently, have been growing less rapidly.

This checking effect on the growth caused by the density, which is most active in the case of the most numerous year class, is also clearly seen in the Figs. 8, 9, and 10 published by Thursby-Pelham, 1928, 1, pp. 42—47, where the rich year classes 1920 and 1922 are characterised by drops in the average length. Thus we may state as a fact that a large stock will have a checking effect on the growth, and in this way will further increase the population of the nursery grounds. As the rich year class, which is the actual cause of the accumulation, grows to become commercial plaice and partly is decimated by the fishing, partly emigrates from the nursery grounds which the plaice leave in considerable numbers, when they attain a length of about 26 cms. (Aage J. C. Jensen, 1931, 1, p. 13), the competition is relieved considerably, and beside the fact that the normal growth would cause a comparatively great recruiting of the commercial plaice, the recruiting increases considerably, as the competition for food is relieved, because the much consuming older plaice (about 5 years old) disappear from the nursery grounds, and hence the growth of those left increases. The rapid growth causes a great increase in the number of the commercial plaice for a year or two, but this causes the stock growing up afterwards to become comparatively sparse and to produce a smaller yield of fishery in the following years (1, 2, or 3 years) in spite of a comparatively rapid growth, until a new rich year class causes a check of the growth. This fact will cause a periodic variation in the yield of the fishery of about 5 years in duration which, however, because of the complicated nature of circumstances cannot be expected to be very conspicuous. For certain areas of the Limfjord H. Blegvad, 1926, 1, p. 50 has been able to demonstrate a distinct connexion between the quantity of plaice food and the yield of the flat-fish fishery, and A. Hagmeier, 1930, has pointed out that the great fluctuations occurring from year to year in the quantity of plaice food in the North Sea possibly influence the growth of the plaice considerably.

No doubt there are variations from year to year in the quantity of plaice food due also to causes independent of the size of the stock of plaice (physical factors and the amount of other consumers), and these variations will also tend to veil the said 5 years' period.

c. The period of about 10 years. Because of the fact that the material comprises a series of years only a little longer than twice the length of the period, the general validity of this period is very uncertain. Possibly it is only due to an error in the drawing of the normal curve.

d. A possible period of 6 or 7 years. It has been pointed out that after the elimination of the period mentioned in the above sections we might possibly still find a periodic variation 6 or 7 years in length, but that the existence of this variation cannot be ascertained. Such a period would be of interest as, on account of its length, it would be naturally explained as a consequence of the effect of the number of spawning plaice on the quantity of fry produced, and hence on the number of plaice in the following years. For plaice in the North Sea arrive at the maturity stage at an age of about 5 years, and the spawning plaice must be supposed to be of about this age[1]. It should be noted that if this cause of periodic variations has at all influenced the changes in the yield of the plaice fishery during these years, it has at any rate played quite an inferior part during the years 1892—1914.

This cause of fluctuations in the fishery seems to have been of special importance in the fluctuations of the stock of plaice after the war (Aage J. C. Jensen, 1928, 1, p. 29).

3. The Stock of Plaice in the Southern Kattegat and the Belt Sea.

A. Catch Figures for the 0- and 1-Groups of Plaice.

As regards the stock of plaice in the southern Kattegat and the Belt Sea we have in the quantitative fishing experiments on plaice fry of the 0- and I-Groups quite another kind of material for the investigation of the variations in the population of a certain area.

Such quantitative investigations of the youngest age-groups at our coasts were started in the beginning of the nineties by C. G. Joh. Petersen (1893, p. 5, and 1894, p. 10 ff.) and Apstein (1905) but only since 1905 they were carried on annually by a uniform method by A. C. Johansen (cp. 1908, 1, and 1927, 2). The catches were made with a fine-meshed otter trawl of a certain size in fishing experiments during the summer months along the coasts at depths of about 2 metres.

The Area. The area considered represents a unity within the stock of plaice. The marking experiments within this area and the adjacent ones have shown that there is only a very inconsiderable emigration from the area and that at any rate during the years up to 1911 a very inconsiderable immigration took place to the area of the sizes of plaice that are marked, i. e. plaice of above 20 cms. As mentioned below there has hardly been any material immigration of the younger age-groups or influx of fry with the possible exception of the southern Kattegat.

The Catch Figures. On the basis of the average catches per hour of the 0- and the I-Groups of the plaice A. C. Johansen, 1927, 2, computed "catch figures" as the sum of the average catch of the 0-Group and 3 times the average catch of the I-Group. Such "catch figures" for the quantity of the fry have been used here because they are likely to express the relative frequency of the year classes in a better way than the quantity of the 0-Group alone.

Against the application of catches of the I-Group in the estimate of the frequency of the year classes A. Bückmann, 1930, has objected that fishing experiments with the young fish trawl at the coast do not, perhaps, give the representative values of the I-Group with so great exactness as in the case of the 0-Group. This is undoubtedly correct, but as the average catch of plaice of the I-Group is only 3 times smaller than that of plaice of the 0-Group, and as we must take into consideration a very high natural mortality within the 0-Group, we cannot suppose the catch values found for the I-Group to be much more misleading than those found for the 0-Group. Moreover, on account of this mortality of the 0-Group undoubtedly varying from year to year, the numerical size of the I-Group is a better expression for the amount of plaice which some years later forms the stock of commercial fish. Finally there is so great an uncertainty in the calculation of the mean number for the quantity of the 0-Group that an increase of the material by the inclusion of mean numbers for the I-Group must be supposed to give a value for the quantity of fry that is more correct than the mean number for the quantity of the 0-Group only.

[1] Attention must be paid to the fact that a larger plaice produces more fry than a younger and smaller one.

As to the Kattegat and the Belt Sea ANTON FR. BRUUN, 1927, has pointed out the fact that in some cases the quantity of the 0-Group and that of the I-Group of the following year do not correspond. He supposes this to be due to the immigration of plaice of the I-Group changing from year to year. Hence the 0- and the I-Groups would possibly express two different things: the 0-Group being in the main representative of the production of fry in the Belt Sea and the I-Group of the immigration of the I-Group.

As BÜCKMANN (1930, p. 70) has pointed out, too, there is a so great uncertainty about the quantitative determinations of the 0- and the I-Groups that this may easily explain the want of correspondence between the quantities of the two age-groups, and a considerable immigration from the north would result in a more pronounced change in the race character from 0- to I-Group than the actual one. This change is so small, that in all probability it does not exceed the systematic error which must no doubt be found in a determination of the racial character (the number of the anal fin rays) when they are determined without a previous staining.

Only to a small part of the area considered, viz. to the southern Kattegat, and especially to the Aalborgbugt, there may probably be a perceptible immigration of plaice of the I-Group from the north like the one proved to take place from the Tannis Bay to the Aalbæk Bay (A. C. JOHANSEN, 1910).

The variations in the number of the plaice of the 0-Group and in the catch figures coincide so exactly, that the correlation coefficient between the two series within the years 1904—1930 is $r = 0.94$, calculated for 17 years on the basis of the revised catch figures given below in Table 8.

In practice the possibility of enlarging the material by including determinations of the relative frequency of the year classes on the basis of catches of the I-Group will be of great importance, the material thus extending over more years.

It is seen from Table 8 that for some years we have only catches of plaice fry from the southern Kattegat, for other years from the Belt Sea, and that on the whole the proportion between the number of stations within the two areas varies greatly from year to year. A direct combination of figures from two areas situated so wide apart is of course permissible only if the catches are of fairly the same size. For nine years both areas have been examined by fishing experiments to such an extent, i. e. with more than 20 stations within each area, that the catches of plaice of the 0- and the I-Groups must be considered fairly representative. On an average for these years the catches of the 0-Group in the southern Kattegat and in the Belt Sea were 17.2 and 16.2, respectively, and those of the I-Group 4.0 and 6.0, respectively. It is seen that the areas are so nearly alike that a combination is permissible. The difference of 2.0 individuals between the I-Group of the Belt Sea and the I-Group of the southern Kattegat is so slight, that it must be estimated to fall within the margin of error.

For the different years the fishing experiments at the coasts have been carried out to a very different extent. From one or two years we have very few fishing experiments, and these must be rejected at once as non-representative. In some cases it is possible by means of age-analyses of catches taken in the scientific fishing experiments or by the fishermen to control the correctness of the determinations of the frequency of the year classes made on the basis of fishing experiments at the coasts.

The fact is that the variations in the frequency of the year classes may to a certain degree be followed from one age-group to another. A. C. JOHANSEN, 1908, 1 proved this to be case of the 1904-year class, which in the catches from 1905—06 was very poor as compared with the neighbouring year classes. In the coastal investigations of 1905 were found very small quantities of the I-Group (cp. Table 8).

From age-analyses of plaice caught in the Belt Sea 1911 appears further that the year classes 1907 and 1909 were poorer than those of 1906 and 1908 (cp. A. C. JOHANSEN, 1912, 2, Table 12—14).

The determination of the catch figure 12 for 1907 being based on 1 fishing experiment only, it is of course of no value. For this year I have used the catch figure 15; for all that we know about this year class is that it was below the average; the lowest catch figure from this series of years is 2.4, and the average value of the catch figures is about 30. Age-analyses from 1920, published by C. G. JOH. PETERSEN, 1921 comprise only few specimens of the 1914-year class and older, and no plaice younger than the 1918-year class. For the years 1921—23 Strodtmann and Langhammer, 1925, have published a number of age-analyses of the catches of plaice in the western Baltic, and for 1922 Kirstine Smith, 1923, has published similar analyses from the western Baltic and the Smaalandshavet. From these analyses it is evident that the 1920-year class yielded a much smaller number of plaice than the 1919-year class, i. e. the inverse of what appears from the catch figures if they are calculated on the basis of the too small number of fishing experiments. The numerical value of the 1919-year class cannot, however, be determined from the material in hand.

Further, H. Blegvad, 1927, 2 has published an investigation of the relative frequency of the year classes based on an examination of plaice caught in the fine-meshed otter seine used by the Danish Biological Station, and on plaice caught by the commercial fishery. For the years 1921—26 his data correspond with those obtained by the fishing experiments at the coasts. For it appears from Blegvad's investigations that the year classes 1923 and 1925 were of nearly the same size and 8 times as rich as the year classes 1924 and 1926, whereas from the quantity of plaice of the II- and the III-Groups taken in fine-meshed otter seine we may conclude that the 1921-year class was poorer than that of 1923 but richer than that of 1922.

As to the 1920-year class the results of the examination of plaice taken in fine-meshed otter seine and that of plaice taken by the commercial fishery disagree. The 1920-year class was scantily represented in the fine-meshed otter seine catches and hence was to be considered below the average. But as III-Group in 1923 it constituted the same percentage of the examined commercial plaice as did the rich 1923-year class as III-Group in 1926. The whole stock of commercial plaice no doubt being smaller in 1926 than in 1923, a conclusion that may be drawn from the decrease continued from year to year in the yield of the fishery of

Table 8. Average catch pr. hour-haul of plaice of the 0- and I-Groups. Averages determined on the basis of less than 20 stations given in brackets. Catch figures calculated as 1 × number of 0-group + 3 × number of I-Group.

Year	S. Kattegat		Belt Sea		S. Kattegat + Belt Sea		Catch figure	No. of Stat.	
	0	I	0	I	0	I		S. Katt.	Belt S.
1904	—	—	—	—	—	—	2.4	0	0
1905	(11.1)	(0.7)	(10.4)	(0.0)	10.9	0.4	24.1	14	8
1906	(20.7)	(2.5)	(23.9)	(7.9)	21.8	4.4	43.6	13	7
1907	(6.0)	(13.2)	—	—	(6.0)	(13.2)	15.0[1]	1—6	0
1908	(23.7)	—	(44.0)	—	(38.9)	—	45.6	3	9
1909	1.9	5.6	(6.0)	(18.6)	2.6	7.6	10.1	27	5
1910	3.2	2.5	—	—	3.2	2.5	7.7	26	0
1911	74.6	1.0	48.4	2.0	61.3	1.5	97.0	34	35
1912	7.4	9.4	2.7	14.0	4.9	11.9	16.9	36	41
1913	11.4	4.3	(19.0)	(0.0)	11.9	4.0	39.8	26	2
1914	(1.5)	(36.8)	6.1	4.1	5.4	9.3	10.8	4	21
..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..
1920	(58.0)	(3.3)	—	—	(58.0)	(3.3)	30.6	3	0
1921	1.5	3.6	5.4	6.4	3.6	5.1	27.6	30	35
1922	1.0	6.7	16.9	8.7	11.5	7.9	23.0	22	43
1923	—	—	—	—	—	—	46.8	0	0
1924	15.5	5.1	18.4	10.0	17.1	7.8	32.7	30	38
1925	—	—	22.8	5.2	22.8	5.2	49.8	0	33
1926	—	—	3.9	9.0	3.9	9.0	9.3	0	28
1927	31.0	3.0	31.6	1.7	31.4	2.0	45.5	21	52
1928	5.9	3.4	9.8	5.5	8.4	4.7	18.9	35	59
1929	3.0	3.2	2.8	3.6	2.9	3.5	7.7	31	59
1930	14.6	1.0	9.4	2.0	11.9	1.6	21.7	31	59

[1] Estimated from the age composition of the stock of older plaice.

this area, we should have to take the said result of the examination of the commercial plaice as evidence of the 1920-year class being above the average. Hence we may suppose the determination of the frequency of the year class, based on 65 fishings for the I-Group at the coast, to be approximately correct as it gives the 1920-year class as an average one. On the basis of fishing experiments with the fine-meshed otter seine during 1927, 1928, and 1929 I was able to demonstrate (AAGE J. C. JENSEN, 1931, 1) that in the stock of plaice older than the I-Group the year classes 1925 and 1927 were richer than those of 1924 and 1926, which agrees with the results of the coastal fishing experiments.

In this investigation we may only use determinations of quantity of fry from the years down to 1928 incl. because of the possibility that the low values for the quantity of fry in the Belt Sea found for the years after 1928 are due to the stock of plaice in the Belt Sea being so greatly reduced by the fishery that the quantity of plaice fry produced is smaller now than formerly. The decreasing yield of the fishery (A. C. JOHANSEN, 1928) and the corresponding considerable decrease of the stock of plaice found in the quantitative fishing experiments (AAGE J. C. JENSEN, 1931, 1) shows that this may actually be the case (cp. AAGE J. C. JENSEN, 1931, 2, p. 20).

B. Periodic Variations in the Catch Figures.

The revised catch figures are shown in Fig. 12, A and in the continuous curves of Fig. 14. We see here, as in Table 8, that there seems to be a periodic variation in the catch figures where the length of period is about 2.5 years, and where, consequently, n is about 145.

A calculation of the correlation coefficients between the catch figures and values determined from sine functions with varying length of period and phase gives the values shown in Table 9 and Fig. 13. The highest correlation coefficient is found for $n = 150°$ (length of period 2.4 years), $\varphi = 280$; for these values we find $r = 0.607$. To this corresponds $t = 3.24$; $P < 0.01$, and thus the correlation is significant.

The values of the sine function are given in the dotted curve of Fig. 15, A, together with the catch figures.

It is seen from Fig. 14 and from Table 9 that there is also a distinct correlation between the catch

Table 9. Revised catch figures correlated with values determined from sine functions with varying lengths of period and phase from 1904.

$n = 120°$		$n = 130°$		$n = 140°$		$n = 150°$		$n = 160°$	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
120	0.274	130	0.351	200	0.299	260	0.577	30	0.336
150	0.308	160	0.510	230	0.383	290	0.593	60	0.346
180	0.267	190	0.497	260	0.354	320	0.432	90	0.250

figures and values determined from sine functions where n is about 130°. Thus the catch figures seem to be varying according to 2 periodic functions the length of period of which are abt. 2.5 and abt. 3.0 years, respectively.

After calculation of the coefficient of regression between the catch figures and the values determined from the sine function $y = \cos(150\,T - 280)$, which is found to be 18.7 and here rounded off at 20, we are able to eliminate the named sine-variation from the catch figures. Hence we get the values shown in Fig. 12, curve B.

It appears from this curve that there seems to be a periodic variation here, the length of period of which is about 3 years.

A calculation of the correlation between the reduced catch figures shown in Fig. 12, B and values determined from sine functions with varying length of period and phase gives the coefficients shown in Table 10.

The maximum for r is found for n being between 110° and 120°. One of the highest values to be found is $r = 0.571$, for $n = 115°$; $\varphi = 115°$. To this corresponds $t = 2.96$ and $P < 0.01$, and consequently we

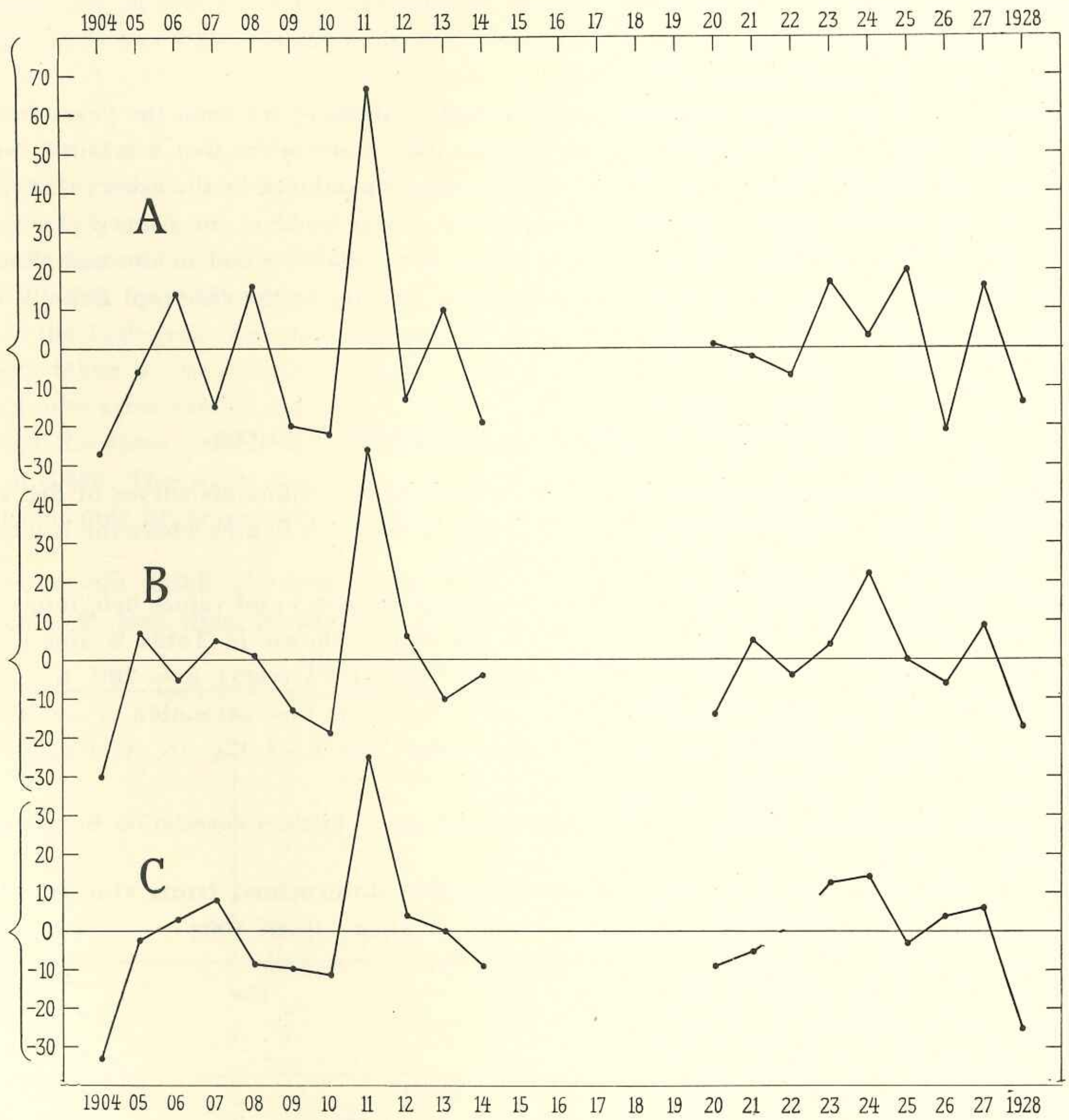

Fig. 12. A: Catch figures for the year classes (0- and I-Group) of the plaice in the southern Kattegat and the Belt Sea.
B: Values determined from $y = 20 \cdot \cos(150\,T - 280)$ eliminated from catch figures.
C: Values determined from $y = 20 \cdot \cos(150\,T - 280) + 10 \cdot \cos(110\,T - 80)$ eliminated.

Table 10. Revised catch figures eliminated for the sine function where n = 150°, φ = 280°, A = 20; correlated with values determined from sine functions with varying lengths of period and phase.

n = 100°		n = 110°		n = 120°		n = 130°		n = 140°		n = 150°	
φ°	r	φ°	r	φ°	r	φ°	r	φ°	r	φ°	r
30	0.165	50	0.237	150	0.413	130	0.373	230	0.382	80	0.045
50	0.184	80	0.433	180	0.444	160	0.393	260	0.430	110	0.060
70	0.089	110	0.324	210	0.362	190	0.294	290	0.352	140	0.064

may consider the last mentioned correlation significant. In the following the calculations has been carried out partly for these values of n and r, partly for $n = 110°$, $\varphi = 80°$ (from 1904).

The regression coefficient between the values of the latter sine function and the reduced catch figures being 10, it may be added to those found from the sine function $y = 20 \cos (150\ T - 280)$. The combined sine curves are presented in Fig. 14 B (the dotted curve) where it is compared with the catch figures (the continuous curve). The correlation coefficient between these values found from the combined sine functions, and the catch figures is 0.694.

In Fig. 12 C also the sine function, where $n = 110°$, $\varphi = 80°$, $A = 10$, is eliminated from the catch figures.

Here it is seen that in the catch figures there is possibly still found a periodic variation of about 5 years.

If we correlate the values given in Fig. 12 C with values found from a sine function where $n = 72°$, $\varphi = 180°$, reckoned from 1904, we get the coefficient $r = 0.473$; t becomes 2.3, and $P = 0.04$.

The regression coefficient between the values of the 5 years' sine function and the reduced catch figures (Fig. 14 C) is about 10.

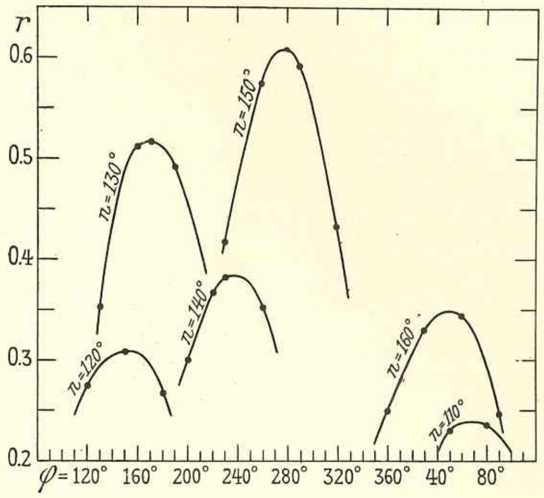

Fig. 13. Correlation coefficients between catch figures and values determined from sine functions with varying length of period and varying phase.

A combination of the three sine functions is compared with the catch figures in Fig. 14 C. A calculation of the correlation between these two groups of values gives $r = 0.777$. While the standard deviation, σ, is 21.9 for the revised catch figures, it is 15.7 for the values shown in Fig. 12 C, where the sine functions $y = 20 \cdot \cos (150\ T - 280)$ and $y = 10 \cdot \cos (110\ T - 80)$ are eliminated, and 12.9 for the values where further $y = 10 \cdot \cos (72\ T - 200)$ is eliminated.

The regression coefficient between the values found from the sine function, where $n = 115°$, and $\varphi = 115°$ and catch figures is 14. The correlation coefficient between the combined sine functions $y = 20 \cdot \cos (150\ T - 280) + 14 \cdot \cos (115\ T - 115)$ and the catch figures is 0.754. After eliminating these combined sine functions from the catch figures no further periodic variations are to be found. The standard deviation for the reduced catch figures is 14.2.

Thus we may take about $^1/_3$ of the variations from year to year in the catch figures to be determined by the periodic variations.

C. The Plaice Fishery in the Belt Sea.

A. C. Johansen (1908, 1) and H. Blegvad (1926, 2 and 1927, 2) have shown that the frequency of the year classes is determined at a very early stage of development, viz., at the egg- and larva-stages in the winter months, and that the frequency of the year classes influences decisively the composition in age-groups of the stock. It may be mentioned that H. Blegvad in the said paper from 1926 also demonstrated quite a corresponding dependence of the relative frequency of the year classes of the cod on the hydrographical conditions. This relative frequency he deduced from the composition of the age-groups of the older stock of cod, and later on it has been possible to demonstrate that the hydrographical factors determining the relative frequency of the year classes are also determinative of the weight yield of the cod fishery some years (about 4) later (Aage J. C. Jensen, 1929). Consequently, one would suppose it possible to demonstrate a similar direct dependence of the weight yield of the plaice fishery on the relative frequency of the year classes, the more so as such a dependence has been demonstrated in the case of the North Sea fishery by D. E. Thursby-

PELHAM, 1930, p. 76 ff., and by the writer in Section 2 of the present paper, and, in the case of the true Baltic, by R. KÄNDLER, 1931, pp. 53—54.

Up to the first part of this century the plaice fishery of the Belt Sea was not very intense, and it was

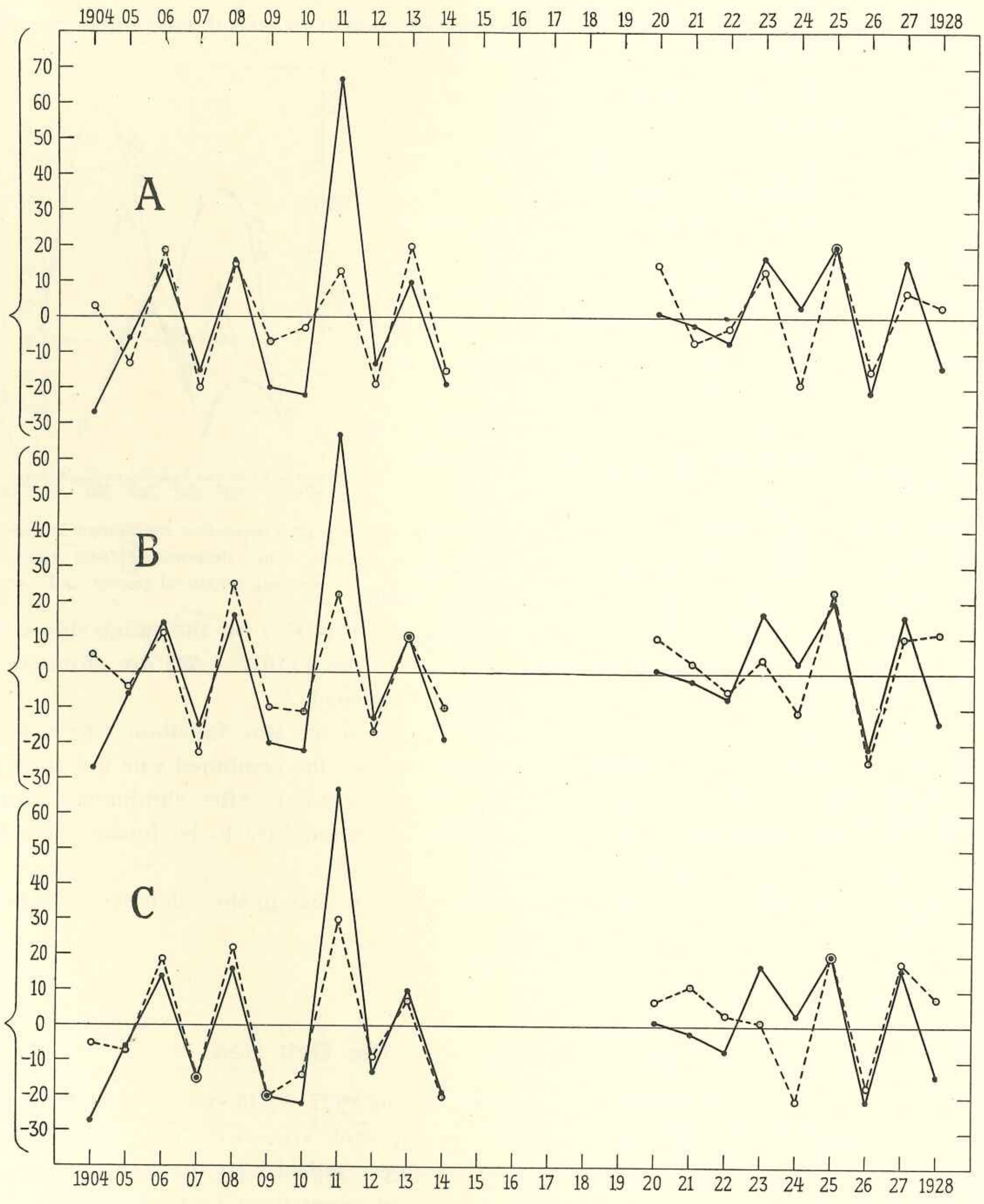

Fig. 14. Catch figures for the year classes of plaice (continuous curves) compared with:
in A: values determined from $y = 20 \cdot \cos(150\,T - 280)$.
in B: values determined from $y = 20 \cdot \cos(150\,T - 280) + 10 \cdot \cos(110\,T - 80)$.
in C: values determined from $y = 20 \cdot \cos(150\,T - 280) + 10 \cdot \cos(110\,T - 80) + 10 \cdot \cos(72\,T - 200)$.

carried out chiefly with plaice nets in some few localities fit for the purpose. The percentage of re-capture at the close of these years in ordinary marking experiments in the Belt Sea (during the spring of 1907) was 34 (A. C. JOHANSEN, 1912, p. 99), i. e. rather considerable, anyhow. About the beginning of the century fishing with the Danish seine and a few years before 1910 fishing with the otter seine were started in the Belt Sea. The number of Danish seines in the Belt Sea attained a maximum in 1912, but decreased to half the number during the years after 1916. The number of otter seines was increasing rapidly up to 1913 and was then rather constant up to 1918, but in 1919 the number of otter seines increased highly once more (cp. C. G. Joh. Petersen, 1921, p. 15).

Because of the intense fishing during the years about 1910 the character of the stock changed rapidly, and from being a dense, slowly growing stock it became a fast growing one, which in the first years after the beginning of the intense fishing was recruited rapidly from the accumulated stock of old fish below the minimum size caught. The yield reached a maximum in 1912 and in 1919, partly because of the changed conditions of growth, partly on account of the increased fishing intensity (C. G. Joh. Petersen, 1921), but also because there was an accumulated stock of small plaice that would grow up to become commercial plaice as soon as the check of growth caused by the competition for food was relieved by the commencing thinning of the stock (Aage J. C. Jensen, 1931, 1, p. 19). This explosion-like increase in the yield of the fishery can only be explained if we take into consideration this last mentioned fact.

During the following years there was a rapid decrease in the yield of the fishery. As late as 1913 the plaice fishery in the Belt Sea was rather profitable, but in 1914 the stock was nearly exhausted. During the war the stock was partially safe from interference on the part of the fishery. In 1919, when the great increase in the number of otter seines took place, the yield was high again, but decreased once more during the following years.

Hence, the yield of the fishery within this area during the years after 1910 does not express the density of the stock in such a way that the successive years may be directly compared.

It is worth noting that W. B. Schostakowitch, 1929, 2 has found a periodic variation in the plaice fishery in the Belt Sea with a length of period of 2.5 years, besides periods of 5.9 and 10.33 years. The data from which Schostakowitch found the said period are derived from the yield of the fishery in the Belt Sea during the years 1885—1926; for the years down to 1910 they are taken from A. C. Johansen and E. Neergaard-Møller, 1913, and for the following years from the Fiskeri-Beretning.

Throughout the whole period down to the time when the intense fishing began, the plaice fishery was one of the more important fisheries within the area, yielding about 600 tons a year on an average up till 1900. Hence, also for these years the variations from year to year in the yield may be considered more or less representative of the variations from year to year in the size of the population.

The periods could not be expected to be very distinct until the intense fishing had thinned the stock, the accumulated population causing a smoothing of the variations from year to year that are due to difference in the quantity of fry.

Yet in the difference between the catch and a three years' smoothing of the catch calculated by Schostakowitch, the periodic variation of about 2.5 years is clearly visible. The length of the period in the years 1885—1900 has been c. 2.7 years, and it is a noticeable fact, that for later years it has been shorter. This is what would be expected from the fact that the intensity of the fishery has been increasing especially since abt. 1900 and has caused the stock to be thinned out and the average age of the year classes, which determine the variations from year to year in the yield of the fishery, to be decreasing, i. e. the phase-difference between a spawning year and the year in which the catch anomaly is determined by this year class has been decreasing. The length of period in the yield of the fishery for this reason must be shorter than in the frequency of the year classes, as was also found to be the case in the North Sea.

D. Discussion of Causes of Periodic Variations in the Stock of Plaice in the Southern Kattegat and the Belt Sea.

1. The 2.4—3.3 years' periods.

Factors influencing the amount of young plaice.

As pointed out by H. Blegvad, 1926, 2, the quantity of fry is dependent on the hydrographical conditions during the early development of eggs and fry, more especially on the temperature.

Hence, there are beforehand two possibilities: the periodicity found is due to a periodic variation with this length of period in the hydrographical conditions, or it is due to a purely biological (physiological) cause. The latter possibility would *a priori* seem to be out of the question, the biological condition of the stock in the area having been subject to a radical change during the series of years considered.

In the investigation of the question which are the hydrographical causes of the variations from year to year in the quantity of plaice it will be necessary to examine directly the correlation between the catch figures and the hydrographical conditions, but, as mentioned in detail below, we must further examine the causes of the changes in the racial character of the plaice, these changes, according to A. C. Johansen, 1929, being apparently closely connected with the changes in the amount of fry.

a. Examination of the correlation between catch figures and hydrographical conditions.

In an investigation of the question how the quantity of plaice fry, determined by the catch figures calculated by him, depends on the hydrographical conditions, A. C. Johansen, 1927, 2 found that the connexion between the salinity and the quantity of fry seems to be more marked than that between temperature and quantity, but he thought it probable that both the low percentage of salt and the low temperature directly and indirectly exercised a checking influence on the quantity of fry, indirectly, because these factors influence the amount of food, the quantity of plankton being negatively correlated with the quantity of outflowing Baltic water, which is poor in salt and plankton. He supposed the indirect effect to be by far the most important one.

On the basis of the critically revised catch figures we shall systematically examine the connexions between catch figures and temperature-salinity. As the eggs and larvae of the plaice are dispersed throughout the body of water and are not found in the upper water layers only, we shall examine the correlation with the hydrographical conditions both in the upper and the lower water layers.

A calculation of the correlation between catch figures and salinity and temperature, respectively, of the surface water at the Schultz Grund will give:

Catch figures correlated with	Dec.	Jan.	Feb.	Mar.	Jan.-Feb.
Surface salinity	—0.008	0.388	0.306	—0.074	0.405
Surface temperature	0.194	0.524	0.403	0.236	0.538

In correspondence with the various higher correlation coefficients we get

for $r = 0.388$	$t = 1.74$	and	$P = 0.1$
$r = 0.405$	$t = 1.83$	—	$0.1 > P > 0.05$.
$r = 0.524$	$t = 2.52$	—	$P = 0.02$, significant.
$r = 0.403$	$t = 1.87$	—	$0.1 > P > 0.05$
$r = 0.538$	$t = 2.63$	—	$0.02 > P > 0.01$, signicficant.

Correspondingly, a calculation of the correlation between catch figures and salinity and temperature, respectively, of the bottom water at the Schultz Grund will give:

Catch figures correlated with	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Bottom salinity	0.057	0.415	— 0.113	— 0.473	— 0.469	— 0.440	— 0.149
Bottom temperature	0.261	0.137	— 0.148	— 0.259	— 0.026	— 0.089	— 0.041

Here we get corresponding to

$r = 0.415$: $t = 1.94$ and $0.1 > P > 0.05$
$r = -0.473$: $t = 2,11$ — $P = 0.05$, significant?
$r = -0.469$: $t = 2.19$ — $P = 0.04$, significant.
$r = -0.440$: $t = 2.08$ — $P = 0.05$, significant?

Finally the calculation of the correlation coefficient between the catch figures and the bottom salinity in Feb.—March—April gives $r = -0.769$, to which corresponds $t = 5.14$; $P < 0.01$, i. e. a significant correlation.

Thus we have found:

1. A doubtful positive correlation with the surface salinity in Jan.—Feb.
2. A significant positive correlation with the surface temperature in Jan.—Feb.
3. A doubtful positive correlation with the bottom salinity in Dec.
4. A significant negative correlation with the bottom salinity in Feb.—March—April.

The connexion between the catch figures and respectively the temperature at the surface in Jan.—Feb. and the salinity at the bottom in Feb.—March—April is shown in Figs. 15 and 16.

As regards the covariation of the catch and the hydrographical conditions at the surface, we note at once that it seems to be more marked in the case of temperature than in the case of salinity.

The doubtful correlations found between the catch figures and respectively the surface salinity in Jan. —Feb. and the bottom salinity in Dec. may be explained as "false" correlations due to the connexion of these conditions with the bottom salinity in Feb.—March—April.

To all probability, however, the amount of fry is actually to a small degree dependent on the surface salinity in Jan.—Feb., as the latter is determined by the intensity of the outflow, so that in years when a comparatively large quantity of eggs and fry are carried away from the area by the current, the amount of fry in the Belt Sea becomes perceptibly smaller. The surface salinity is low when the outflow is intense, and high when the outflow is weak.

That there is a considerable transport of fry of Belt Sea plaice to the northern Kattegat appears directly from the race investigations, as the fry of the Belt Sea plaice in some years may be traced as far as the Aalbæk Bay (cp. A. C. Johansen, 1929, Fig. 5, p. 89). When e. g. the number of anal fin rays in one year shows an average value that is lower than the normal of the area, the dispersion is of such a kind that it appears that the stock investigated is mixed up of the fry of North Sea plaice with about 54 anal fin rays and of Belt Sea plaice with about 50 anal fin rays. In this connexion it is worth noting that the amount of fry in the northern Kattegat (and Skagerak) very frequently fluctuates from year to year independently of the amount of fry in the southern Kattegat and the Belt Sea, as has been pointed out by H. Blegvad, 1926, 2 and Anton Fr. Bruun, 1927, p. 8.

Finally we have the connexion of the catch figures with the surface temperature in January—February and with the bottom salinity in February—March—April. These hydrographical conditions vary practically independently of each other.

A dependence of the catch figures on the surface temperature must be expected chiefly from the influence of the temperature throughout the period of development of eggs and fry, the mortality being the higher, the longer the period of development. The eggs of plaice of the Baltic race being hatched after about 27.5 days at 4° C., the same stage is reached after about 50.4 days at 2° C., 121 day-degrees (reckoned from

÷ 0.4° C.) being required for the hatching (A. C. JOHANSEN and AUGUST KROGH, 1914). The surface temperature in January showed the closest connexion with the catch figures as a natural consequence of the fact

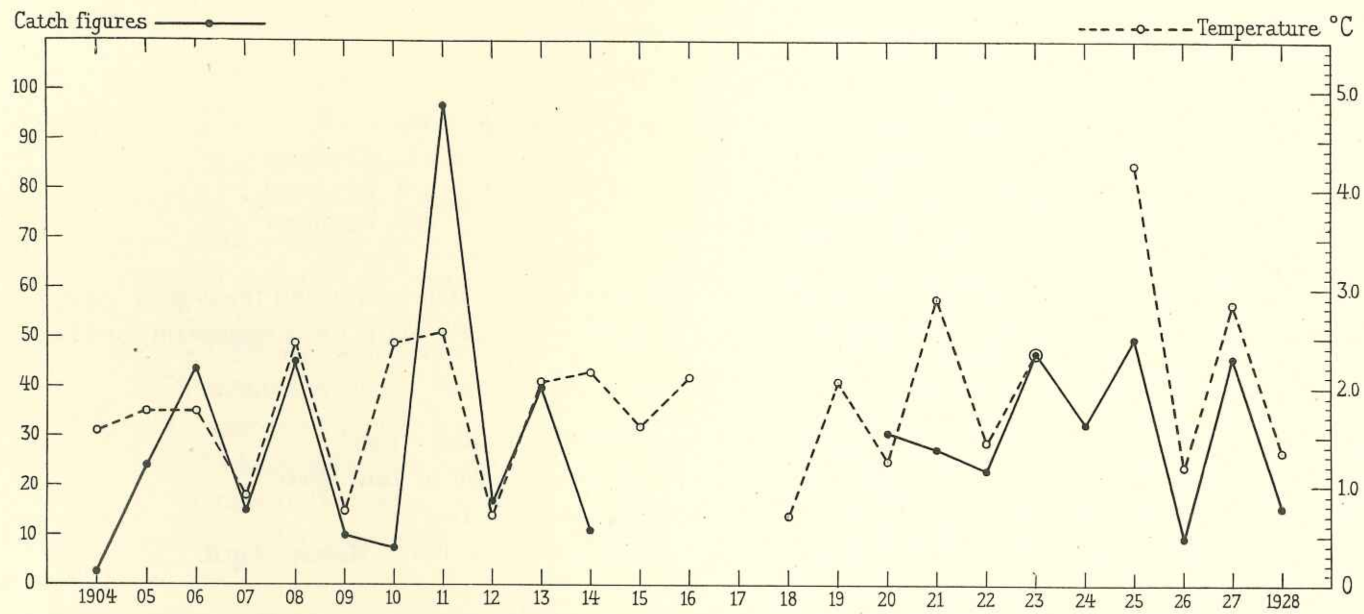

Fig. 15. Catch figures for the year classes of plaice (0- and I-group) compared with surface temperature at Schultz's Grund Light Vessel in January-February.

that the low surface temperatures, which are mainly determined by the temperature of the air, only gradually spread to the deeper layers, the bulk of the eggs at the same time being found at a constantly increasing depth, as their specific gravity increases during their development, as pointed out by J. P. JACOBSEN and A. C. JOHANSEN, 1908, p. 10.

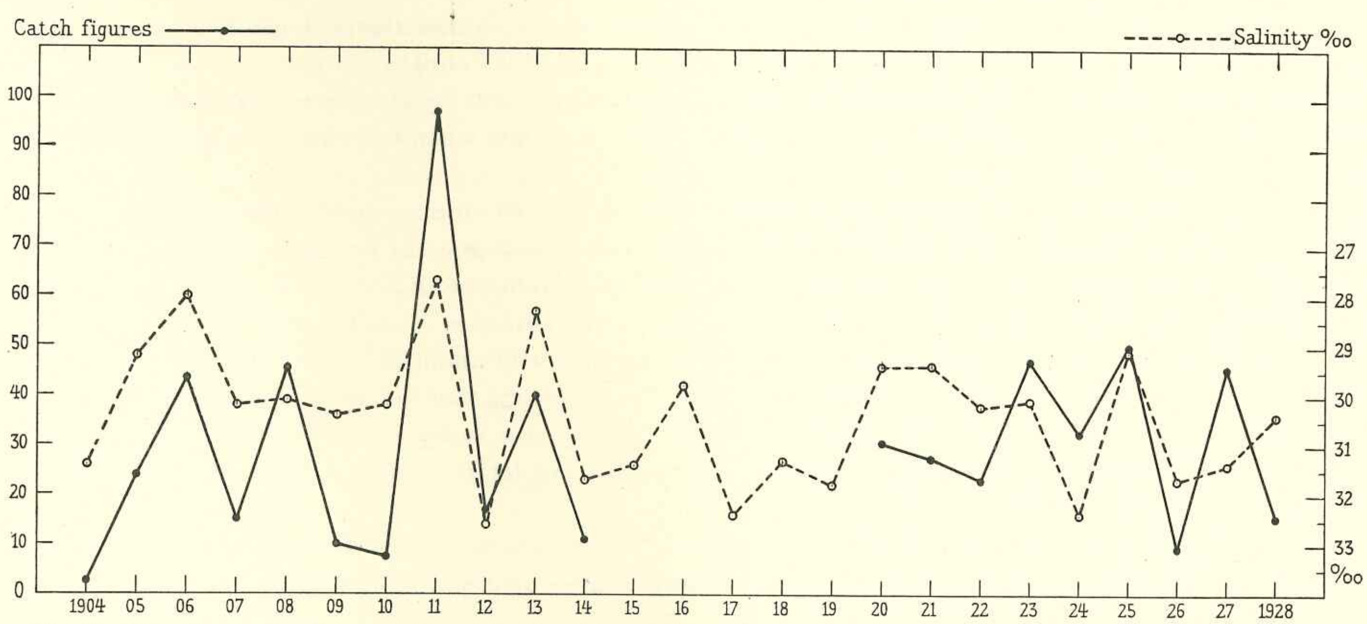

Fig. 16. Catch figures for the year classes of plaice (0- and I-group) compared with bottom salinity at Schultz's Grund Light Vessel in February—March—April.

According to J. GEHRKE, 1922 the temperature of the bottom water at Schultz Grund at a depth of 26 metres in the first and second month after an ice winter shows an average of respectively 0.29° and 0.09° C.

above the normal. Not until the third and fourth month will the temperature be 0.67° and 1.28° C. below the normal.

According to J. P. JACOBSEN, 1908, pp. 23—26, the shifting of phase between the occurrence of the minimum temperature at the surface and at a depth of 20 metres in the Belt Sea averages 1—1$^1/_2$ month and shorter at smaller depths in correpondence with the degree of intermixture of the Kattegat water, which predominates in the bottom layer, and the Baltic water, which predominates in the surface layer.

A dependence of catch figures on bottom salinity in Feb.—March—April must be expected from the fact that the bottom salinity being expressive of the intensity of the inflow and from the fact that an intense inflow of salt bottom water will carry eggs and larvae of plaice from the Belt Sea towards the Baltic, or rather, that more larvae normally are carried away from the Belt Sea by the bottom current than are carried into the Belt Sea from the north.

It should, however, be noticed that as to this explanation a difficulty would seem to arise, because the drift of eggs and larvae away from the Belt Sea would seem to have a material influence on the quantity of plaice fry in this region, while these eggs and larvae, which are carried into the Baltic, do not perceptibly influence the quantity of plaice fry in the Baltic. The year 1924, which showed a high salinity and consequently an intense inflow into the Belt Sea in Feb.—April, according to H. BLEGVAD, 1927, 1 was extremely poor in fry in the Baltic, whereas 1925, which showed an inconsiderable inflow, was a particularly rich spawning year in the Baltic as in the other Danish waters.

Thus it would seem that the changes in the quantity of plaice in the Baltic depends only to a slight degree on the inflow to the Belt Sea carrying plaice eggs towards the Baltic, but *chiefly* on other factors, e. g. the strength of the ingoing current at Drogden (and Gedser cp. below) and the temperature, as stated by H. BLEGVAD, 1927, 1. This is explained, however, by the fact that during a transport by the current towards the Baltic a large number of the eggs, which, as mentioned above, increase in specific gravity during their development, sink to the bottom while transported towards the less saline water of the Baltic and hence partly will travel towards the Baltic at a slower rate, partly are very liable to perish. According to J. P. JACOBSEN, 1908, Table VIII, and R. RUPPIN, 1912, the bottom salinity in February at the Fehmarnbelt is the same as the surface salinity in the northern part of the Great Belt (abt. 20 pro mille) cp. A. OTTERSTRØM 1906. On the other hand a rather large number of larvae will necessarily be carried to the Baltic by the under-current.

It is a well-known fact (cp. e. g. A. C. JOHANSEN, 1912, pp. 10—13) that the bulk of the eggs and fry of plaice in the Belt Sea are found in the lower water layers. Hence, the intensity of the outflow in the surface layer does not naturally exercise a very perceptible influence on the catch figures. Further an intense outflow will cause the salinity of the upper water layers to become low, and comparatively large quantities of eggs will therefore sink towards the lower water layers and thus avoid being carried outwards.

As mentioned above, A. C. JOHANSEN arrived at the result that it was the surface salinity that exercised the greatest influence on the frequency of the plaice fry. He explained the effect of the salinity as being either a direct or an indirect one.

The effect might be a direct one, as a low salinity, especially in the shallower parts of the Belt Sea and the Kattegat might cause a considerable quantity of pelagic plaice eggs to sink to the bottom, where they are easily preyed upon by the numerous predatory animals of the sea floor.

As, however, throughout extensive areas the eggs will only sink down to the lower and salter water layers, he thought this direct effect to be of secondary importance.

The effect might be an indirect one by influencing the physiological conditions of the fry, the salinity together with the temperature, which is positively correlated with the salinity, being highly determinative of the quantity of plankton, and A. C. JOHANSEN, 1927, 2, pp. 13 ff. supposed this fact to be of decisive importance.

These causes, too, probably do play a part although, as was pointed out, the covariation with the surface salinity is much less than that with the temperature.

b. Investigation of causes of changes in the racial character of the plaice.

The question of the causes of the changes in the racial character of the plaice in this area is closely connected with the question of the causes of the changes in the quantity of fry.

A. C. Johansen, who proved that the racial character of the Belt Sea plaice varies from year to year, at the same time pointed out that it varied from year to year parallelly to the changes in the salinity of the surface water in January—February, and thought these changes to be due to the fact that considerable quantities of larvae of the North Sea race are carried from the eastern Kattegat to the Belt Sea and the Baltic with the surface current (cp. A. C. Johansen, 1929, p. 93). Such an indrift of larvae that influences the race character must, however, at the same time be expected to influence the quantity of fry considerably (cp. A. Bückmann, 1930, p. 70). In itself as stated by W. Schnakenbeck, 1931, p. 455, this goes very well with the positive correlation between the quantity of fry and the surface salinity, which was pointed out by A. C. Johansen. However, we have seen above that this connexion in the reality is very loose.

In addition, the salinity at the surface can not be taken as a measure of an inflow of larvae or eggs from the north. The resulting water movement at the surface is outgoing though the current is shifting very much between in- and outgoing (cp. M. Knudsen, 1905, and J. P. Jacobsen, 1925), but the inflow will excercise the most marked influence on the salinity of the bottom layer where the main ingoing current is found. Not until the bottom layer in the course of the next time is mixed up with the surface layer, is the inflow felt by an increase of the salinity of the surface layer (A. C. Johansen and Aage J. C. Jensen, 1926). As was the case with eggs carried from the Belt Sea towards the Baltic, the eggs, which from the northern Kattegat are carried southward, on account of the decreasing salinity will sink to the bottom, where the movement of the water is slow, and where a great many of them will be devoured by predatory animals. The fry, as mentioned above, is most numerous in the lower water layer and is only for a small part exposed to a transport towards the south *with a surface current.*

Thus there is apparently a contrast between the ways in which the changes from year to year in the quantity of fry and in the race character must be explained, and hence we must examine more closely the causes of the changes in the race character of the plaice.

Beside the irregular variations from year to year A. C. Johansen, 1929, p. 97, has demonstrated a change in the race character during the whole of the post-war period as compared with the years before the war, and he ascribes this to a supposed increased indrift of larvae of the North Sea race.

We shall first inquire into the causes of this last mentioned change in the racial character of the plaice.

The post-war change in the racial character might be brought about in the following ways:

1. The indrift of eggs or fry of the North Sea race has been increased by
   a. a richer occurrence of fry in the northern Kattegat and the same intensity of the inflow,
   b. an increased inflow and unaltered amount of fry in the northern Kattegat.
2. An increased immigration of plaice of the 0- and I-Groups.
3. The production of fry in the Belt Sea has decreased.
4. The race character of the indigenous population has altered because of changed biological conditions.
5. Increased crossing in the Belt Sea with plaice of the North Sea race.

ad 1 a. An increase in the indrift of eggs and larvae of the North Sea race on account of a richer occurrence of fry in the northern Kattegat cannot be the cause; for the fishing experiments at the coasts on the 0- and I-Groups of plaice show that there has been no demonstrable change in the quantity of fry after the war as compared with pre-war quantities (Anton Fr. Bruun, 1927).

Outside the coastal areas, too, a change in the production of fry would result in a change in the density of the population, thus in the Aalbæk Bay—Herthas Flak area, but as to this population, too, fishing experiments did not show any change in the density (Aage J. C. Jensen, 1931, 2).

ad 1 b. An increased indrift of eggs and fry caused by an increased inflow from the north has not, on the

Table 11. Mean salinity (tenths of pro mille) at Schultz Grund Light Vessel at surface and bottom in each five-year 1901—1930 (figures in brackets from less than five years).

	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
At surface												
1901—1905.......	200	208	157	184	163	153	171	185	171	174	196	207
1906—1910.......	226	215	184	155	163	156	169	185	178	164	197	219
1911—1915.......	210	209	200	178	180	156	160	166	179	173	208	232
1916—1920.......	213	(194)	173	177	155	166	176	180	196	202	195	207
1921—1925.......	(228)	(204)	180	177	162	182	179	183	189	201	205	202
1926—1930.......	193	(185)	(170)	178	168	170	173	181	182	201	204	185
At bottom, 26 metr.												
1901—1905.......	290	290	307	320	326	327	324	307	289	315	318	293
1906—1910.......	292	291	(297)	305	324	326	322	306	292	299	316	306
1911—1915.......	287	(294)	306	304	317	319	322	317	310	300	318	304
1916—1920.......	294	(295)	297	329	323	328	320	312	301	288	289	303
1921—1925.......	(293)	(273)	301	317	332	323	312	311	304	286	281	297
1926—1930.......	294	(305)	(311)	327	326	329	323	311	304	294	293	291

whole, taken place after the war. This appears from the fact that during Jan.—Feb.—March, i. e. the months when large quantities of pelagic eggs or larvae of the plaice are found in the water, there can neither at the surface, nor at the bottom be demonstrated any rise in salinity or temperature (cp. Tables 11 and 12). An increase of the inflow would appear most markedly in a rise of temperature or salinity at the bottom, the current here being inwards bent, and less distinctly at the surface, where the current has an outward direction, as the water of the bottom layer is being mixed up with the surface water. According to the correlation found, an increase in the salinity (the inflow) at the bottom influences the quantity of fry *in an opposite way.*

In an earlier paper (Aage J. C. Jensen, 1929), I have pointed out that during later years (after about 1914) there has been a rise of temperature in the bottom water of the Belt Sea during the following months, i. e. April—July, and that this caused an increase of the stock of cod in the waters within the Skaw by affording better conditions for the survival of the cod fry. At the same time an increase in the salinity of the bottom water

Table 12. Mean temperature at Schultz Grund Light Vessel at surface and bottom in each five-year 1901—1930 in °C. (figures in brackets from less than five years).

	Jan.	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
At surface												
1901—1905.......	2.0	1.3	1.8	4.3	8.9	14.2	16.6	16.4	14.0	10.7	7.0	3.6
1906—1910.......	2.2	1.2	1.8	4.5	8.8	13.9	16.5	16.2	14.2	12.0	7.5	4.5
1911—1915.......	2.4	1.3	2.3	4.9	9.7	13.9	17.0	17.3	14.9	10.7	7.0	4.8
1916—1920.......	1.9	(1.2)	1.5	4.6	9.5	13.8	16.4	16.6	14.3	10.6	6.8	4.1
1921—1925.......	(3.1)	(2.6)	1.8	4.6	9.5	13.4	15.7	16.0	14.0	10.8	6.8	3.8
1926—1930.......	2.0	(1.7)	(2.6)	4.8	9.2	13.2	16.2	16.7	14.8	11.2	7.8	4.4
At bottom												
1901—1905.......	5.1	4.1	4.2	4.3	4.6	5.3	7.1	10.7	12.6	11.5	10.1	7.0
1906—1910.......	5.3	3.9	(4.6)	3.9	4.7	5.5	6.7	10.4	12.2	11.7	10.4	7.7
1911—1915.......	5.1	(4.6)	4.7	4.4	4.8	5.7	6.9	9.5	11.4	11.7	9.7	7.2
1916—1920.......	4.9	(3.8)	3.9	4.5	5.2	5.7	7.5	9.8	12.0	11.8	9.9	7.7
1921—1925.......	(5.2)	(3.7)	4.5	5.0	5.5	6.7	9.2	10.7	12.5	12.3	9.7	8.0
1926—1930.......	6.0	(5.0)	(4.6)	5.3	5.4	6.0	8.0	11.3	12.9	12.2	10.3	7.9

has taken place, although mainly in April only (Cp. Table 11). But this increase has been rather slight, and e. g. in the quinquennium 1921—25, the bottom salinity at Schultz Grund was on an average lower than in the quinquennium 1901—05.

From the table it is seen that in recent years, i. e. after about 1916, the outflow in September—October from the Baltic has been slower than in the previous years, and, consequently, the inflow at the bottom has been slower, too.

ad 2. As mentioned above, Anton Fr. Bruun, 1927, p. 6, has pointed out the possibility of an immigration of plaice of the 0-Group from the Skagerak and the northern Kattegat to the southern Kattegat and the Belt Sea during the period after August—September, i. e. after the termination of the fishing experiments at the coasts by which the quantity of the 0- and the I-Groups is determined. It would correspond to the immigration of small plaice of the I-Group to the northern Kattegat from the Tannis Bay that was demonstrated by A. C. Johansen (1906, p. 77). It has not been proved that such an immigration to the Belt Sea takes place, as there is a considerable uncertainty in the determinations of mean numbers for the quantity of plaice of the 0-Group and perhaps to a still higher degree for the I-Group, which are based on coastal fishing experiments (cp. p. 30). As mentioned above, it is very improbable that the immigration should be of any practical importance for the population, with the possible exception of the Aalborg Bay.

ad 3. The approximation in race character of the stock of plaice in the Belt Sea to the North Sea plaice both in the case of younger and older age-groups might further be explained on the assumption that the stock of indigenous plaice has been so greatly thinned out that the quantity of its fry has become perceptibly smaller in comparison with the quantity of fry that is carried into the area with the southward current.

If, however, we take 50 rays of the anal fin to be characteristic of the Belt Sea plaice and about 54 for plaice of the North Sea race, it is seen that while the normal admixture in the Belt Sea of the North Sea race during the years 1894—1907 was extremely small (nearly 0 per cent.), it was about 10 per cent. during the years 1920—25 and about 25 per cent. during 1927—28, the number of rays of the anal fin during the three periods being 49.96, 50.38, and 51.00, respectively (A. C. Johansen, 1929, p. 84).

The decrease of the quantity of fry in the Belt Sea, however, which has taken place during these years has not by far been so great, because the numerical value of the average catch in the quantitative fishing experiments at the coasts on plaice of the 0- and the I-Group has not changed. Still, a slight decrease may be said to have taken place, because a limited increase in the catch per time unit of the 0- and I-Group was to be expected, the fishery to an increasing degree being carried out in places where experience has shown that great quantities of fry might be expected to occur.

All these explanations discussed above presuppose a change in the "mechanical" admixture of North Sea plaice with the stock of indigenous plaice of the southern Kattegat and the Belt Sea, which possibly, though not necessarily, is connected with a certain degree of crossing.

If, on the other hand, an attempt is made at a mechanical intermixture of plaice of the North Sea race with plaice of the Belt Sea race in such a proportion that the intermixed stock will get a number of rays of the anal fin which on an average equals the one found for the Belt Sea plaice during the years 1920—25 and 1927—28, we get dispersion curves showing a distinct skewness and flatness. In Fig. 17 they are compared with the dispersion curves found in the race investigations of plaice in the Belt Sea carried out by A. C. Johansen during the two periods. The dispersions in the various samples of plaice considered here are shown in Table 13.

The difference between the dispersion of frequency of anal fin rays found in the Great Belt 1927—28 (column 4) and the one to be expected if this dispersion were due to the stock in the Belt Sea in 1927—28 being a mixture of Belt Sea plaice with about 50 anal fin rays, and plaice of the North Sea race which had drifted in from the Kattegat and had about 54 anal fin rays (column 3), may be tested by a computation of χ^2 for the two dispersion curves (cp. R. A. Fischer, 1930, Ch. IV. Ex. 9). By this computation is found $\chi^2 =$

121.2, and P, which here denotes in what proportion of cases this value for χ^2 will be exceeded if the dispersion in column 4 follows that in column 3, is by far less than 0.01 (P is 0.01 for χ^2 = abt. 25), and the probability

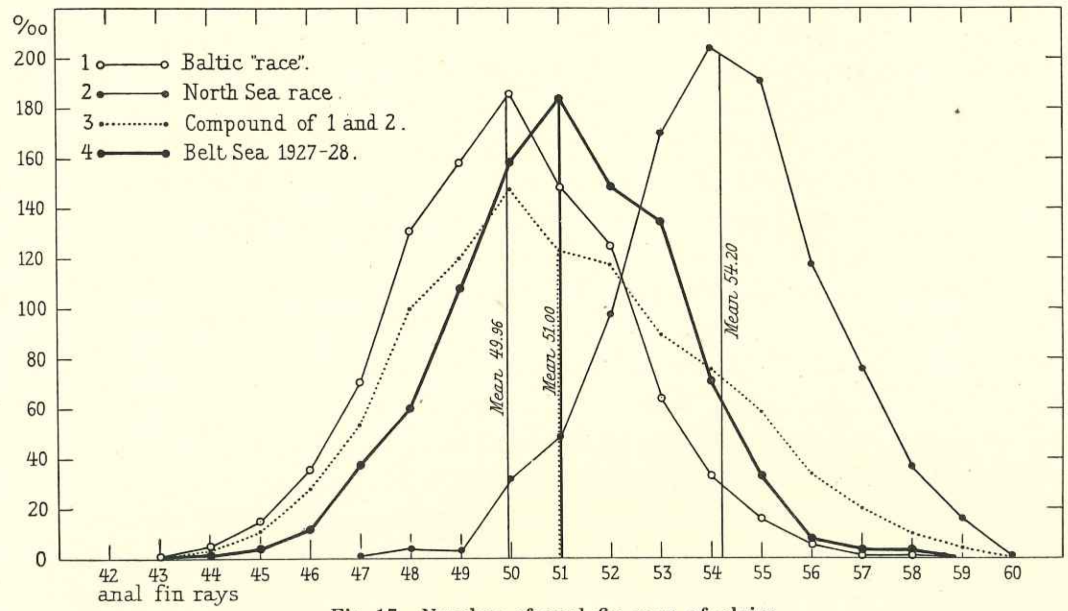

Fig. 17. Number of anal fin rays of plaice.

that the dispersion, which was found in the Great Belt in 1927—1928, is a consequence of a mixture between Belt Sea plaice and larvae (or other stages of development) of North Sea plaice, therefore is exceedingly small.

Table 13. Number of anal fin rays, in pro mille, 1) of plaice of the North Sea race (0-Group in the Aalbæk Bay, 1924—1930), 2) of plaice caught in the Great Belt 1894—1907, 3) of a mixture of the plaice under headings 1 and 2, 4) of plaice caught in the Great Belt 1927—1928 (from investigations by A. C. Johansen).

Number of anal fin rays	1 Aalbæk Bay 1924—1926	2 Great Belt 1894—1907	3 Mixture between 1 and 2	4 Great Belt 1927—1928
43	..	1	1	..
44	..	5	4	3
45	..	15	11	4
46	..	37	28	12
47	1	71	54	38
48	4	131	100	61
49	3	159	120	118
50	32	186	148	169
51	49	148	123	184
52	98	125	118	159
53	170	64	90	135
54	204	33	76	71
55	191	16	59	33
56	118	6	34	8
57	76	1	20	3
58	37	1	10	3
59	16	..	4	..
60	1	..	..	..
Average	54.20	49.96	51.00	51.00
Number of plaice examined	696	1443	..	735

Moreover we have seen above in the examination of the salinity that the physical basis of such an increased inflow from the north during the months Jan.—Feb.—March cannot be established for recent years. Hence, the change must be due to the race character not being constant or an increased crossing having taken place.

ad 4. We have seen that in the Belt Sea there has only been a very inconsiderable change in temperature or salinity during the period when the racial character considered might possibly be determined by the environments, viz., during Jan.—Feb.—March, i. e. there is no basis of a change of race character due to changed physical conditions.

ad 5. An increased crossing with plaice of the North Sea race may arise, as in the Belt Sea there is normally a crossing of the two races, if the proportion of quantity during recent years has changed in favour of the North Sea race.

No doubt a crossing between the two races takes place normally, a certain number of the North Sea race every year immigrating to the Belt Sea (A. C. Johansen, 1912, p. 78), and no doubt some of the immigrated plaice spawn in the Belt Sea. Thus a rather considerable number of the plaice transplanted from the North Sea to the Belt Sea have proved to spawn in the Belt Sea, and A. C. Johansen, 1929, p. 95, has demonstrated directly that the race character of the spawning plaice of the Belt Sea in 1928 proved them to be a mixture of Belt Sea plaice and plaice of the North Sea race. In a sample of 214 individuals the average number of anal fin rays was found to be 51.34. In this year, at any rate, only a negligible number of the transplanted North Sea plaice might be found among these spawning plaice. That a number of hybrids are found among these plaice is stated by A. C. Johansen (l. cit., p. 96).

At the same time as the stock of plaice of the Belt Sea has been rapidly decreasing, the immigrating fish have necessarily constituted an increasing part of the population — provided the immigration is the same — and hence comes to be a more distinctive feature in the race character of the population of this area.

Further, *the fact that the conditions of nutrition have improved greatly by the rapid thinning of the stock of plaice in the Belt Sea, has probably caused more stray plaice of the North Sea race to stay within this area than was formerly the case.*

The migration tendency of the plaice is no doubt inversely proportional to the quantity of food (cp. Aage J. C. Jensen, 1928, 3, pp. 97—98, where the demonstrated connexion between temperature during the autumn months and the catch is most likely to be explained by the fact that a higher temperature will cause a more rapid growth of the food animals of the plaice, and hence a delay in the emigration of the plaice).

In the Belt Sea the change of the racial character has taken place simultaneously with the thinning of the population within this area, and it is worth noting that in the true Baltic the change did not begin until the thinning of the stock which was caused by the intense fishing, had reached this region. According to H. Blegvad the intense fishing within this region began in 1919—23. As late as 1927 there seemed to be no change in the racial character of plaice of the 0-Group caught in the coastal water to the south of Møen (A. C. Johansen, 1929, p. 94), but at that time a change in the racial character of the older plaice was beginning to appear in the true Baltic, caused no doubt by an increased immigration of older fish (cp. l. cit., Table 5, p. 86). After the thinning had become very distinct within this area (R. Kändler, 1931), a change in the racial character has taken place as stated by A. C. Johansen, 1931, p. 184: "The plaice in the Baltic proper has in recent years undergone remarkable changes. It grows more rapidly and is now larger on reaching sexual maturity than it used to be. Also the number of anal fin rays has increased in a similar manner to those of the plaice of the Belt Sea".

A change in the salinity of the bottom water during the autumn months might possibly be the cause of the change in the race character, as more plaice would stay in order to breed within the area if the salinity was higher. The change which has taken place in the hydrographical conditions during this season is, however, to the effect that the salinity of the bottom water is lower now than at the beginning of the century (cp. Table 11).

While the change that has taken place after the war in the racial character of the plaice of the Belt Sea and the Baltic would thus seem for the most part to be independent of the hydrographical conditions, it is possible that the variations from year to year are to some degree connected with the hydrographical conditions. During the years for which he was able to determine the racial character of the year classes, i. e. the years 1924—27, A. C. JOHANSEN, as mentioned above, found a distinct co-variation with the salinity of the surface water. But we have seen above that an explanation to the effect that there is a dependency on an indrift in the surface of larvae of the North Sea race must be rejected.

In fact, for the fluctuations in the race character there is an equally good co-variation

1. with the bottom salinity in Nov.—Dec.
2. with the surface temperature in Jan.—Feb.
3. (negative correlation) with the bottom salinity in Feb.—March—April (see Fig. 18).

The fact that a higher salinity at the beginning of the spawning period would cause more plaice of the North Sea race to stay in the Belt Sea for the sake of breeding, would directly explain a connexion with the bottom salinity in Nov.—Dec. Most likely such a connexion exists (cp. a connection between number of cod-larvae and bottom salinity in Nov.—Dec. shown by ERIK M. POULSEN, 1931, p. 97). A connexion with the surface temperature in January—February like the one seen in Fig. 18 cannot be explained from our present knowledge of the biological demands of the plaice eggs of the two races. Beforehand one would expect the biological zero to be lower for the eggs of the Belt Sea plaice than for those of the North Sea, the Baltic race spawning in an area where the temperature during the spawning time is lower than in the areas where the spawning of the North Sea plaice normally takes place. However, the observations in hand show the opposite state of things, for A. C. JOHANSEN and A. KROGH, 1914, found that the biological zero for the development of the eggs of the Baltic plaice must be put at —0.5°, while DANNEVIG puts it at —2.4° C. on the basis of his experiments on plaice of the northern North Sea. The question whether the temperature during the first stages of development of the fry to some degree influences the racial character has not yet been settled.

A connexion between the salinity of the bottom water, i. e. the intensity of the inflow in Feb.—March—April, and the race character, as the one seen in the figure, cannot be explained. One would expect an intense inflow to increase the number of anal fin rays by an increased indrift of larvae of the North Sea race, but apparently we find the contrary. That the racial character does not seem to be dependent on the inflow from the north corresponds fully to what we found above, viz., that an indrift from the north does not perceptibly increase the amount of fry in the Belt Sea.

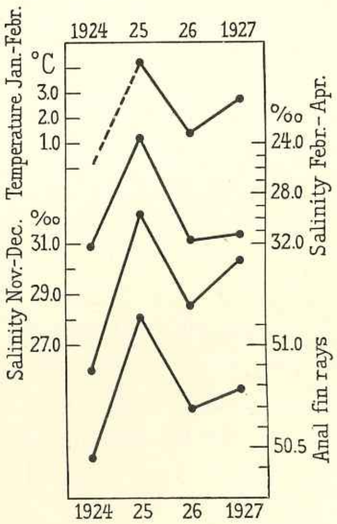

Fig. 18. Variation of the number of anal fin rays (from A. C. JOHANSEN, 1929) compared with bottom salinity in Novbr.—Decbr., surface temperature in Jan.—Febr., and bottom salinity in Febr.—April.

The series of years considered is of course too short for any definite statements, but we may lay down that there is no contrast between the explanations that must be given as to the changes in race character and quantity of fry. The changes in racial character stated after the war must be supposed mainly to be due to the varying extent of the crossing between plaice of the Belt Sea race and of the North Sea race, brought about by the fact that the amount of North Sea plaice breeding in the Belt Sea changes from year to year. Changes in certain hydrographical conditions probably influence the race character of the stock in the area to some extent while at the same time hydrographical factors are greatly affecting the alternations in the amount of fry.

Hence, the connexion between the hydrographical conditions and the quantity of fry must be attributed mainly to the fact that the quantity of eggs hatched is determined directly by the temperature through the influence of the latter on the time of development of the eggs, and that the intensity of the inflow influences the quantity of fry, as there seems to be a southgoing transport in the area of eggs and fry, this transport being determinative of the quantity of fry. Another factor of special importance is, no doubt, the quantity of food, i. e. the contents of plankton in the water, which is mainly determined by the hydrographical conditions. The influence of the salinity at the surface seems to be of less importance than that of the temperature. There is no indrift at the surface of eggs and larvae of any importance for the supply of the area with fry.

Periods in the hydrographical conditions.

Having made sure which hydrographical conditions are determinative of the amount of fry, we shall have to examine whether in these conditions there are periodic fluctuations that may explain the found periodicity in the amount of fry.

A calculation of the correlation coefficient between the surface temperature at Schultz Grund in Jan.—Feb. and values determined from sine functions with varying period and phase for a longer series of years, viz. 1898—1931, will give the figures shown in Table 14.

Table 14. Surface temperature at Schultz Grund in January—February of the years 1898—1931 correlated with values determined from the sine function with varying length of period and phase (phase reckoned from 1898).

$n = 110°$		$n = 120°$		$n = 125°$		$n = 130°$		$n = 135°$		$n = 140°$		$n = 150°$		$n = 160°$	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
350	0.081	0	0.173	70	0.289	190	0.299	225	0.212	230	0.012	80	0.374	40	0.227
20	0.100	30	0.221	100	0.388	220	0.347	255	0.213	260	0.118	110	0.414	60	0.238
50	0.094	60	0.212	130	0.384	250	0.301	285	0.181	290	0.032	140	0.406	80	0.183

For all values of $r > 0.338$ the correlation is significant, P being then less than 0.05. The highest values are found for $n = 125°$ and $\varphi =$ abt. 115°, and for $n = 150°$; $\varphi = 110°$

We find for $n = 125°$

$$\text{for } \varphi = 110°\colon r = 0.404$$
$$\text{for } \varphi = 120°\colon r = 0.405.$$

In both cases the corresponding value of t is 2.40 and $P = 0.02$, and consequently the periodic variation of abt. 2.4 and abt. 3 years in the surface temperature are significant. By eliminating the periodicity of about 2.4 years we shall find a 3.1 years period as in the case of the catch figures.

For the bottom salinity at Schultz Grund in Feb.—March—April the corresponding calculation of the correlation with values from sine functions with varying lenghts of period and phase is given in Table 15.

Table 15. Bottom salinity at Schultz Grund February—March—April 1903—1931, correlated with values determined from sine functions with varying lengths of period and phase (phase reckoned from 1904).

$n = 110°$		$n = 120°$		$n = 130°$		$n = 140°$		$n = 145°$		$n = 150°$		$n = 160°$	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
330	0.089	180	0.132	350	0.324	350	0.363	45	0.572	90	0.488	240	0.203
0	0.119	210	0.186	10	0.341	0	0.371	55	0.585	110	0.534	260	0.216
30	0.114	240	0.152	30	0.317	10	0.366	65	0.580	130	0.509	280	0.194

In this case the calculation is made for the series of years 1903—1931, because the observations of salinity before 1903 must be supposed to be less exact (cp. A. C. JOHANSEN and AAGE J. C. JENSEN, 1926, p. 117).

For $n = 147°$, $\varphi = 83°$ (or $\varphi = 230°$, reckoned from 1903) we get the correlation coefficient $r = 0.591$.

For all values of $r \geqq 0.367$ is $P < 0.05$, and consequently the correlation is significant.

The periodic variation in the temperature and salinity is, however, rather irregular.

For the years 1904—14 and 1920—28, for which the correlation between the hydrographical conditions and the catch figures have been examined the correlation between surface temperature at Schultz Grund in Jan.—Feb. and values from sine functions with varying length of period and phase is shown in Table 16, and the corresponding correlation between bottom salinity at Schultz Grund in Feb.—March—April and values from sine functions with varying length of period and phase in Table 17.

Table 16. Surface temperature at Schultz Grund, January—February of the years 1904—1914 and 1920—1928 correlated with values determined from sine functions with varying length of period and phase (phase reckoned from 1904).

$n = 120°$		$n = 130°$		$n = 140°$		$n = 150°$		$n = 160°$	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
30	0.193	130	0.318	140	0.172	230	0.346	110	0.293
60	0.236	160	0.394	170	0.193	260	0.540	140	0.326
90	0.197	190	0.383	200	0.168	290	0.564	170	0.280
120	0.126	220	0.242	230	0.097	320	0.423	200	0.200

Table 17. Bottom salinity at Schultz Grund in February—March—April of the years 1904—1914 and 1920—1928 correlated with values determined from sine functions with varying length of period and phase (phase reckoned from 1904).

$n = 120°$		$n = 130°$		$n = 140°$		$n = 150°$		$n = 160°$	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
240	0.042	340	0.328	340	0.279	70	0.493	200	0.197
270	0.194	10	0.354	0	0.344	90	0.582	220	0.260
300	0.109	40	0.379	20	0.368	110	0.610	240	0.262
330	0.004	70	0.146	40	0.287	130	0.552	260	0.217

Both the surface temperature in Jan.—Feb. and the bottom salinity in Feb.—Mar.—Apr. showed the greatest co-variation with a sine function where n was about 150°, i. e. the length of period was abt. 2.4 years, and for the years 1904—14 and 1920—28, too, they shows the greatest co-variation with a sine function with about this length of period. Here, too, there is within the considered values for n a less pronounced secondary maximum for $n =$ abt. 130°. Moreover, as in the case of the catch figures, if the period of c. 2.4 years is eliminated, the period with $n =$ c. 130° becomes less distinct and we find a period of abt. 3.1 years ($n =$ c. 110°).

The cause of the periodic variation in the catch figures.

Thus, between the catch figures and respectively the surface temperature in Jan.—Feb. and the bottom salinity in Feb.—Mar.—Apr. we find a very clear correspondence as regards the length of the periodic variations, the catch figures showing a primary maximum for the size of the correlation coefficient for a periodicity of about 2.4 years and a secondary maximum for a periodicity of about 3 years.

Accordingly, the periodic variations in the catch figures the length of period of which is about 2.4—3 years, are naturally explained by the fact that in the hydrographical factors determining the variations from year to year in the catch figures there are the same periodic variations.

Possibly these periodic variations are intensified here, as in the North Sea, by the influence of purely biological conditions, viz., the competition between the two youngest age-groups. As appears from the fishing experiments at the coasts, we find in summer a comparatively large number of plaice of the I-Group at a depth of 1 or 2 m., on an average no less than $^1/_3$ of that of the 0-Group. In many years we find in the coastal fishing experiments a rich I-Group that is even more numerous than the 0-Group that will make a poorer I-Group in the following year. Hence, as each plaice of the I-Group consumes much more food than a plaice of the 0-Group, a rich year class will undoubtedly be able to check the growth of the plaice of the 0-Group to such a degree that comparatively many of them perish. That the density of plaice in the coastal regions perceptibly influences the growth of the plaice has been pointed out by H. Blegvad, 1927, as mentioned above.

2. The period of about 5 years.

This periodicity is not very easily ascertained, and its reality cannot actually be demonstrated on the basis of the material in hand, as it is quite obvious that a variation like the one shown in Fig. 12 C might be due to either non-periodic or periodic conditions. In the hydrographical conditions I have not been able to find any acceptable explanation of such a variation. Possibly it is associated with a period of about 2.5 years, but because of the uncertainty of the periodicity we shall make no further mention of the possible causes, but only point out the possibility that it might also be connected with the average age of propagation of the plaice, this being about 6 years at the beginning of the series of years considered (the years about 1904) and about 4 years at the end of the series.

4. The Stock of Mackerel in the Kattegat and Skagerak.

A. The Yield of the Mackerel Fishery as Representative of the Stock.

The mackerel fishery in the northern Kattegat and the eastern Skagerak is carried on intensely both by Danish and Swedish fishermen. It takes place during the period from May to Sep.—Oct., the mackerel in May—June migrating into this area, where the spawning takes place in June—July. Not only mature, but also young immature mackerel migrate into the Skagerak—Kattegat during May—June (cp. David Nilsson, 1914). The most important gear of the Danish cutters is the drift-net, although during later years considerable quantities of mackerel have been taken in pound net, and also some part in purse-seine and with trolling lines (F. V. Mortensen and A. C. Strubberg, 1931). The Swedes generally use drift-net till the spawning time is over; after this time they use the trolling lines. Further especially seine fishing in the fiords and purse seine fishing play a role (David Nilsson, 1914, Nils Rosén: Årsbok).

After the spawning time part of the mackerel also disperse over the southern Kattegat, the Belts, and the Baltic as far as the mouths of the Gulf of Bothnia and the Finnish Gulf (Embrik Strand, 1931).

Statistics of the yield of the mackerel fishery have been worked out and published in the Bulletin statistique since 1903.

The total yield of the Swedish mackerel fishery in the Kattegat and Skagerak has in the years after 1903 always been greater than that of the Danish mackerel fishery. The Swedish fishery mainly takes place in the eastern Skagerak and the adjacent regions of the Kattegat, while the Danish mackerel fishery is chiefly carried on in the northern Kattegat. Throughout the period after 1903 some mackerel were taken by Danish fishermen also in the central and southern part of the Kattegat and during recent years in the eastern Skagerak, too. Beforehand probably the variations in the yield of the mackerel fishery in the southern Kattegat are de-

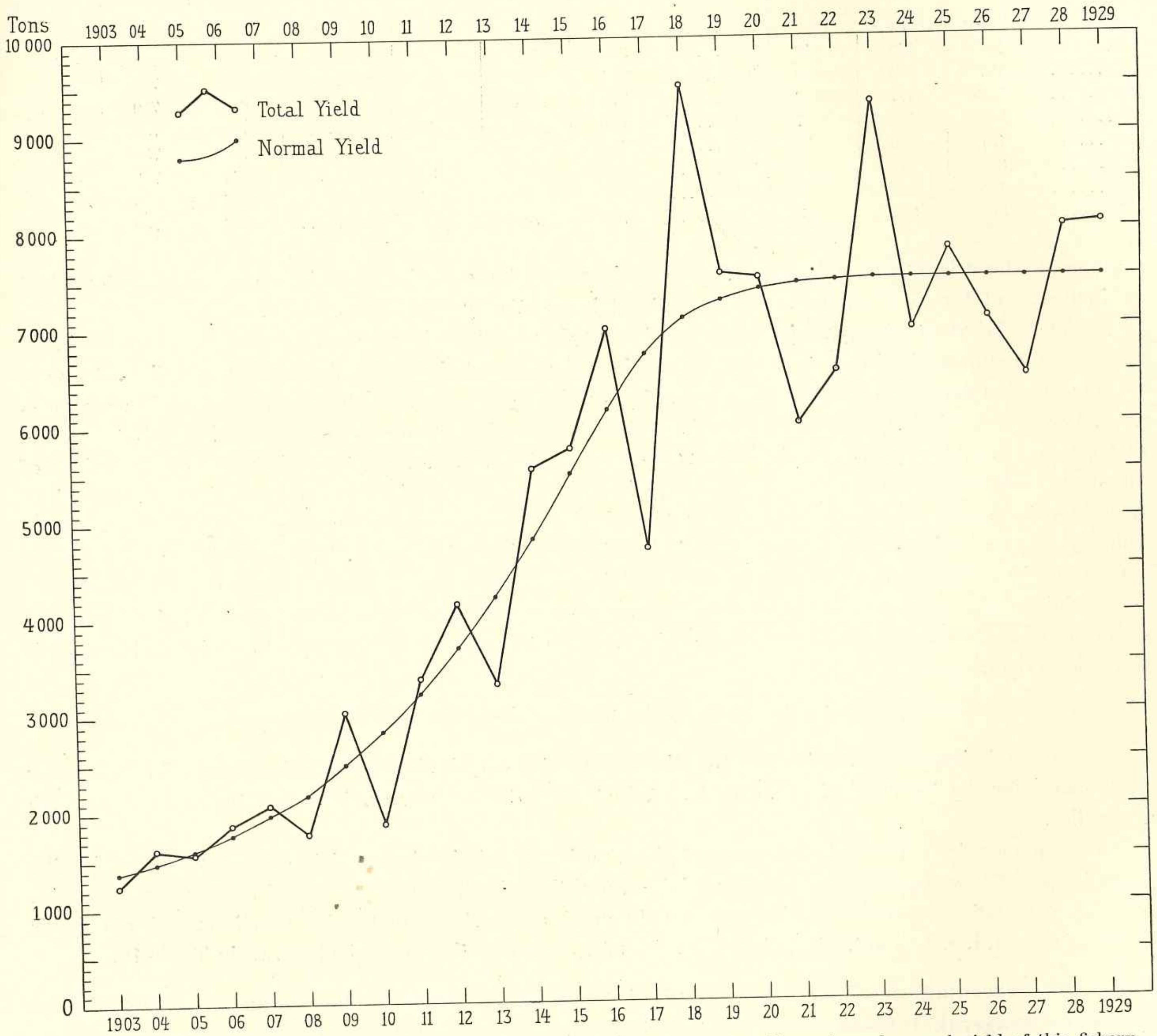

Fig. 19. Total yield of the Danish and Swedish mackerel fishery in the Kattegat—Skagerak, and normal yield of this fishery.

termined by other factors than the variations of the mackerel fishery in the eastern Skagerak and the adjacent part of the Kattegat. As to these latter areas it has been shown by A. C. Johansen, 1925, that the immigration of the mackerel is determined by the hydrographical factors during the spawning time. For one of the areas where mackerel are caught after they have dispersed in search of food, I have been able to make out that the variations from year to year in the yield of the fishery are due to the variations in the hydrographical conditions during the months when this fishery is carried on (Aage J. C. Jensen, 1930), and *a priori* one would expect the same to be true of the southern Kattegat. The quantity of mackerel taken by the Danish fishermen in the

Table 18. Total yield of the Danish and Swedish mackerel fishery in the Kattegat and Skagerak in 10.000 kgs., normal yield for this fishery and per cent. anomalies.

Year	Yield	Normal yield	Per cent. anomalies	Year	Yield	Normal yield	Per cent. anomalies	Year	Yield	Normal yield	Per cent. anomalies
1903......	125	138	— 9	1912......	415	370	12	1921......	600	745	— 19
1904......	162	148	10	1913......	329	423	— 22	1922......	655	749	— 13
1905......	157	161	— 3	1914......	554	483	15	1923......	932	750	24
1906......	188	177	6	1915......	576	551	5	1924......	698	750	— 7
1907......	209	195	7	1916......	701	616	14	1925......	780	750	4
1908......	191	218	— 12	1917......	471	673	— 30	1926......	708	750	— 6
1909......	305	248	23	1918......	951	710	34	1927......	647	750	— 14
1910......	189	283	— 33	1919......	756	728	4	1928......	804	750	7
1911......	338	323	5	1920......	752	739	2	1929......	806	750	7

southern Kattegat is, however, so small in comparison with the quantity taken in the northern Kattegat that an inclusion of the yield of the southern Kattegat is practically of no importance.

The total yield of the Danish and Swedish mackerel fishery in the Kattegat and Skagerak must, on account of the intense fishing on the stock, be considered representative of the size of the population. It should be kept in mind that the records on the yield of the Danish fishery down to 1915 incl. are given in scores and are here converted into kilogs. by means of a certain "conversion number", 20 pieces being put at a weight of 8 kilogs. (A. C. Johansen and E. Neergaard-Møller, 1912, p. 87). For the estimate of the variations of the stock a statement of the yield of the fishery in weight or number is, of course, of different value. The variations from year to year in the number of individuals depend on the quantity of fry produced in the different years to a higher degree than the variations in the weight of the stock. As each individual of the older age-groups is of a far greater weight than an individual of one of the younger ones, while the number of individuals of a year class at the same time decreases from year to year, the effect of the relative frequency of the individual year class is more or less reduced when the yield of the fishery or the size of the stock is given in weight.

B. Periodic Variations in the Yield of the Fishery.

The total yield of the Danish and Swedish mackerel fishery is shown in Table 18 and Fig. 19 together with values for the "normal yield". In Fig. 20, in the continuous curves, is shown the percentage catch anomalies.

It appears from this that there seems to be a periodic variation in the yield of the fishery. During the years 1903—1929 we count 11 maxima or minima, and thus the length of the period approaches 2.5 years.

A calculation of the correlation between the catch anomalies and the sine functions with about this length of period, i. e. $n =$ abt. 145°, gives the values for the correlation coefficient shown in Table 19.

Table 19. Percentage anomalies for the yield of the Danish and Swedish mackerel fishery in the Kattegat—Skagerak, 1903—1929, correlated with values determined from sine functions with varying length of period and phase from 1903.

n = 90°		n = 100°		n = 110°		n = 120°		n = 125°		n = 130°		n = 140°		n = 145°		n = 150°		n = 155°		n = 160°	
φ°	r	φ°	r	φ°	r	φ°	r	φ°	r	φ°	r	φ°	r	φ°	r	φ°	r	φ°	r	φ°	r
340	0.147	100	0.262	200	0.130	120	0.136	320	0.176	40	0.317	80	0.034	120	0.208	140	0.542	190	0.622	250	0.513
0	0.186	120	0.320	230	0.250	150	0.167	350	0.267	70	0.389	110	0.047	130	0.235	150	0.548	200	0.645	260	0.523
20	0.201	140	0.338	260	0.286	180	0.151	20	0.302	100	0.338	140	0.057	140	0.202	160	0.540	210	0.648	270	0.519
40	0.196	160	0.303	290	0.268	210	0.097	50	0.258	130	0.236	170	0.048	150	0.181	170	0.518	220	0.626	280	0.498

It is seen that the highest values are found for the length of period 360:155° = 2.32 years and the phase 210° (reckoned from 1903). For the series of years in question all correlations where the coefficient $r > 0.381$ must be considered significant, P being in this case < 0.05. For the coefficients $r > 0.445$ is $P < 0.02$, and for the coefficients $r > 0.487$, is $P < 0.01$. Thus the periodic variation in the yield of the mackerel fishery

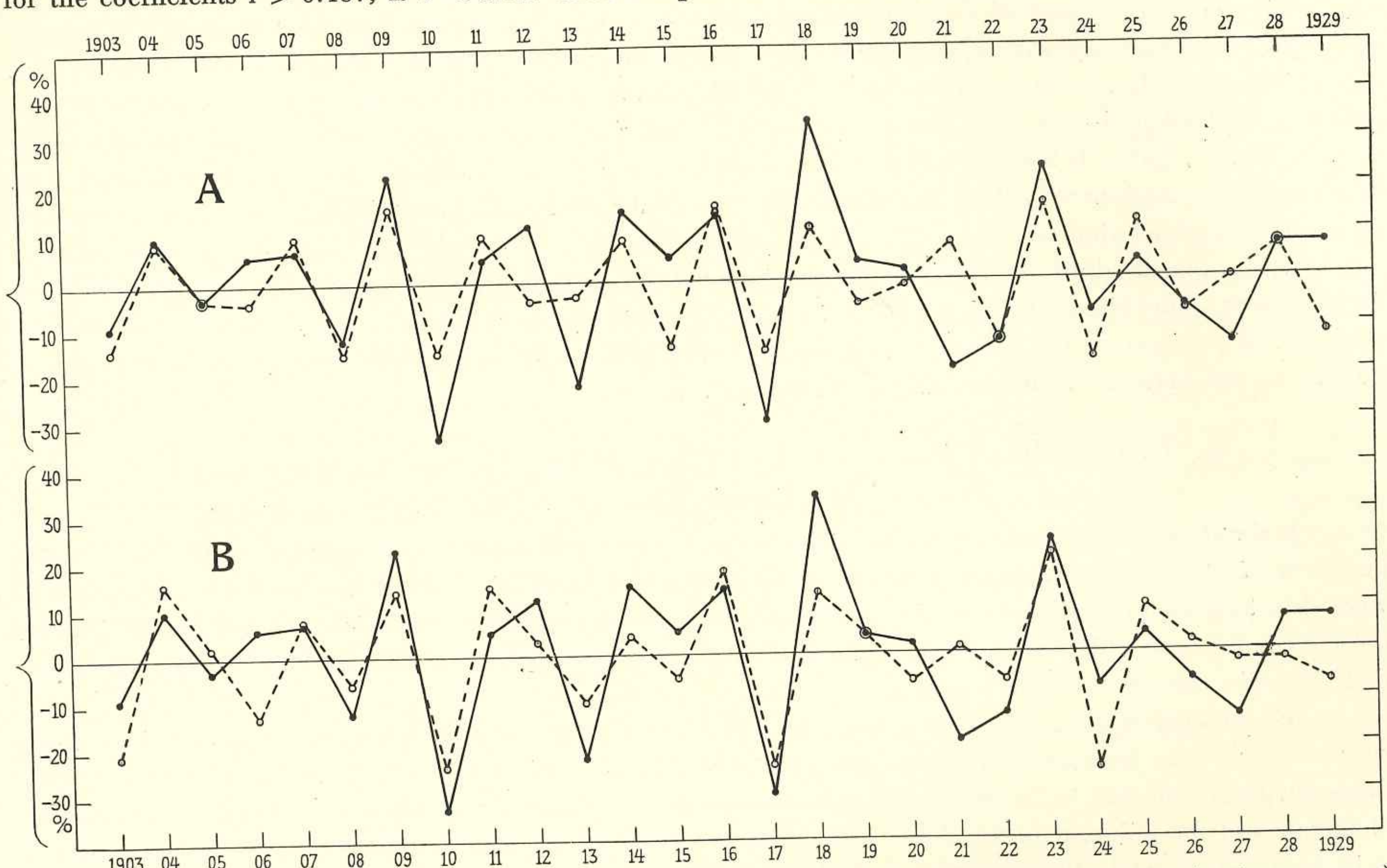

Fig. 20. Per cent. anomalies of the yield of the Danish and Swedish catch of mackerel in Kattegat—Skagerak (continuous curves) compared with
in A: values determined from the sine function $y = 15 \cdot \cos(155\,T - 210)$.
in B: values from $y = 15 \cdot \cos(155\,T - 210) + 8 \cdot \cos(100\,T - 140)$.

with a period of about 2.3 years must be considered a reality, but further there seems to be found periodic variations where $n = 130°$ and where $n = 100°$.

The regression coefficient between the values of the sine function $y = \cos(155\,T - 210)$ and the catch anomalies is 15.

In Fig. 20, A the sine function with these values is compared with the catch anomalies.

Table 20. Catch anomalies reduced for $y = 15 \cdot \cos(155\,T - 210)$ correlated with values determined from sine functions with varying lengths of period and phase from 1903.

n = 90°		n = 100°		n = 110°		n = 120°		n = 130°		n = 140°	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
320	0.176	120	0.428	230	0.329	300	0.313	40	0.333	50	0.050
350	0.250	130	0.438	260	0.401	330	0.324	70	0.404	80	0.065
20	0.261	140	0.443	290	0.419	0	0.248	100	0.383	110	0.062
50	0.205	150	0.440	320	0.315	30	0.106	130	0.242	140	0.042

A curve of catch reduced for the sine curve seems to indicate the existence of a periodic variation with a length of period of abt. 3.5 years. A calculation of the correlation between the catch anomalies, where the values determined from sine function $y = 15 \cdot \cos(155\ T - 210)$ are eliminated, and values determined from sine functions with varying lengths of period and phase, gives the coefficients shown in Table 20.

We note that the best co-variation is found for n = c. 105°, i. e. with a length of period of c. 3.4 years, and that the periodicity with n = c. 130° found in the original catches of mackerel is also distinct here.

The regression coefficient between the reduced catch anomalies and the sine function, where $n = 100°$ and $\varphi = 140°$ is found to be = 8, and the values of the last sine function may then be combined with the first one. In Fig. 20, Curve B these combined sine functions are compared with the percentage catch anomalies. The correlation coefficient between the actual catch anomalies and the theoretical catch anomalies determined from the combined sine functions (Fig. 20, B) is 0.729.

While the standard deviation for the percentage catch anomalies is 16.1 per cent., it is 11.0 per cent. for the catch values eliminated for $y = 15 \cdot \cos(155\ T - 210) + 8 \cdot \cos(100\ T - 140)$. Consequently, we may take abt. 30 per cent. of the variations from year to year in the statistic statements of the size of the catch to be due to the periodic variations in the catch yield.

C. Discussion of the Causes of the Periods Found in the Fishery.

Factors influencing the yield of the fishery.

It should be noted that the lengths of the periods stated are nearly the same as two of those found for the stock of plaice in the southern Kattegat and the Belt Sea. As to this stock it was shown that the periods were due to periodic variations in the hydrographical conditions, and so there is a *priori* a possibility that the same is the case with these periodic variations in the yield of the mackerel fishery in the eastern Skagerak and the adjacent parts of the Kattegat.

As mentioned above A. C. Johansen has demonstrated a connexion between the variations from year to year in the hydrographical conditions in the Kattegat and in the yield of the mackerel fishery. He supposed the connexion to be due to the fact that the greatest quantity of mackerel migrate to the eastern Skagerak and the adjacent parts of the Kattegat in the years when the temperature of the surface water is at its lowest, because in those years they find the best spawning conditions. It will be worth while to make this connexion the object of a closer investigation on the basis of the material from a longer series of years that is now available.

At a calculation of the correlation between Danish and Swedish catches in the Kattegat and Skagerak in 1903—1929 and respectively temperature and salinity at the surface in the Kattegat, calculated as the average of temperature and salinity at the Skagens Rev, Anholt Knob, and Schultz's Grund Light Vessels, we get the coefficients shown in the below Table 21.

Table 21. Danish and Swedish catch of mackerel in the Kattegat—Skagerak, 1903—1929, correlated with temperature and salinity at the surface.

		Feb.	March	April	May	June	July	Aug.	Sep.
Kattegat	Temperature	— 0.365	— 0.299	— 0.073	— 0.029	— 0.438	— 0.260	— 0.193	— 0.280
	Salinity	— 0.064	— 0.362	— 0.313	0.204	0.400	0.375	0.331	0.331
Skagens Rev	Temperature	— 0.298	— 0.295	— 0.058	— 0.073	— 0.323	— 0.295	— 0.202	— 0.348
	Salinity	— 0.117	— 0.392	— 0.329	— 0.042	0.208	0.475	0.452	0.326

As mentioned above all coefficients higher than 0.379 are significant when calculated for 27 years, P being in this case smaller than 0.05. It is seen that a significant correlation exists between catch and respectively temperature and salinity in June but in no other case.

If we correlate the Danish and Swedish catches with respectively temperature and salinity at surface at the Skagens Rev, we get the correlation coefficients also given in Table 21. It is seen that there is here a significant correlation with the surface salinity both in March and in July—August but not with the temperature. The correlation coefficient between catch and mean salinity in July—August is 0.489. That we cannot demonstrate any connexion with the temperature is explained by the fact that the temperature at the Skagens Rev and the surface temperature in the Kattegat do not correspond very well, because, with a westerly and south-westerly current, the water here often comes direct from the Skagerak. If we correlate the catch with the surface temperature in June at the Læsø Trindel and at Schultz's Grund we get the coefficients 0.438 and 0.463, respectively.

The statistical statements for recent years are more exact than for the first of the years considered here. If, therefore, we calculate the correlation coefficients for the years after 1909 only, we get higher coefficients than those found above in the cases where the correlation was significant. Thus, if the catch is correlated with surface temperature and salinity in the Kattegat in June during the years 1909—1929, we get $r = 0.455$ and $r = 0.477$, respectively.

If we inquire into the biological cause of the significant correlations found, it should be kept in mind that the stock of mackerel dealt with in the preceding cannot be considered a biological unity, as it consists partly of mackerel which have entered the area for the sake of spawning, partly of spent mackerel straying in search of food, and finally of some young immature fish which must be supposed to have immigrated into the area in search of food. We may get a somewhat purer material by separately considering partly the yield of the Danish fishery in the Kattegat, and partly the yield of the rest of the fishery considered above. A correlation of the yield of the Danish fishery in the Kattegat with respectively the surface temperature and salinity in the Kattegat gives the coefficients shown in the below Table.

Table 22. Danish catch of mackerel in the Kattegat, 1916—1930, correlated with the surface temperature and salinity.

	Feb.	March	April	May	June	July	Aug.	Sep.	Oct.
Temperature	0.247	0.245	0.217	0.155	— 0.185	— 0.115	— 0.163	— 0.550	— 0.112
Salinity	0.348	— 0.637	— 0.632	— 0.184	0.602	0.350	0.234	0.098	..

All coefficients higher than 0.513 being significant here, because P for these is smaller than 0.05, it is seen that there is a real co-variation with the salinity in March, April and June but not with the temperature in June, like the one found for the combined Danish and Swedish fishery in the Kattegat—Skagerak. For $r > 0.591$ is $P < 0.02$. There is, however, a significant correlation with the temperature in September.

A corresponding calculation of the correlation with the surface temperature and salinity in the Kattegat made for the rest of the Danish-Swedish mackerel fishery in the Kattegat—Skagerak, i. e. the one which mainly takes place in the Skagerak, gives the coefficient shown in the below Table 23.

Table 23. Swedish catch of mackerel in the Kattegat—Skagerak and Danish catch of mackerel in the Skagerak, 1916—1929, correlated with the surface temperature and salinity in the Kattegat.

	Feb.	March	April	May	June	July	Aug.	Sep.
Temperature	..	..	..	0.000	— 0.502	— 0.306	— 0.136	— 0.233
Salinity	— 0.292	— 0.560	— 0.567	— 0.195	0.427	0.243	0.325	0.324

After some time the surface of the Eastern Skagerak is made out to a considerable degree by the same bodies of water as were representative of the surface of the Kattegat (namely the outflowing water from the Baltic, the "Baltic current"), so that we may use the hydrographical conditions of the Kattegat as a measure of the hydrographical conditions of the Skagerak.

It is seen that there is here a distinct negative correlation with the salinity of March—April and a positive correlation with the salinity of June quite similar to those found for the Danish fishery in the Kattegat, but further there seems to be a connexion with the temperature of the surface in June. There is no significant correlation with the surface temperature in September.

We see then that in the fishery of the Skagerak there seems to be a connexion with the surface temperature, but the same is not the case with the fishery in the Kattegat. This no doubt means that the explanation of the cause of the variations from year to year in the yield of the mackerel fishery given by A. C. Johansen holds good of the fishery carried on in the Skagerak, while the fishery in the Kattegat depends on other causes. In both areas the yield of the fishery is negatively correlated with the surface salinity in March—April and positively correlated with the salinity in June. The salinity is a measure of the intensity of the current, and hence the found connexions indicate that the yield of the mackerel fishery is great in years with an intense outflow of Baltic water in March—April and a weak outflow in June. The former takes place at a time when the mackerel of the North Sea have not yet immigrated to the Skagerak—Kattegat, and consequently the connexion must be an indirect one, or must be due to the fact that the salinity in March—April is negatively correlated with the salinity in June (cp. A. C. Johansen, 1925). The connexion may be an indirect one, as an intense outflow of Baltic water will cause a comparatively intense inflow of North Sea water to the Skagerak—Kattegat during the following time. If we correlate the catch with the bottom salinity at Schultz's Grund we get the following coefficients.

Table 24. Catch of mackerel correlated with bottom salinity at Schultz's Grund.

Salinity in:	April	May	June
correlated with			
Danish catch in the Kattegat (1916—30)	— 0.058	0.467	0.099
Danish-Swedish catch in the Kattegat—Skagerak (1903—29)	0.275	0.563[1]	0.370

[1] For the years 1916—1929 the coefficient becomes $r = 0.670$.

The displacement in an inward direction of the waters of the bottom layer which takes place as a reaction against an outflow, occurs so soon after the outflow in question, that we get a very small shifting of phase between the oscillations in the salinity of the surface layer and the bottom layer. Hence an intense outflow in the surface layer in March—April will bring about an intense inflow in the southern Kattegat as early as April—May. Therefore, as might be expected, there is a positive correlation between the catch and the bottom salinity at Schultz's Grund during these months. An intense outflow through the Kattegat in March—April of a certain year will make itself felt in the Skagerak one or two months later, i. e. in April—May, and cause an intense inflow from the North Sea into the Skagerak, especially in May. This is the very time when the mackerel immigrate to this area, and the connexion between the yield of the mackerel fishery and the intensity of the outflow must no doubt partially be explained as a consequence of an intense outflow causing a more intense inflow, which again causes a comparatively large number of mackerel to migrate into the Skagerak—Kattegat area. But as pointed out by A. C. Johansen, 1925, p. 17, such an inflow will further contribute to the surface water becoming colder than normally, which will no doubt make more mackerel enter the Skagerak for the sake of spawning.

It is worth noting that for the yield of the mackerel fishery in the Kattegat there was found a negative correlation with the surface temperature in September, i. e. the same conditions as were found for the mackerel fishery in the Sound (AAGE J. C. JENSEN, 1930, 2).

Periodic Variations in the Hydrographical Conditions.

Having investigated which hydrographical conditions must be supposed to influence the yield of the mackerel fishery in the Kattegat—Skagerak, we shall now examine whether in these conditions there are periodic variations of the same length as those found in the mackerel fishery.

In the below Table are shown the correlations between the surface salinity at Skagen in March and values determined from sine functions with varying length of period and phase. It is seen here that the correlations show maxima for very nearly the same values of n as the correlations between the catch of mackerel and the sine functions.

Table 25. Salinity at Skagens Reef, surface, in March 1903—1929, correlated with values determined from sine functions with varying length of period and varying phase from 1903.

n = 90°		n = 100°		n = 110°		n = 120°		n = 130°		n = 140°		n = 150°		n = 160°	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
260	0.248	0	0.297	30	0.098	300	0.190	120	0.174	260	0.184	300	0.385	30	0.235
280	0.262	20	0.310	50	0.105	330	0.218	150	0.186	290	0.207	330	0.412	60	0.259
300	0.240	40	0.276	70	0.094	360	0.179	180	0.131	320	0.176	360	0.363	90	0.218

From this table it is seen, that the correlation between the surface salinity and sine functions with a period of abt. 3.5 years is rather small. Some other hydrographical factors, however, which were found to co-variate with the yield of the mackerel fishery, exhibit a significant correlation with the sine functions with this length of period, e. g. the surface salinity at Skagen in July—August.

Table 26. Salinity at Skagens Reef, surface, July—August 1903—1929, correlated with values determined from sine functions with varying length of period and varying phase from 1903.

n = 100°		n = 110°		n = 120°	
$\varphi°$	r	$\varphi°$	r	$\varphi°$	r
90	0.177	260	0.386	60	0.220
100	0.180	270	0.388	70	0.226
110	0.175	280	0.377	80	0.225

It has been shown above that in the salinity in the southern Kattegat (Schultz's Grund) during the winter and spring months there exist periodic variations with about the same lengths of period as those found for the mackerel fishery.

Thus we may conclude, that the periodic variations of c. 2.3—3.4 years, periodicity stated above in the mackerel fishery are due to periodic variations in the hydrographical factors determining the variations from year to year of the same lengths in the stock of mackerel worked.

5. The Stock of Herring at Bornholm.

A. Periodic Variations in the Yield of the Herring Fishery.

As mentioned above it has been possible to demonstrate a variation with a length of period of 3.7 years in the yield of this fishery (AAGE J. C. JENSEN, 1927, 1).

The herring caught in the true Baltic by Danish fishermen probably belong to two different races one of which lives in the Baltic during the whole of its life, viz., the herring at Bornholm which is called the Kivik Herring (S. NILSSON, 1855) or the Baltic Bank Herring (FR. HEINCKE, 1898), whereas the herring at the eastern coasts of Seeland, Møen, and Falster is a Herring, which lives in the Kattegat outside the spawning time (A. C. JOHANSEN, 1927, 1).

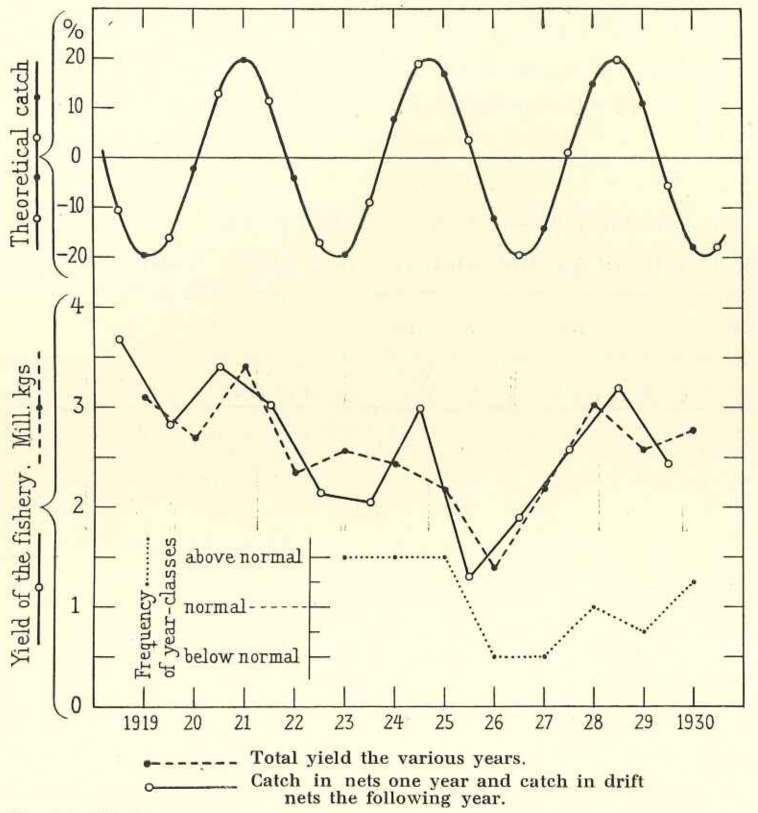

Fig. 21. Yield of the herring fishery at Bornholm compared with a sine curve of 3.7 years periodicity, and with the frequency of the year classes.

The above mentioned investigation of the periodic variation covered the years 1885—1914 only, as there seems to have been so considerable irregularities in the fishery during the war and the first years after the war, that an inclusion in the investigation of the years after 1914 would seem to serve no purpose.

However, we have now statistic reports on the yield of the fishery for 12 years after the war, i. e. up to 1930 incl. Hence it would be of interest to make the alternations in the yield of the fishery during the war and later years the object of a closer investigation. It should be remembered, however, that the yield of the herring fishery down to 1915 incl. is given in numbers and after this year in cubic measures or weight; this causes that the statements of the statistics from the time before 1916 express the yield in another way than after this year (cp. p. 52).

The yield of the herring fishery at Bornhom during the years 1918—30 is given in Fig. 21, and it is seen here that maxima appear also for the years 1921, 1923—24, 1928, and 1930, so that the period of 3.7 years would seem to assert itself within this series of years, too. A normal curve for this series of years cannot, however, be drawn on the basis of the variations in the fishing intensity as was possible for the period 1885—1914 (a rather isolated case). During the years after 1919 the number of fishing boats increased rapidly because an intense plaice fishery was commenced in this area, and during recent years this plaice fishery has occupied a varying number of boats. For these years, however, there have probably been rather small changes only, in the intensity of the herring fishery.

The herring fishery at Bornholm is partly a drift-net fishery carried on during May—August with a maximum in July—August, partly a net fishery during the rest of the year (F. V. MORTENSEN and A. C. STRUBBERG, 1931, p. 30). I have previously pointed out that the variations in the yield of the drift-net fishery in the Sound and the true Baltic are uniform with those of the net and pound-net fishery one or two years before, which is a natural consequence of the herring caught in the drift-net fishery being mostly one or two years older than those caught in the net and the pound-net fishery (AAGE J. C. JENSEN, 1929, 2, p. 6). If we combine the yield of the net and drift-net fishery of Bornholm in such a way that the yield of the net fishery is added to that of the drift-net fishery of the following year, we get the catches shown in Table 27. In this Table is also shown the total yield of the herring fishery at Bornholm from each of the years 1919—1930. In Fig. 22 the variations from year to year in the catch is compared with a sine function, the length of period of which is 3.7 years and the phase 1.90 years, reckoned from 1885. It is seen that for the years after the war there has been a periodic variation in the yield of the herring fishery at Bornholm with the same length of period as the one found for the years 1885—1914. At the investigation of the periodicity in the fishery during the latter series of years was found the best correspondence with a sine function where the phase was 1.8 years, reckoned from 1885. But also when values from a sine function with a phase of 1.9 years were correlated with the catch anomalies of the herring fishery, a real co-variation was found, r in this case being 0.569, with $\sigma_r = 0.124$ (calculated for 30 years). For the rest, the difference in phase is so small that most probably it is only due to the fact that we should have substituted a period of abt. 3.72 years for that of 3.70 years. Thus there is no indication of a change of phase due to a changed fishing intensity.

Table 27. Catch of herring at Bornholm.

Total catch		Catch in nets one year and in drift-nets next year	
Year	Tons	Years	Tons
1919	3090	1918—19	3680
1920	2701	1919—20	2827
1921	3425	1920—21	3418
1922	2348	1921—22	3039
1923	2577	1922—23	2149
1924	2449	1923—24	2046
1925	2192	1924—25	2998
1926	1409	1925—26	1301
1927	2203	1926—27	1908
1928	3022	1927—28	2578
1929	2578	1928—29	3192
1930	2773	1929—30	2449

In my above cited paper from 1927, it could be shown that in the years considered there seemed to be a periodic variation of about 11 years; the reality of this periodicity was very uncertain on account of the great length of the period in proportion to the length of the series of years considered. It was shown in a figure that there was no co-variation with the sun-spots.

If these variations were of a cyclic-like periodicity, the fishery would have shown a maximum between 1925 and 1930, but it has not done so.

The variations in the yield of the herring fishery in the other parts of the Danish waters are so greatly influenced by the size of the stock of cod, that only an insignificant periodicity in the yield of the herring fishery may be expected here. The rapid increase in the size of the stock of cod after 1918 has caused a very great reduction of the stock of herring (Aage J. C. Jensen, 1929, 2).

B. The Cause of the Periods in the Herring Fishery at Bornholm.

In my 1927 paper quoted above I explained the period of 3.7 years to be a consequence of the quantity of spawning herring influencing the quantity of fry and hence the size of the stock of herring some years later.

K. A. Andersson, 1930, has not been able to ascertain whether the hydrographical changes are the cause of these oscillations in the yield of the herring fishery, but has pointed out that a rich spawning year of the autumn spawning herring in the Baltic seems to be followed by a rich spawning year of the Norwegian spring herring in the following year, and that this would seem to indicate that the oscillations are caused by meteorological-hydrographical factors.

I have tried to find a period of 3.7 years in the hydrographical conditions of the Baltic, but without success. Still it should be noted that the regular observations in the true Baltic only reach a depth of 45—50 m., i. e. only some way down into the upper water layers, and further have taken place during the years after 1923 only (Svenska Hydrografisk-biologiska Kommissionens Fyrskeppsundersökning, Göteborg), whereas regular measurings of temperature and salinity covering a longer period have been carried out only in the surface water (Nautisk-meteorologisk Aarbog, København). In some hydrographical conditions in the Kattegat and the Belt Sea, I have found (cp. above) periodic variations with lengths of period differing not very much from 3.7 years.

We shall inquire more closely into the possibility that a purely physiological cause is determinative of the periodic fluctuations in the yield of the herring fishery.

The fluctuations are not due to a biocoenosis with another species of fish as was the case in the investigation of VOLTERRA's. Among the fish of the Baltic the cod is by far the most conspicuous enemy of the herring. The yield of the cod fishery (and the stock of cod) is subject to a variation totally different from that of the herring fishery at Bornholm, with maxima within this century in 1909, 1915, 1920, and 1926.

In the Danish waters Copepodes are by far the most important food matter of the herring (P. JESPERSEN, 1928). According to JESPERSEN Copepodes are found on an average in abt. 75 per cent. of the herrings examined, and quantitatively, too, they constituted the greater part of the food. Thus there is a possibility that the biocoenosis with the Copepodes is the cause of the periodic fluctuation in the fishery, but we cannot decide on this cause until quantitative determinations of the variations from year to year in the quantity of Copepodes during a longer series of years are available.

Another possibility is the above mentioned explanation formerly pointed out as the natural one by the writer, viz., that the variations are due to the fact that the quantities of fry produced by the herring are dependent of the quantity of spawning herring, and that the stock of herring during the following years, and hence the stock of spawning herrings — and therefore also the yield of the fishery — some years after the spawning year in question are determined by the quantity of fry.

If this be the case, the length of the period must be equal to the average age of the spawning herring.

In the below Table are compared the age-analyses in hand from the Bornholm Basin, and it is seen that the average age is abt. 3.8 years. For kind information on the maturity of the herring and the composition of the catches in 1926—1929 I am indebted to CHR. HESSLE.

The calculation of the average age is based on age-analyses made for 5 years, and considering the small length of this series of years the correspondence with the length of period (about 3.7 years), found for the herring fishery at Bornholm, is quite satisfactory.

Table 28. Per cent. composition in age groups of autumn spawning herring from the Bornholm Basin according to Chr. Hessle and K. A. Andersson.

Year	Date	Age, years							Average age years
		2	3	4	5	6	7	8	
1924	4/11	57	7	2	7	7	14	5	3.6
1926	10/8	1	22	72	3	1	..	1	3.8
1927	31/8, 8/9, 18/10	4	58	30	6	0.5	0.5	1	3,5
1928	6/9	..	10	73	13	4	..	..	4.1
1929	18/12	7	18	32	34	7	2	..	4.2
Mean...	..	..	..	..	..	..	..	..	3.8

Finally it is of interest to examine the relation between the quantity of herring fry of the different years and the yield of the fishery. A. C. Johansen, 1930, has made such a comparison as regards the Sound and found that the quantity of fry during the years 1925—28 varied in accordance with the quantity of spawning herring so that the investigation would seem to be in favour of the view set forth by the present writer.

According to kind information from Dr. H. Blegvad the frequency of the year classes in the true Baltic in the years 1923—1930 was:

1923 above normal
1924 above normal
1925 above normal
1926 below normal
1927 below normal
1928 about normal
1929 somewhat below normal
1930 somewhat above normal.

These frequencies are presented graphically in Fig. 21 together with the catch yield of the various years (the dotted curves), and actually there seems to be a correspondence between the catch yield of a certain year and the amount of herring fry in this area of the same year too, so that a comparatively large catch, (i. e. a great stock of herring) will produce comparatively much fry and, inversely, a small population will produce a comparatively small quantity of fry. This, then, would support the supposition that the periodicity in the yield of the herring fishery at Bornholm depends on the quantity of spawning herring, i. e. on a purely biological cause.

A periodicity caused by this reason, naturally will run only a few periods before damped by the effect of the fact that the spawning of a certain year class ranges over more than one year, if the amount of fry produced by a stock of spawning herring is linear proportionate with the size of the stock. If it increases proportionately very much when the stock of spawning fish becomes larger, the variations will not be damped That this is the case until a certain size limit of the stock, is very natural, in that the conditions for fertilization of the eggs are better if there are many fish spawning, than if there are a few only. If the size of the stock is very large in proportion to the areas where the eggs are deposited, many eggs will always be fertilized, but in this case only proportionately few come to development on account of the eggs then being deposited in thick layers where only the superficial ones develop (E. Lea, 1930, p. 114). As far as is known, this has never been the case at Bornholm.

If the connexion between the amount of spawning fish and the amount of fry, as set forth above, is not linear, associated periods should be a consequence. It is very possible, that the variations from year to year, which for the years 1885—1914 exhibited a periodicity of 11 years, are due to such associated variations

6. Summary. Causes of Periodic Variations in the Yield of the Fisheries.

In the investigations made in the preceding chapters it has been shown, by using the calculation of probabilities as an objective criterion, that in the various stocks of fish and fisheries there are periodic variations from year to year with a length of period of some few years.

In the Danish plaice fishery in the North Sea was found a period of about 2.7 years.

In the stock of plaice in the southern Kattegat and the Belt Sea were found periods of about 2.4 years and about 3.3 years, and in the mackerel fishery in the Kattegat—Skagerak periods of about 2.3 and about 3.4 years.

It was shown that in each case there were corresponding periods in the hydrographical conditions, which determine the variations from year to year in the stocks of fish and in the fisheries, and hence the periods found here must be ascribed to the periodic variations in the meteorological-hydrographical conditions.

The causes of the periodic variations found in the meteorological-hydrographical conditions are not discussed here. Suffice it to mention that various authors have examined periodic variations with about the same lengths of period as those found here. Thus it has been shown by FRIDTJOF NANSEN and BJ. HELLAND-HANSEN, 1917, p. 259, that in the meteorological conditions we may expect to find lengths of periods of between 2 and 3 years, in consequence of the fact that in the solar spots there are periods of 2 years and of between 3 and 4 years. A two years' period has been demonstrated by B. HELLAND-HANSEN (MURRAY and HJORT, 1912, p. 301) in the temperature of the water at the coasts of Norway, by JEE in the surface temperature of the Atlantic in 50° N. 20° W., by MATTHEWS in the salinity of the Channel, and by D'ARCY THOMPSON in the surface temperature of the southern North Sea. W. B. SCHOSTAKOWITCH has thought it possible to demonstrate periods of about 3 years in a great many meteorological (and biological) conditions. It is worth noting that theories on the existence of periods of 4.5 and 9 years due to the tide-effecting forces, have been put forth by B. STORROW and ED. LE DANOIS. Such periods can hardly be demonstrated in the meteorological-hydrographical conditions of the waters round Denmark; at any rate they are so insignificant that they cannot be supposed to be the cause of periodic variations in the yield of the fisheries. Periods of longer duration, as demonstrated by H. W. HARVEY, HANS PETTERSSON, OTTO PETTERSSON, D'ARCY THOMPSON and B. STORROW, no doubt exist, but cannot be traced in the material treated here.

However, the periodicities discussed in the meteorological-hydrographical conditions in this paper are not very regular, and for various series of years we may find somewhat differing values of the lengths of period.

Biological conditions are of considerable importance for the variations. The period of 2 and 3 years in the size of the stocks of plaice is intensified by the competition for food among the two youngest age-groups.

In the yield of the herring fishery at Bornholm there is a periodic variation of about 3.7 years. Most probably it is due to purely biological causes and must be explained as the effect of the quantity of spawning herring on the size of the stock some years later. As mentioned on p. 5 J. P. JACOBSEN and A. C. JOHANSEN have pointed out a similar periodicity of about 5 or 6 years in the salmon fishery in the Gudenaa, which has now practically come to an end.

In the Danish plaice fishery in the North Sea was found a period of about 5 years which must be supposed to be due to purely biological conditions, viz. the competition for food among the plaice on the nursery grounds.

Further we found in this fishery a periodic variation with a length of period of about 10 years. Even if the latter could be proved significant, it cannot be concluded that it should represent a real periodic variation; for within the series of years considered we have only about $2^1/_2$ periods of the said length, and it may be due to a mere error in the construction of the normal curve and thus will not correspond to any change in the stock of plaice. In the catch per cutter day (cp. Fig. 7) there was apparently no such periodicity. Furthermore the variation might be due to causes which actually are non-periodic.

It has been pointed out (p. 6) that periodic variations (associated periods) may arise when the original periodicity does not cover a whole number of years. Such periodic variations seem to be the cause of variations in the herring fishery at Bornholm. However from the statistical material treated here, it is not possible to decide whether dependencies determining the periodic variations from year to year in the stocks of fish and fisheries are linear, but we may expect by the method applied in this paper, to get information as to this point in the future.

On the basis of the investigations made we may lay down that in the waters round Denmark there are periodic variations in various stocks of fish and fisheries which are due to the fact that in the meteorological-hydrographical conditions influencing the said variations from year to year there are periodic variations with lengths of period of about 2.5—3.5 years. Biological conditions play a great part.

Further there are periodic variations from year to year in various fisheries, which are due to purely biological conditions within the stock of fish in question, viz.:

1. Periods brought about by the quantity of spawning fish (which appears from the yield of the fishery) determining the amount of fry and hence the size of the stock and the yield of the fishery some years later.
2. Periods brought about by the competition for food within the same species.

But I have not found any periodic variations identic to those treated by Volterra, which are due to the fact that one species lives on the other.

7. Dansk Resumé (Danish Summary).

Undersøgelsen af de biologiske Aarsager til Variationerne i Fiskebestandene og dermed i Fiskeriernes Udbytte er en af Fiskeribiologiens vigtigste Opgaver. Biologiske Aarsager kan fremkalde Ændringer i Fiskebestandene, dels fordi Fiskene er afhængige af de hydrografiske Omgivelser, dels fordi de er afhængige af de biologiske Omgivelser og dels fordi selve Fiskens Livscyclus betinger Ændringer.

De fysiske Forhold spiller navnlig en Rolle under Yngelens Udvikling og de enkelte Aargange bliver, paa Grund af de fysiske Forholds Variation fra Aar til Aar, af ulige Hyppighed. Betydningen heraf er navnlig paavist af Johan Hjort, 1914. Men de fysiske Forhold influerer ogsaa paa de ældre Fisk. Som Eksempel herpaa kan nævnes, at Havstrømmene synes at have en afgørende Indflydelse paa Sildens Vandringer (sml. A. C. Johansen, 1927).

Rent biologiske Forhold, hvor de fysiske Omgivelser spiller en ganske underordnet Rolle eller er helt uden Betydning, har i adskillige Tilfælde vist sig at være Aarsagen til Ændringer i Fiskebestandene og Fiskerierne. Saaledes kan Forskelligheder, der engang er opstaaet i de enkelte Aarganges Hyppighed være Aarsag til stadig fortsatte Ændringer i Fiskebestandene, efter som Fiskene vokser op, formerer sig og dør, og disse Ændringer vil i det Tilfælde, at den ynglende Mængde Fisk bestemmer Yngelmængden, fortsættes i de næste Generationer. Enhver Ændring i Fiskenes Biocønose vil fremkalde nye Ændringer i Fiskebestandene. Fiskene er afhængig af Mængden af Næring, men ogsaa af Fjender. Det første er navnlig fastslaaet ved C. G. Joh. Petersens Undersøgelser. Det sidste er paavist af Umberto d'Ancona, 1926, for Biocønosen mellem Hajer og forskellige andre Fiskearter, af H. Blegvad, 1928, for Aalekvabbens og den sorte Kutlings Afhængighed af Torskebestanden, og af Aage J. C. Jensen, 1929, for Sildens Afhængighed af Torskebestanden. Vito Volterra, 1928, har givet en teoretisk Behandling af disse rent biologiske Variationer, der skyldes Ændringer i Biocønosen.

Vekslinger i Fiskebestandene kan desuden fremkomme paa Grund af Indgreb fra Menneskets Side, ved Udplantning eller ved Fiskeri.

En særlig Gruppe af Variationer i Fiskebestandene og i Fiskeriernes Udbytte danner de periodiske Variationer. Teorier om, at saadanne periodiske Variationer i Fiskebestandene eller i Fiskerierne eksisterer, er fremsat af forskellige Forfattere og enkelte af disse periodiske Variationers Eksistens er hævet over al Tvivl, saaledes de sekulære Variationer i Sildebestanden og Sildefiskeriet ved Bohuslän paavist af Ljungman, 1879, og Otto Pettersson, 1922.

Et objektivt Kriterium for Sandsynligheden for at periodiske Variationer fra Aar til Aar findes, har man i Fejlberegningen; og ved Hjælp heraf har jeg for forskellige Fiskebestande og Fiskerier i de danske Farvande undersøgt, om der i disse findes periodiske Variationer fra Aar til Aar, der omfatter Periodelængder paa et mindre Antal Aar. Ved Hjælp af denne Metode har jeg tidligere paavist, at saadanne Perioder findes i det bornholmske Sildefiskeri (Aage J. C. Jensen, 1927, 1).

I de Tilfælde, hvor saadanne periodiske Variationer findes, maa vi dernæst undersøge, hvad Aarsagen er til disse Variationer.

Valget af de her behandlede Fiskebestande er foretaget dels efter, hvor der fandtes et for Undersøgelsen egnet Materiale d. v. s. hvor der var gode statistiske Oplysninger for en enkelt Fiskebestand, og hvor vedkommende Fiskebestands biologiske Forhold var kendt i en saadan Grad, at Undersøgelsen her kunde forventes at give et positivt Resultat, og dels endelig saaledes, at saavidt muligt forskellige Fiskebestande og Fiskerier blev undersøgt for at give et Indtryk af de opnaaede Resultaters almindelige Gyldighed.

Det paavistes, at der i det danske Rødspættefiskeri i Nordsøen er en periodisk Variation med en Periodelængde paa ca. 2,7 Aar. En Undersøgelse af, hvilke meteorologisk-hydrografiske Forhold, der bestemmer Variationerne fra Aar til Aar i Fiskebestanden, viste, at det danske Rødspættefiskeris Udbytte afhænger i væsentlig Grad af hvor megen Yngel, der af Havstrømmene føres til det sydlige Horns Rev Omraade.[1] I Hyppigheden af de Vindretninger, der bestemmer Havstrømmenes Variationer fra Aar til Aar, er der en periodisk Variation med en Periodelængde paa ca. 3,1 Aar. Paa Grund af den gradvise Foryngelse, Bestanden har været underkastet som Følge af Fiskeriets Indvirkning paa Bestanden i den betragtede Aarrække, er Periodiciteten i Fiskeriets Udbytte kortere end Periodiciteten i de meteorologisk-hydrografiske Forhold, der bestemmer Variationerne fra Aar til Aar i Yngelmængden. Forbindelsen mellem Variationerne i Hyppigheden af bestemte Vindretninger og i Fiskeriets Udbytte kan paavises.

I Rødspættefiskeriet og Rødspættebestanden i den sydlige Nordsø findes en periodisk Variation med en Periodelængde paa ca. 5 Aar. Den kan forklares som en Følge af Næringskonkurrencen mellem Rødspætterne paa Opvækstgrundene.

I Mængden af Rødspætteyngel i det sydlige Kattegat og Belthavet er der Perioder af Længderne ca. 2,4 og ca. 3,3 Aar. Ved Undersøgelse af Aarsagerne til Yngelmængdens Variationer fra Aar til Aar paavistes, at Overfladens Temperatur i Januar, som paapeget af H. Blegvad, 1926, 2, samt Indstrømningen i det nedre Vandlag i Februar—Marts—April spiller en meget væsentlig Rolle. Ved Undersøgelsen viste det sig, at Aarsagen til at Rødspættens Racekarakter i Bælthavet efter Krigen, som paavist af A. C. Johansen, 1929, har vist en Forandring i Retning af Nordsørødspættens Racekarakter, ikke er en forøget Tilførsel af Yngel Nord fra, men at den Mængde Rødspætter af Nordsøracen, der i Belthavet bastarderer med Belthavsrødspætterne er forøget paa Grund af en øget Indvandring af ældre Fisk. Belthavet faar en mindre Forsyning af Yngel Nord fra end der føres bort. Fra Bælthavet eller det sydlige Kattegat føres derimod i visse Aar en følelig Mængde Rødspætteyngel til det nordlige Kattegat.

I de hydrografiske Forhold, der viste sig at have Indflydelse paa Variationerne fra Aar til Aar i Mængden af Rødspætteyngel, fandtes periodiske Variationer med de samme Periodelængder som de, der fandtes i Rødspætteyngelen. Disse sidste Variationer maa skyldes de periodiske Variationer i de hydrografiske Forhold.

Makrelfiskeriet i Kattegat—Skagerak viser periodiske Variationer fra Aar til Aar med Periodelængder paa ca. 2,3 og ca. 3,4 Aar. Dette Fiskeri viser en udpræget Covariation med Udstrømningen gennem Kattegat i Marts—April, hvilket maa antages at skyldes, at Mængden af Makrel, der indvandrer til Omraadet, influeres af den indgaaende Reaktionsstrøm, der fremkaldes af Udstrømningen. Desuden er Udbyttet af Makrelfiskeriet i Skagerak afhængigt af Overfladetemperaturen i Juni Maaned, som paavist af A. C. Johansen, 1925. Udbyttet af Makrelfiskeriet i Kattegat er derimod uafhængigt heraf, men viser en negativ Korrelation med Overfladevandets Temperatur i September, ligesom jeg tidligere har paavist, at dette var Tilfældet for Makrelfiskeriet i Sundet (Aage J. C. Jensen, 1930, 2). I de hydrografiske Forhold er der ogsaa her de samme periodiske Variationer som i Fiskeriet.

Rent biologiske Forhold spiller dog en væsentlig Rolle for Variationerne i Rødspættebestandene. En Periodicitet paa mellem 2 og 3 Aar maa nemlig forstærkes ved Virkningen af Næringskonkurrencen mellem de to yngste Aldersgrupper af Rødspætter, idet en rig Aargang vil hæmme Væksten af den følgende Aargang og foraarsage en større Dødelighed mellem denne Aargangs Rødspætter ved at forlænge Væksttiden.

Den tidligere paaviste periodiske Variation i det bornholmske Sildefiskeri, hvor Periodelængden var ca. 3,7 Aar, er undersøgt nærmere. Af Aldersanalyser af Silden i Bornholmsbassinet, der er foretaget af Hessle og K. A. Andersson, fremgaar, at den gennemsnitlige Alder af de Sild, der yngler her (og hvorpaa Fiskeriet ved Bornholm drives) er ca. 3,8 Aar beregnet paa Grundlag af Undersøgelser i de fem Aar 1924, 1926, 1927, 1928 og 1929. Der er altsaa en meget god Overensstemmelse med Længden af den Periode, der er

[1] En Formodning om en Forbindelse mellem Variationerne fra Aar til Aar i Havstrømmene og i Hyppigheden af Rødspættens Aargange i den sydøstlige Nordsø er tidligere fremsat af D. E. Thursby-Pelham, 1928, 2 og af Ad. Bückmann, 1930.

fundet i Fiskeriet. Det fremgaar endvidere af en direkte Sammenligning mellem Yngelmænden og Fiskeriudbyttet, at Yngelmængden synes at være i væsentlig Grad bestemt af Mængden af ynglende Sild. Denne periodiske Variation synes altsaa at skyldes rent biologiske Aarsager, nemlig at Mængden af ynglende Sild bestemmer Mængden af Yngel, der fremkommer og dermed den ynglende Bestands Størrelse nogle Aar senere. En ca. 11-aarig Periode i dette Fiskeri, som syntes at fremgaa af Fiskeriudbyttet i 1885—1914 eksisterer vistnok ikke. Et forholdsvis stort Fiskeriudbytte er ikke fremkommet mellem 1925 og 1930, som man skulde have ventet, tværtimod har Udbyttet i dette Tidsrum været forholdsvis ringe.

I Tilfælde af at den periodiske Variation ikke dækker et helt Antal Aar kan der, hvis den biologiske eller hydrografiske Afhængighed, der betinger de periodiske Variationer i Fiskebestanden ikke er lineær, findes sekundære periodiske Variationer i Fiskebestanden (associerede Perioder). Saadanne er vistnok Aarsagen til Variationer i det bornholmske Sildefiskeris Udbytte. Det foreliggende statistiske Materiale er dog ikke tilstrækkeligt omfattende til, at man paa Grundlag af denne Undersøgelse kan afgøre, om man kan betragte de fundne Afhængigheder som lineære eller ikke, men man kan vente, i Fremtiden ad denne Vej at faa Oplysning herom.

En Beregning af Standardafvigelsen viser, at mellem 30 og 55 % af Variationerne fra Aar til Aar i de statistiske Oplysninger om Fiskebestandene og Fiskeriudbyttets Størrelse skyldes periodiske Variationer. Det maa antages at de Aarsager, der bestemmer Variationerne, vilde træde endnu tydeligere frem, hvis de Mangler, der klæber til Materialet, kunde afhjælpes. De daglig gentagne hydrografiske Observationer fra de danske Fyrskibe byder et enestaaende Materiale for fiskeribiologiske Undersøgelser, men saadanne Observationer mangler desværre for betydningsfulde Omraader. Ligeledes vilde det, hvis Fiskeristatistiken i endnu højere Grad end nu var anlagt efter biologiske Synspunkter, betyde en stor Fordel for Undersøgelser af Aarsagerne til Variationerne fra Aar til Aar. De hidtil opnaaede Resultater viser, at saadanne Undersøgelser kan give et Grundlag for Prognoser for Fiskeriernes Udbytte i et saadant Omfang, at det vil have praktisk Betydning.

De fundne periodiske Variationer synes alle at være en Følge af Fiskenes fysiologiske Krav, og der synes at være to væsensforskellige Arter af disse Variationer, nemlig nogle, hvor Aarsagen er at søge alene i Fiskenes biologiske Forhold, andre hvor den Aarsag, der fremkalder den periodiske Variation, er af terrestrisk-kosmisk Natur.

Af den Gruppe, hvor den Aarsag, der fremkalder Perioden og bestemmer dens Længde, er af terrestrisk-kosmisk Natur er det lykkedes at paavise tre Eksempler:

a. en periodisk Variation i Rødspættebestanden i den sydlige Del af Nordsøen med Periodelængde ca. 2,7—3,1 Aar.
b. Perioder i Rødspættebestanden i det sydlige Kattegat og Belthavet, hvis Periodelængde er ca. 2,4—3,1 Aar.
c. Perioder i Makrelfiskeriet i Kattegat—Skagerak, hvis Periodelængder er ca. 2,3—3,4 Aar.

Rent biologiske Forhold kan i væsentlig Grad spille ind ved disse Variationer.

Af den Gruppe, hvor rent biologiske Forhold alene er Aarsagen, er der hidtil paavist tre Eksempler, der falder i to Grupper, nemlig:

1. hvor Aarsagen er at Mængden af ynglende Fisk bestemmer Mængden af Yngel, der fremkommer og dermed den ynglende Bestands Størrelse nogle Aar senere.
   a. En Periode paa 5—6 Aar i Laksefiskeriet ved Gudenaa paavist af J. P. Jacobsen og A. C. Johansen, 1921.
   b. En Periode paa ca. 3,7 Aar i Sildefiskeriet ved Bornholm.
2. hvor Aarsagen er Næringskonkurrencen mellem Individerne af samme Art.
   a. En Periode i Rødspættebestanden i den sydlige Nordsø, hvor Periodelængden er ca. 5 Aar.

Periodiske Variationer, der skyldes, at en Art lever hovedsagelig af en anden Art, hvis teoretiske Mulighed er paavist af V. Volterra, 1928, har jeg ikke fundet ved de her behandlede Fiskebestande.

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