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COLLOQUE INTERNATIONAL DE BIOLOGIE MARINE
STATION BIOLOGIQUE DE ROSCOFF
(27 juin-4 juillet 1956).

## I. — REPRODUCTION ET CYCLES BIOLOGIQUES EN RELATION AVEC LES DISTRICTS GÉOGRAPHIQUES ET LA TEMPÉRATURE

# WATER TEMPERATURE AND BREEDING THROUGHOUT THE GEOGRAPHICAL RANGE OF *OSTREA EDULIS*

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It has often been stated that water temperature is a factor of paramount importance in the breeding of marine invertebrates and fishes. Though there are species which breed the year round, the majority of these creatures reproduces at a particular temperature only, which temperature may be either high or low. It has often been assumed that such a definite temperature is a physiological constant for the species throughout its range (Orton 1920, Runnström 1927). This entails that the breeding season is of longer duration and starts earlier in the year in the warmer part of the range. Evidence has been adduced that such a pattern may hold good for a variety of species. Runnström demonstrated that species which breed in arctic waters in mid-summer reproduce in winter, but at about the same water temperature, in the southern parts of their range. Conversely, species which breed in early spring in the Mediterranean area, reproduce in late summer further north, but again at approximately the same water temperature. Experimental evidence has been adduced by Runnström that these organisms are forced to follow such a pattern since normal larval development can be accomplished within a rather narrow range of temperatures only, whereas the adults are less exacting and can endure both higher and lower water temperatures.

There is some difference of opinion on the exact way the temperature exerts its influence at the outset of the breeding season. Some authors think in terms of a « trigger » mechanism, released at the moment a given temperature has been reached; others, dealing with organisms which breed at higher temperatures, assume that the ripening of the sex products may require a given amount of warmth, a time-temperature effect, which could be expressed in day-degrees. If the temperature of the water rises slowly, breeding may accordingly begin at a lower temperature than in case of a more rapid rise. However this may be, one needs a wealth of accurate quantitative data to find out exactly how each organism reacts to water temperature under fully natural conditions.

Among the invertebrate denizens of the sea the oyster has, for obvious reasons, attracted the greatest attention of the scientists. Therefore the oyster-data could perhaps inform us on the correctness of the theories mentioned above. ORTON, the British oyster authority of the nineteen-twenties and 'thirties, wrote that his exhaustive investigations on the degree of correlation between breeding and water temperature throughout *Ostrea edulis*' geographical range had enabled him to conclude that this species begins to breed at 15 to 16° C. and continues to do so as long as the temperature remains above this figure (ORTON, 1920, 1937). As far south as Naples *Ostrea edulis* begins to breed in April, several months earlier than the British oysters do, but at about the same water temperature of 15 to 16° C. Accordingly the breeding season is said to be of much longer duration in the southern part of the range of *Ostrea edulis*. ORTON stated further that a temperature stimulus of some kind is the normal impulse for inducing sexual activity in marine animals.

Since ORTON carried out his investigations an impressive amount of evidence on *Ostrea edulis*' breeding behaviour has been accumulated. For the Oosterschelde, the Dutch centre of oyster cultivation, we possess, for instance, quantitative data on the reproductive activities of the oysters, collected on a daily or twice-daily basis, and covering 20 complete seasons. These data demonstrate that ORTON's assumption holds good for this area, even though only in a very general way. The oyster never did spawn here before the water temperature had surpassed a level of some 15 to 16° C. But attainment of this temperature level did not automatically release the sex products. Some time, up to several weeks, had to elapse before the first larvæ made their appearance in the water. It further became clear that breeding does not go on and on until the water temperature drops again under the so-called « critical » level. As a rule the production of larvæ decreases considerably after about August 10th, and dies down practically completely in the first week of September, even if water temperatures are over 18° C. at that time. The 15° C. level is not passed before about October 1st in the Oosterschelde. Only a very occasional oyster may release its sex products so late in the season. The height of the spawning season is invariably located somewhere between the last ten days of June and the first ten days of August.

A closer investigation reveals, however, that the correlation between the oyster's breeding and water temperatures cannot be a very close one. Among the seasons covered there are some with an unusually cold spring, and others which show an exceptionally early rise in water temperature. Peculiarly enough this entails neither a late breeding season in the former, nor an early one in the latter years (KORRINGA, 1951, 1952, 1953, 1954, 1955). We further are in a position to conclude that once the breeding season has begun the course of the actual water temperature in the summer months does not influence appreciably either the total number of larvæ released, or the usual ups and downs in the appearance of the larvæ during the breeding season. It appears to be the number of mother oysters rather than weather conditions which governs the total number of larvæ produced in a given season, and a lunar periodicity pattern rather than fluctuations in the actual water temperature which brings about the ups and downs in the number of newly released larvæ (KORRINGA, 1947). Some swarming takes place on almost every day, but maxima of greater and lesser importance are observed every year. By pooling the numerous data of all these years the unavoidable irregularities due to imperfections of the sampling can be smoothed out. Thus the underlying pattern is clearly revealed, demonstrating that the spawning of *Ostrea edulis* in the Oosterschelde tends to attain maxima at *both* spring tides, which leads to the appearance of great numbers of larvæ about 8 days later. The greatest peak in spawning occurs between 18. June and 2. July, irrespective of the actual course of the water temperature and regardless of cold or mild weather in spring and early summer.

The extent and the pattern of spawning are not the only factors involved in success or failure in the reproduction of the oyster. Much depends on the way the young larvæ grow up and settle. Larval development in a species like *Ostrea edulis* is without any doubt to a considerable extent dependent on water temperatures and feeding conditions. The extensive data on the development of oyster larvæ in the Oosterschelde reveal that water temperature is a very important factor indeed. If the larvæ are liberated at water temperatures of 20° C. and higher, larval development will be fast, provided there are enough suitable flagellates to feed on. At temperatures of about 19° C. the rate of development is modest, at 18° C. slow. At 17.5° C. the growth has virtually come to a standstill and at 17° or lower we invariably found that the larvæ remained unchanged for quite a while. We are sure that at such low temperatures even the greatest production of larvæ, excellent feeding conditions, and the utmost care of the oyster farmers will never lead to settlement of oyster spat in the Oosterschelde. Peculiarly enough, spawning and incubation go on at water temperatures of 16 and 17° C. Evidently, the most sensitive period in the life of *Ostrea edulis* is not the early development within the maternal mantle chamber, but the stage immediately after expulsion of the straight hinge larvæ. Once the larvæ have reached the umbo-stage they can proceed to grow and settle even if they hit a rather cold spell. The young larvæ are not killed by low water temperatures as such, as has often been assumed. It is possible to keep oyster larvæ in any developmental stage alive under refrigeration, and to revive their activities by transferring them to water of normal temperature. Evidently the bottle-neck is formed by the sensitivity of the growth process.

We may safely conclude from the Oosterschelde data discussed above, that *Ostrea edulis* is very fussy indeed in its breeding. Reproductive activities have been observed only at water temperatures over 15 to 16° C., but larval development appeared to be normal only at temperatures over 17 5° C. There is not such a thing as a « trigger » mechanism producing and releasing sex products from the very moment a given temperature has been reached. Nor is there a definite time-temperature period after the lapse of which the larvæ appear almost automatically. Neither does breeding go on and on as long as water temperatures are higher than 16° C. Breeding seems rather to be confined to a given part of the year, irrespective of minor temperature fluctuations, but with a lunar periodicity pattern, and is in its success or failure in the very first place dependent on the temperatures and feeding conditions the larvæ meet with during their pelagic life.

Does this detailed analysis of the influence of temperature on the breeding behaviour in *Ostrea edulis* allow us to conclude that the requirements recorded above are characteristic for this species ? If so, these data should hold good for this species in all parts of its geographical range. That would tally with ORTON's conclusion « these temperatures appear to be physiological constants for the species. » More recently this view has been supported by RANSON (1948), who stressed again that the normal development of oyster larvæ can take place within a narrow range of temperatures and salinities only : « Chaque espèce d'huître réclame une salinité et une température spéciales. Le développement de l'œuf et de la larve a lieu entre des limites assez étroites eu égard à ces deux facteurs. L'adulte en admet de plus larges. »

A comparison with several other centres of oyster culture seems to confirm that the temperature requirements mentioned above are indeed a physiological constant for the species :

1. Observations concerning the oyster's breeding in the Essex rivers Crouch and Roach (WAUGH, 1952, 1953, 1954, 1955) reveal a striking similarity with the Oosterschelde data. Here too it is the second half of June and the first part of July which give the greatest production of oyster larvæ, and that at temperatures over 15 to 16° C. Here too food conditions and water temperatures are considered the main factors governing larval development. At temperatures of 17° and lower larval growth is hardly perceptible. At most the Essex larvæ appear on an average a few days ahead of those in the Oosterschelde and may still develop very slowly at about 17° C. whereas 17.5° C. seems to be the lower limit in Holland. Even if these slight differences are statistically reliable, they seem hardly worth mentioning.

2. In the main centre of spat production in France, the Morbihan area (Brittany), the staff members of the Institut Scientifique des Pêches Maritimes have made numerous observations. The pre-war data only have been published in full in the *Revue des Travaux*, but repeated verbal information from the staff members and from the local oystermen make it safe to conclude that the breeding pattern in the Morbihan waters strikingly resembles that in the Oosterschelde. Here too, the bulk of the oysterlarvæ appears late in June or in the first half of July, at which time water temperatures are well over 16° C. If the veligers meet with a very cold spell, so that water temperatures drop below the 18° C. level, larval development slows down, and setting becomes a failure.

3. In the Bay of Arcachon, on the other hand, the larvæ of *Ostrea edulis* make their appearance in the water some 14 days ahead of those in Brittany.

This Bay being situated further south, water temperatures rise early, so that the « critical » temperature of 15 to 16° is reached some 2 or 3 weeks earlier than in Brittany. Therefore this advanced breeding seems to confirm that the Arcachon oysters react in exactly the same way to water temperatures as those in Holland, Brittany, and Essex.

4. Information on the oyster's breeding in two Italian centres : the Lago Fusaro near Naples (MAZZARELLI, 1913) and the Mare Grande at Tarento (verbal information given by Prof. A. CERRUTI) reveal that the larvæ appear much earlier in the year there than in France, England and Holland, viz. in April and May. Occasionally the very first make their appearance late in March. This corresponds, however closely with the water temperature, which rises earlier there, so that the 15° C. level is usually reached late in March or early in April. At the time the pelagic larvæ are numerous water temperatures of 18 to 22° C. prevail. MAZZARELLI found actively swimming larvæ when water temperatures had dropped to 13 or 14° C. in a cold spell, but this does not mean that the larvæ can grow and develop normally at such low temperatures. In the laboratory MAZZARELLI observed that setting can be accomplished at 18° C., occasionally even at 17°. The Italian oysters therefore seem to behave exactly similar to the oysters from the Atlantic coasts of Europe. It is of interest to note that the oyster's breeding in Italy does not go on and throughout the entire summer season, until the temperature drops again under the 15° C. level late in the year. At the end of May most of the spawning is over, though an occasional oyster bearing larvæ may still be found in summer and autumn. This tallies very well with the detailed information gathered in the Oosterschelde, but differs from ORTON's original hypothesis that high water temperatures force the oysters to reproduce almost automatically.

5. For the Yugoslavian oyster area in the Bistrini Bight near Ston I received interesting verbal information from Prof. M. MIHAILINOVIC to the effect that there too the months of April, May and June constitute the major breeding period. Spawning dies down in mid-summer, but it may happen that a second, though minor, spatfall occurs as late as October. Water temperatures are said to fluctuate from about 17 to 22° C. during the height of the breeding period. Apart from the occasional recurrence of spawning in October, the Yugoslavian data prove the rule. It seems very probable, indeed, that temperature requirements for breeding are a physiological constant for the species.

*Do all these data suffice to prove our case?* The decision whether or not the breeding temperature is a physiological constant for the species is of considerable practical and theoretical importance. The practical point is evident : if *Ostrea edulis'* breeding behaviour is fundamentally the same in all parts of its range, this factor need not be taken into account in purchasing elsewhere oysters for relaying. As for the theoretical importance of the conclusion, we should consider that for few, if any, denizens of the sea has there been accumulated such a wealth of quantitative data on breeding as for the oyster, *Ostrea edulis.* Any definite conclusion on the oyster's breeding behaviour will therefore be useful in interpreting the more scanty data relating to other creatures.

The case of the American Atlantic oyster, *Crassostrea virginica*, especially throws doubt on the assumptions of Orton and Runnström that the temperature range for breeding is a physiological constant for the species, and that one needs not assume that there are within a given species several physiological varieties breeding at different temperatures. It is true, that Th. C. Nelson stated in 1928 that « the American oyster spawns after the water temperature reaches 20° C., over all parts of its range, with no adjustments to the extremes of the distribution. » This conclusion was based on his own observations in Barnegat Bay (New Jersey), and on observations made by his father (J. Nelson, 1917) in Richmond Bay (Prince Edward Island, Canada). Nelson admitted later (in litt. 14-3-1956) that extrapolation of these data in framing the statement above was unwarranted. For Stauber (1950) pointed out that the time of initiation of spawning is nearly coincident in such widely separated areas as Prince Edward Island, Long Island Sound, and Delaware Bay, though temperature conditions at the time were considerably different, viz. 20°, 16.4°, and 25° C. respectively. This made Stauber deduce tentatively that there might be several physiological spawning varieties in *Crassostrea virginica.* Ingle's finding (1951) that mass spawning of this oyster in Apalachicola Bay (Florida) takes place invariably above the 25°C. level seems to support Stauber's view. Ingle rightly remarked, however, that one should not focus only on the temperatures at which spawning proceeds, but that one should also take into account the conditions during maturation of the gonads. Loosanoff and Nomejko (1951) kept oysters originating from different sites on the Atlantic coastline in trays in Milford Harbor (Connecticut), and that for a prolonged period. Thus conditions for maturation of the gonads were identical. Still there was a marked difference in breeding behaviour between the groups, the oysters of northerly origin definitely spawning at lower temperatures than the southern oysters. These observations seem to confirm the existance of several physiological varieties initiating spawning at about 17, 20, and 25°C. It is of considerable practical importance to know that southern oysters may not spawn at all when relaid in cooler northern waters, and conversely that northern oysters will spawn earlier in the season after having been relaid in southern waters. Nelson informed me recently (in litt. 14-3-1956) that different physiological varieties may even exist in such geographically adjacent places as Delaware Bay (New Jersey) with its typical « bay » oysters spawning at 25° C., and the area below the jetty of the Cape May Canal, where can be found typical « coastal » oysters, spawning at about 20° C.

*Is there any evidence that the European flat oyster* Ostrea edulis, *though belonging to a different genus from the American Atlantic oyster, should also be split up into several physiologically different varieties?*

I believe there is :

1. If Orton's graphs (Orton, 1928, reproduced in Orton, 1937, p. 101) repre-

senting the breeding periods in 3 populations of British oysters (A. Thames estuary, B. Varne Lightship in the Channel, representing a typical deep-sea oyster bed, C. Fal estuary) depict the facts correctly, we can see that the deep-sea oysters breed at water temperatures hardly surpassing the 15° C. level. It seems hardly possible that the larvæ of these deep-sea oysters do require 17.5° C. as minimum level for their normal development. The summer of the chosen year 1926 not being a cold one, we should either presume that successful breeding of deep-sea oysters occurs very exceptionally only, viz. in unusually warm summers, or that the larvæ of these populations are not as exacting as the coastal varieties seem to be.

2. The Heligoland beds were once well populated with oysters (Caspers 1950). Evidently successful larval development and setting occurred at least occasionally there. This in spite of the dispersing action of the currents through which only a very few larvæ get the opportunity to settle in the vicinity of the place they were born. We are well informed about water temperatures in the Heligoland area (Böhnecke and Dietrich, 1951, Gœdecke, 1956). Data covering the period 1872-1950 reveal that temperatures of 16° C. and higher occur during a few weeks only, cold summers excepted. A water temperature of 17° C. occurs only occasionally, but temperatures of 18° C. are very rare indeed. The data refer to the surface layer; without doubt lower values will hold good for the deeper layers where the oysters live. It seems hardly credible that an oyster requiring 17.5° C. as a minimum temperature for a normal larval development can eke out its existance in waters as cool as those which bathe the Heligoland beds. Or should we presume with Caspers that nearly all the oyster spat which settled on these beds originated from parent stocks living in warmer coastal waters, and that larvæ in advanced developmental stages were brought in by the currents?

3. The Scottish oyster beds were once reckoned among the richest of Europe. Millions of oysters were fished there annually. It was the Firth of Forth area which ranked first in productivity of the Scottish oyster districts, according to information kindly provided by Dr. R. M. Millar of the Scottish Marine Biological Station at Millport. Some data have been published on water temperatures in the Firth of Forth (Fulton, 1895), dealing with the period 1890-1894, inclusive. Comparison with Gœdecke's data for the Heligoland Roads (1956) demonstrates that water temperatures in the above-mentioned period cannot have deviated much from a general average over a greater number of years. But even if we assume for a moment that temperatures may have been up to 1° C. higher in several years preceding 1890, we have to conclude that summer temperatures are almost incredibly low for a productive oyster area :

*Firth of Forth* (1890-1894 incl.).

| | |
|---|---|
| June-average . . . . . . . | from 10.9 to 13.2° C. |
| July-average . . . . . . . | from 11.6 to 15.1° C. |
| August-average . . . . . . | from 10.7 to 14.6° C. |
| September-average . . . . . | from 11.2 to 13.5° C. |

*Highest temperatures recorded :*

| | 1890 | 1891 | 1892 | 1893 | 1894 |
|---|---|---|---|---|---|
| June . . . . . . | 12.6 | 14.6 | 12.6 | 15.0 | 12.4 |
| July . . . . . . | 13.3 | 17.2 | 13.8 | 15.0 | 13.8 |
| August . . . . . | 13.0 | 16.4 | 14.4 | 15.5 | 14.4 |
| September . . . . | — | 14.4 | 11.9 | 14.9 | 13.2 |

If *Ostrea edulis* really spawns only at temperatures above 15° C. and never shows normal larval development and setting at temperatures under 17 to 17.5° C. one fails to see how breeding can once have taken place on a large scale in the Firth of Forth, where the 15° C. level is reached only occasionally.

We may safely assume that relaying of oysters from Essex, Holland or Brittany in the cool waters of the Firth of Forth will never lead to a noteworthy setting of spat. At most spawning might proceed normally, at least in the warmer summers; a normal larval development cannot be expected. It seems only logical to assume that the Scottish oysters did breed at lower water temperatures than those from the areas further south. It would be very interesting, indeed, to collect some really native Scottish oysters and to study their breeding behaviour under laboratory conditions.

4. More convincing still is the information relative to the Spanish oyster areas. In a paper presented at the 1955 meeting of the Shellfish Committee of the International Council for the Exploration of the Sea Andreu and Arté informed us that larvæ of *Ostrea edulis* can be found in the Bay of Vigo on the Atlantic coast of Spain from late in March or early in April till late in November or even in December. The numbers of larvæ and the intensity of setting may, however, fluctuate considerably in the course of this prolonged season.

At first sight all this seems rather normal for a place so far south as Vigo. A closer inspection of the temperature data reveals, however, a great discrepancy with the oyster's breeding in French, British and Dutch waters. Water temperatures in the Bay of Vigo rarely drop below the 12° C. level in winter but in the summer season they do not invariably reach or surpass the 18° C. level every year. Dr. Andreu kindly informed me that the water temperatures recorded are not those of Atlantic water coming in with the flood, but refer to real bay-water in which the oyster larvæ live and develop. Dr. Andreu not only observed repeatedly that large numbers of oyster larvæ make their appearance in the water at temperatures of 13 to 14° C. but that the larvæ may even develop apparently normally at such low water temperatures! In November and December, 1955, for instance, at water temperatures of 12 to 14° C., the number of larvæ equalled that observed in July 1955 and was much higher than that recorded in August and September (Andreu, in litt. 23-12-1955). Experimental tiles put out at intervals throughout the summer revealed a profuse setting in November (188 per tile), whereas they caught only 1 to 7 spat in September and October. Factors other than water temperature (e. g. the food factor) probably predominate in bringing about success or failure in the breeding of the Spanish oysters, for, the years 1953 and 1954, in which the water temperature at Vigo reached the 17° C. level for a short period only, did not give smaller numbers of spat on the experimental tiles than the warm year 1955 with its prolonged period of temperatures of 18 and even 19° C.

The extensive and accurate data collected by ANDREU and ARTÉ leave no doubt that there are physiological varieties in *Ostrea edulis* which breed at different water temperatures. That it is exactly at the southernmost fringe of the oyster's Atlantic range that breeding takes place at the lowest temperatures seems rather paradoxical at first sight, but can easily be explained in terms of oceanic hydrography.

ANDREU's data throw more light on the oyster's breeding in the British deep-sea beds, the Heligoland oyster banks and the formerly very rich Scottish oyster grounds, depleted by overfishing. Most probably these oysters could also breed successfully at rather low water temperatures. Laboratory experiments to be carried out with survivors of these populations may confirm this in due course, to the benefit of our oyster industries.

*That breeding temperature is a physiological constant for the whole species* Ostrea edulis *is apparently nothing but a myth.* All this makes it easier to trust in the rather scanty information on the Chilean oyster (*Ostrea chilensis* Philippi), which is said to breed successfully at water temperatures well below the 15° C. level (CASTILLO and VERGARA 1907) (*).

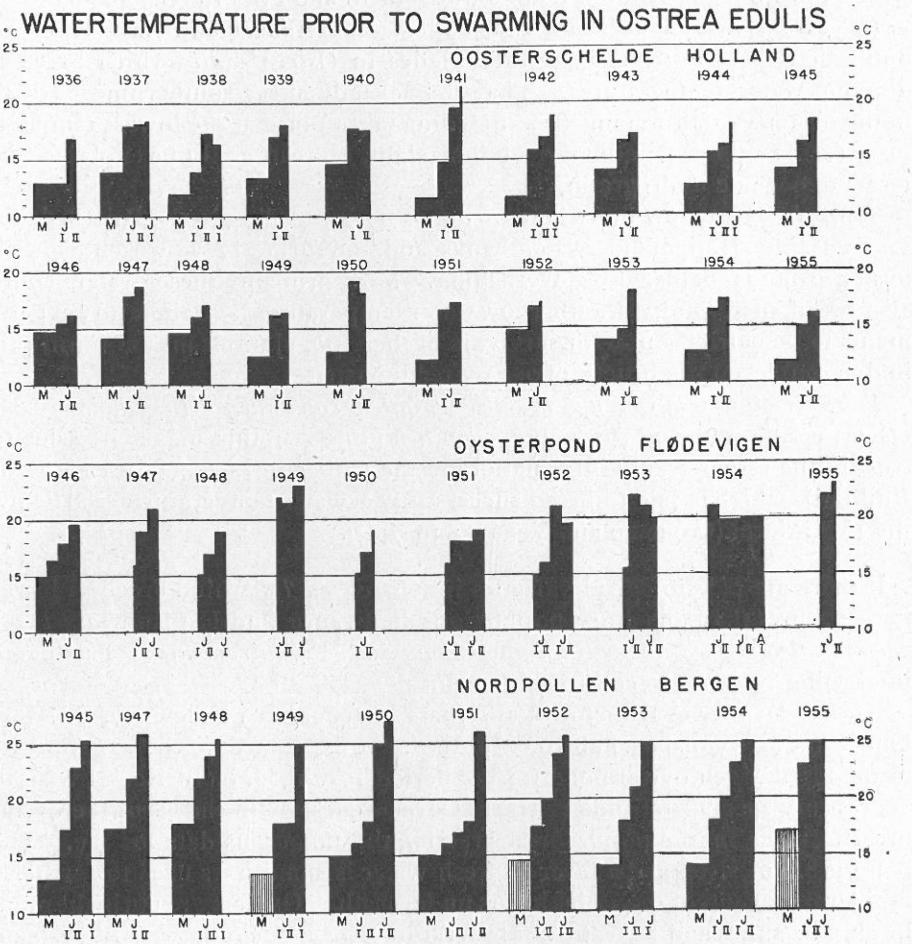
If there are physiological varieties in *Ostrea edulis* which breed at lower temperatures than the huge populations in France and Holland, *are there perhaps also populations with higher temperature requirements?* I gathered interesting evidence to confirm this point :

5. Dr. DANNEVIG, Director of the State Hatchery at Flødevigen, Norway, kindly put at my disposal abstracts of the records related to the experiments in the Flødevigen oyster pond for the period 1946-1955, inclusive. I wish to express my special gratitude to Mr. F. OTTERBECH, now in charge of the oyster investigations in the pond, for abstracting the numerous data for me. The pond is 3,5 m. deep and a layer of fresh water is sometimes used to further a rapid warming up of the saline layers underneath. Oysters are put in the pond in May or June, and henceforth observations are made on a weekly basis on water temperatures and on the number of oyster larvæ at 0, 1, 2, 3, and 3,5 m. depth.

Though it is therefore hard to decide on which particular day a given group of larvæ made its appearance in the water of the pond, the data suffice to conclude that nearly all major batches of larvæ came at water temperatures of 20° C. and higher. This was rarely in June (1948), usually in July and

(*) Mr. Cecil MILES, Regional Fisheries Officer of the F. A. O. for Latin America, kindly passed on to me information on inshore water temperatures in Chilean waters, procured by Mr. M. H. PONCE, Director General de Pesca y Caza of the Republic of Chile. Evidently water temperatures in the Chilean oyster district rarely, if ever, surpass the 14° C. level.

sometimes in August. Comparison with the oyster's breeding behaviour in Holland demonstrates that the first major groups of larvæ usually make their appearance in the Oosterschelde at water temperatures of about 18° C. Since




Water temperature prior to swarming in *Ostrea edulis*. Average temperature in May (M), first half of June ($J_I$), second part of June ($J_{II}$), first and second part of July ($J_I$, $J_{II}$), and first part of August ($A_I$) until the moment when great numbers of larvæ appear in the water. Hatched : conjectured. The Flødevigen oysters lived in water under 10° C. before being put in the pond early in June, 1946 excepted.

the year 1937 I observed only once (1941) that the water temperature was over 20° C. at the arrival of the first larval peak.

Before we conclude that the oysters at Flødevigen have higher temperature requirements for breeding than those in the Oosterschelde, we should consider the course of the water temperature during the weeks preceding breeding.

For it could be that low temperatures slowed down gonad maturation. We have, unfortunately, no information on temperature conditions for the period prior to the sojourn in the pond (without doubt below the « critical » 15° C. level, for surface temperatures in the sea at Flødevigen were on an average 9.8° C. for the month of May and 13.7° C. for the entire month of June, according to data provided by Dr. DANNEVIG), but water temperatures in the first half of June appear to be about 1° C. higher in the pond than in the Oosterschelde; the second half of June is on an average even 1.5° C. higher. Nevertheless the first major group of larvæ arrives nearly always later at Flødevigen than in the Oosterschelde, and at considerably higher water temperatures, instead of arriving earlier and at lower temperatures through a more rapid gonad maturation brought about by the higher temperatures in the month of June.

The Flødevigen data do not suggest that there exists a close correlation between the amount of warmth the oysters receive and the day they produce their offspring. That the larvæ arrived early in a given year (1948), and unusually late in another year (1954) does definitely not correspond with prolonged high temperatures in the weeks preceding spawning in 1948, or many weeks of rather low temperatures in the year 1954. Evidently other factors, presumably the food factor, exert a great influence on the process of gonad maturation.

6. More convincing still are the data related to the breeding of *Ostrea edulis* in the Nordpollen near Bergen, Norway. Mr. P. A. SOLEIM, the secretary of the Selskapet for de norske Fiskeriers Fremme, has been so kind as to provide me with the data collected there. These most interesting data, also collected on approximately a weekly basis, reveal that the appearance of important groups of oyster larvæ occurred here year after year at water temperatures of about 25° C. or higher! In the years under consideration, 1945-1955 inclusive, the larvæ arrived in the month of July, often in its first half, occasionally late in July, but never at water temperatures under 25° C. It is a superficial layer of fresh water, acting like the glass of a hot-house, which makes it possible for the saline layers underneath to attain such high values year after year in the Nordpollen.

A closer study of the water temperatures in the month preceding the emission of larvæ clearly demonstrates that the months of May and June were definitely warmer in the Nordpollen than in the Flødevigen pond, and very much warmer than in the Oosterschelde:

| *Month* | *Oosterschelde, Holland* 1937-1955, incl. | *Oysterpond Flödevigen* 1946-1955, incl. | *Nordpollen Bergen* 1945-1955, incl. |
|---|---|---|---|
| — | — | — | — |
| May. . . . . | 13.2° C. | — | 15.1° C. |
| June, first half. . | 16.4° | 17.3° | 18.8° |
| June, second half. | 17.5° | 19.2° | 21.2° |

It therefore cannot have been a retarded maturation of the sex products through lower temperatures which prevented the Nordpollen oysters from producing larvæ late in June or early in July at water temperatures which at that time often had surpassed the 20° C. level.

Evidently the oysters in the Nordpollen are very exacting indeed.

The Nordpollen data further reveal that the larvæ do not appear automatically as soon as the 25° C. level has been reached. A certain time-temperature factor seems to operate here, for the larvæ appear later in July when water temperatures in June are lower :

| *Year* | *Time of swarming* | *Average water temperature in June* |
|---|---|---|
| 1947 . . . . . . | 1. July | 24° C. |
| 1945, 1948, 1955. . | first ten days of July | 22° |
| 1949, 1952, 1953. . | mid-July | 19° |
| 1950, 1951, 1954. . | late in July | 17° |

This is the more interesting since a time-temperature factor does not seem to be of major importance in the Oosterschelde. The greatest peak in larval production comes there year after year on schedule : between 24. June and 10. July, some to days after full and new moon. Peculiarly enough it does not seem to matter whether the months preceding swarming are warmer or colder than usual. If, however, we do not focus on the greatest peak in larval production, but on the time the first major group of larvæ makes its appearance in the Oosterschelde, the picture is slightly different. Usually there are already quite a few larvæ in the last ten days of June, but in some years it is in the first ten days of July that numbers of larvæ worth mentioning arrive in the plankton :

| *First larval peak* (Oosterschelde) | *Temp. May* | *Temp. June* |
|---|---|---|
| Last ten days of June (11 years) . | 14.0° C. | 17.2° C. |
| First ten days of July (8 years). . | 12 2° | 16.6° |

Though the difference is not so striking as in the Nordpollen it seems reasonable to assume that in the Oosterschelde too gonad maturation in the period preceding spawning is speeded up by higher water temperatures.

The amount of warmth the oysters receive before they proceed to eject their larvæ is much greater at Fløedevigen than in the Oosterschelde, and in the Nordpollen again very much greater than at Fløedevigen. *The three populations of* Ostrea edulis *under consideration apparently differ not only in the temperature level at which swarming can be repeatedly observed (17.5°, 20° and 25° respectively) but also in the amount of warmth required for maturation of the sex products.*

All this evidence is convincing enough to make us reject the hypothesis that a given breeding temperature is a physiological constant within the species *Ostrea edulis*. Just as has been made clear for the American Atlantic oyster, *Crassostrea virginica*, one should distinguish several physiologically different varieties in the European flat oyster, *Ostrea edulis*, races breeding at different water temperatures.

One may wonder why the oyster populations in England, France and Holland are so strikingly identical in their breeding behaviour that it made us almost inclined to accept the view of ORTON, RUNNSTRÖM, and RANSON that there is but one biologically established breeding temperature for the species. This is not so peculiar as it seems at first sight. In the first place, hydrographical conditions in the Essex rivers, in the Gulf of Morbihan, and in the Oosterschelde do not differ noticeably in the summer season. In the second place, there has been considerable transplantation and interbreeding in this century. At the time the Morbihan population was almost wiped out by the disastrous mortalities caused by a disease in 1921 and 1922, many millions of Dutch oysters from the Oosterschelde have been relaid there in several consecutive years. Without doubt this has exerted a great influence on the genetical pattern of the present oyster population in Brittany. The same disease had virtually wiped out the scanty remains of the once flourishing beds of *Ostrea edulis* in the Bay of Arcachon. Up till then a special variety of *Ostrea edulis*, known as the « gravette » had eked out its existance there. For many years flat oysters were virtually absent in the Bay. Enterprising French oyster farmers relaid large quantities of Brittany oysters in the Bay of Arcachon in the years 1931 and 1932, which led to a successful revival of the cultivation of flat oysters there, but not to a come back of the ancient « gravette » (BOMPAYRE 1955). It seems very probable that the recent Arcachon oyster has genetically much in common with the Brittany oyster, as this latter has with the Dutch oyster.

Though it seems very paradoxical that the variety with the highest breeding temperature (25° C.) is to be found at the northernmost fringe of *Ostrea edulis'* range, near Bergen in Norway, and the race able to breed successfully well under the 15° C. level at the southernmost end of the Atlantic range, near Vigo in Spain, this can easily be explained in terms of the hydrographical conditions prevailing there. NELSON (in litt. 14-5-1956), discussing the finding of STAUBER that the variety of the American Atlantic oyster with the lowest spawning temperature (Long Island Sound) is peculiarly enough to be found some 600 miles south of the northern geographical range (Prince Edward Island, Canada), call this « a situation which, I believe, is unique in the geographical distribution of marine animals, the spawning of which depends upon temperature. » I regret that I have to disappoint my dear old friend NELSON in this respect, but the data presented in this paper demonstrate that it is the European oyster which wins easily : Vigo is more than 2,000 kilometers further south than Bergen, and still the Norwegian oysters breed at water temperatures more than 10° C. higher than those from Spain ! Further, is it not amazing that three varieties of *Ostrea edulis* breed at virtually the same water temperatures as the three major varieties of the American Atlantic oyster ?

I believe that the conclusions reached in this paper are of great practical and scientific importance :

Knowing now that there are different varieties of *Ostrea edulis*, oystermen purchasing stocks abroad for relaying on their beds at home, should be very careful not to select oysters which will not breed in their own waters. Not only will they fail to collect any spat from oysters breeding at higher temperatures, but the oysters will also suffer and fail to fatten as they cannot get rid of the accumulated spawn. This may explain several cases of disappointing results of relaying of oysters imported from other countries, but also the successful transplantation of Brittany oysters in Holland in the years when shell disease had decimated the Dutch oyster population. For waters with low summer temperatures the Spanish oysters seem very promising indeed, but one should not omit to study winters conditions and resistance to low temperatures too!

The scientific interest is clear from the fact that more data have been accumulated on the breeding of oysters than on any other marine creature. That we, nevertheless, were almost led astray in the case of the oyster is a sound warning against the drawing of too hasty conclusions from too scanty data, however difficult it may be to get sufficient supplementary material from many other places.

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## Discussions.

**M. Prosser.** — I have two questions. First, you mentioned transplantation in Europe by commercial oystermen ; should there not be controlled transplantation under experimental conditions before concluding that populations differ as physiological or geographic races ? Second, LOOSANOFF's observations have been criticized because he transplanted only adults ; might not the case for racial differences be better had spat been transplanted ?

**M. Korringa.** — The experience of large-scale transplantation by the European oystermen is very instructive, because they kept the oysters under natural conditions on beds. There are transplantations to waters which are so much colder in summer that spawning stays away (Holland-Germany ; Norway-Denmark) and reabsorption of spawn should then precede growth and fattening. There are also successful transplantations which bring spawning, spatfalls and, shortly after, growth and fattening (France-Holland). The great resemblance in behaviour between oysters in Holland and France has presumably been brought about by these large-scale transplantations. I do not believe that small-scale introductions under controlled conditions can make us much wiser.

As to criticism on LOOSANOFF's work, we can remark that transplantation of seed-oysters (over one year old) is exactly what the oystermen often do and which often led to failure when spawning stays away. It might be that introduction of spat gives different results, or perhaps that a second generation reacts differently. This is the question : are the differences observed genetically established or should they be considered as modifications brought about by conditions during their youth ? LOOSANOFF did not decide on this matter, nor did I ; still I believe that our conclusions are very important for the oystermen. We should however welcome a better knowledge on genetical patterns in oysters.

**M. Lubet.** — Je souligne l'importance des observations du Docteur KORRINGA sur la première critique de ponte des différentes populations d'*Ostrea edulis* L. Il ne peut être question d'un « seuil » mais d'une « zone » sensible à partir de laquelle les différents stimuli provoquant l'émission des gamètes, sont efficaces.

Cette zone semble déterminée par l'intensité du produit de neurosécrétion des ganglions cérébroïdes. Celui-ci semble inhiber la maturation des gamètes et conditionner (par une incidence sur le métabolisme) la « zone » sensible de ponte. Les animaux (*Mytilus edulis* L.) témoins émettent leurs gamètes de 8° à 10° (seuil thermique) et pas au-dessous de 8°. Chez les décérébrés (plus de neurosécrétion) la ponte peut être provoquée à 1-5°. Je compare ces résultats à ceux obtenus par le Professeur P. DRACH sur les crustacés (*Xantho Leander*) où l'organe X paraît conditionner la limite thermique des mues. Après l'ablation de cet organe, la limite thermique de ces mues est abaissée.

**M. Korringa.** — C'est très intéressant de savoir que des produits de neurosécrétion des ganglions cérébroïdes peuvent déterminer la période sensible des Huîtres. Il est fort possible que des différences dans de telles sécrétions produisent les différences observées parmi les diverses populations des Huîtres en ce qui concerne la température de leur ponte.

Il est pourtant question non seulement d'une température d'émission de gamètes mais aussi d'une température spéciale requise par les larves après leur période embryonnaire dans la phase pélagique. Les différences sont vraiment énormes et ne peuvent probablement être expliquées par des sécrétions des jeunes ganglions cérébroïdes, encore peu différenciés, des larves.

En ce qui concerne l'absence de ponte de l'Huître portugaise (Gryphées) dans des eaux trop froides en été, nous avons eu exactement la même chose dans un lot d'Huîtres portugaises importées par hasard parmi des Huîtres plates de Bretagne. Elles peuvent très bien être nourries, mais leurs gonades sont encore pleines de gamètes en automne et en hiver, et de ce fait elles sont impropres à la consommation.

**M. Lubet.** — Je signale que les *Crassostrea* (*Gryphœa*) *angulata* L. d'Arcachon reparquées à Cancale, n'émettent plus leurs gamètes, la température des eaux n'étant pas suffisamment élevée (inférieure à 20-21°). L'étude cytologique de ces individus a révélé que l'accroissement des ovocytes était aberrant et que les gamètes étaient phagocytés par des amœbocytes.

**M. Weill.** — J'estime critiquable le terme de « races physiologiques » employé par l'orateur; rien ne prouve, pour l'instant, qu'il s'agisse de différences éthologiques ou physiologiques définitives, inscrites dans le patrimoine génétique de l'individu et de sa descendance. Il pourrait ne s'agir que d'un « accommodat » plus ou moins temporaire, comme en présentent par exemple, divers végétaux austraux transplantés dans les régions boréales en ce qui concerne leurs époques de floraison; peut-être aussi d'une « Dauermodifikation » persistant pendant une génération ou deux. En assimilant le phénomène à une caractéristique raciale (*sensu stricto*), M. Korringa semble répondre, par anticipation, à une question qui, pour l'instant, reste posée.

**M. Korringa.** — Il est vrai que nous ne sommes pas sûrs que les différences observées sont fixées génétiquement. Il est bien possible qu'un séjour d'une ou plusieurs générations conduise à des modifications, à des adaptations aux conditions nouvelles. Quand on veut réserver le terme de « races physiologiques » pour des différences vraiment héréditaires, il serait peut-être préférable de parler ici, provisoirement, de « populations d'un comportement physiologique différent ».

Il est intéressant d'observer que dans le cas de mortalité par des températures basses, nous avons déjà observé que la jeunesse de l'Huître peut avoir une grande influence. Des Huîtres du Morbihan introduites en Hollande sont très sensibles pendant l'hiver, beaucoup plus que les Huîtres indigènes; mais quand elles ont survécu un hiver, elles sont déjà beaucoup plus fortes au cours du second hiver. On peut alors douter que cette sensibilité soit vraiment un caractère stable de la population; elle serait plutôt conséquence des influences pendant la jeunesse de l'Huître.

**M. Hörstadius.** — Dr. Korringa mentioned the results of Sven Runnström (1927) according to which it seems that each marine invertebrate species may have a rather definite breeding temperature range, either high or low, and that such a temperature is a physiological constant for the species throughout its range. On the other hand, Dr. Korringa told us that there are populations of *Ostrea edulis* with different temperature requirements for maturation of the products and for swarming.

In this connexion, it may be interesting to mention the sea-urchin *Paracentrotus lividus* which shows an adjustment to the temperature at the different seasons of the year.

In Roscoff, *Paracentrotus lividus* is ripe from June to August; in Naples all year round. Although it cannot be proved, there is no doubt that every specimen breeds several times a year. In Naples the temperature of the sea-water is 13° C. in the winter and 26° C. in the summer. It appears (Hörstadius, *Biologia Generalis*, 1926) that the winter eggs cannot cleave normally at 26°, nor the summer eggs at 13°. The temperature range of the cleavage processus, particularly those in the cytoplasm, is in fact adjusted to the prevailing temperature of the season.

**M. Bullock.** — I understood you to say that transplantation of spat had not generally been done here, is that correct? I wonder if you can tell us what the results have been of the frequent importation of the Japanese *Ostrea gigas* to the Pacific Coast of the United States. This might be of interest especially because it has been done over more than 1,000 kilometers of latitude from Puget Sound in Washington to Morro Bay, half way between San Francisco and Los Angeles.

**M. Korringa.** — Spat of the Pacific oyster, *Crassostrea gigas* is introduced annually into the waters of the Pacific coasts of the United States and Canada from Japan. This oyster requires rather high water temperatures for its reproduction, which temperatures are not always realized in the waters of British Columbia and Washington. In such cases, the oysters fail to spawn, so that one cannot collect its spat in such years, which makes importation of Japanese spat necessary. Moreover the oysters still full of spawn try to reabsorb this spawn, which does not improve their market-quality. In such years one has to wait for a new period of intensive feeding in the spring to make the oysters « fat » enough for sale. Therefore the introduced oysters are often in their best quality in April and May, unlike oysters which did spawn in summer and reach their best quality in October or November. On a smaller scale this oyster spat is relaid in Californian waters but I have no information on their growth and fattening. If water temperatures are higher further south (as in some inlets on the continental coast of British Columbia) spawning will occur normally in summer and oysters will fatten soon after, provided the coastal water is rich in suitable food.