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The influence of temperature on the behaviour of fish

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1. Introduction

Environmental conditions and their seasonal and/or aperiodic changes have a profound influence upon the seasonal occurrence and migrations of fish. In order to locate aggregations of fish for economic catch, and to predict their migrations and abundance, a detailed knowledge of fish behaviour in different hydrographic conditions is necessary.

Temperature is the most easily determined environmental factor. Therefore, numerous workers have attempted to correlate the behaviour of fish with the sea water temperature and its changes. Such changes in oceanic environment are, of course, very often only due to concomitant changes in other factors, such as currents, whose influence may be considerable; in these cases the actual influence of temperature itself may be of relatively limited significance. Nevertheless, in most cases the temperature may serve as an extremely useful indicator of the prevailing and changing ecological conditions. Finally, when using temperature as a direct or indirect ecological indicator, not only the distribution of the actual values, with their range of variation, but also the horizontal and vertical gradients and their variations from place to place must be taken into account.

The close interrelation and mutual dependence of the several marine sciences, indicating, among other things, the significance of ecological factors in marine life, have long been recognized (SVERDRUP 1942). Thus, the first report, in 1902, of the administration of the International Council for the Exploration of the Sea states:

. . . it was seen from the beginning that the study of the physical conditions, of the chemical nature of the ocean waters, of the currents, etc., was of the greatest importance for the investigation of the problems connected with life, that on the other hand, the study of the floating organisms had particular worth for the solution of hydrographic problems, and consequently that a sharp line should never be drawn between these two main divisions . . .

Of the long list of successful studies which have proved the validity of the above conclusions, only three examples will be given here. SHAPIRO (1950) stated that in Japanese long-line fishing for tuna, the data on the locality for the best catch, when correlated with information on optimum water temperature for tuna, configuration of ocean bottom and type of ocean current, have proved useful in indicating to fishing vessels the situation under which the long-line gear can be operated to maximum advantage. Knowledge of currents, convergences, divergences, reefs, banks, and islands are also important to Japanese fishermen for the location of schools of tuna and other fish.

TAIT (1952) in his book, Hydrography in Relation to Fisheries, made a successful attempt to list the different factors affecting the behaviour of fish.

The Norwegian fishery biologists (DEVOLD 1951 and 1959), in intimate cooperation with their hydrographer colleagues, have made use of the close correlation between the temperature distribution and the migrations of the herring for the prediction of the latter. Beyond any doubt, the Soviet scientists are using a more or less analogous method for the benefit of their herring fisheries; however, the present authors are not sufficiently acquainted with the Soviet literature.

It is definitely felt by the present authors that in the very near future hydrographic experience and knowledge will be submitted more and more generally to fishermen in the form of synoptic or quasisynoptic presentations, which they will be able to use most profitably in their work. It is anticipated that the different national attempts at »thermometric methods» of fish location and related predictions will be coordinated internationally (as is already the case with the meteorological services). Proposals to this effect have already been put forward by the Commission of Maritime Meteorology of the WMO (World Meteorological Organization) and by the International Council for the Exploration of the Sea.

One of the present authors (Laevastu 1960) has been engaged in a comprehensive study of the synoptic approach to hydrographic (thermal) conditions (termed hydropsis by Lyman, 1958) and of the prediction of their future changes. This and other related studies definitely indicate that in hydrography the time is approaching when the step from the study of the marine »climate» to the marine »synopsis», that is, to the actual event taking place in the sea, can be taken. This possibility makes it desirable to review the influence, either direct or indirect, of temperature upon the behaviour of fish. A summary and analysis is given below of the influence of temperature on the behaviour and survival of fish, with emphasis on the value of this information for ascertaining fish concentrations by »thermometric methods».

2. Influence of temperature on fish and their reactions

The sense of temperature in fish seems to be well developed. Bull (1952) concluded from his careful and extensive experiments that individual teleosts perceive and react purposively to a change in water temperature of 0.03° C.

Sullivan (1954) summarized the findings of various workers on the effects of temperature on the movement of fish and the influence of temperature on the distribution of fish in nature, and discussed the rôle of the receptor mechanism of the central nervous system in temperature response. He stated that fish select a certain temperature because of its effect on movement (activity), and concluded that the temperature change may act on fish as:

(1) a nervous stimulus;
(2) a modifier of metabolic processes, and
(3) a modifier of bodily activity.

In addition, it has been shown by Schmidt (1931) and various later workers that the temperature of the environment also has a definite effect on the meristic characters of fish; e.g., the number of vertebrae and fin rays increases as the temperature decreases.

3. Influence of temperature on spawning, and on development and survival of larvae

The influence of the temperature of the environment on fish behaviour is at its most pronounced during spawning. But the temperatures prior to spawning are also highly *significant, since they influence the ripening of the sexual products.* Poulsen (1944) stated that cold months preceding the spawning of cod may have a considerable effect in delaying the maturation of the gonads. Every stock of fish has a »normal» temperature range, possibly with a seasonal cycle. At temperatures below this range the ripening of the sexual products is delayed, and the opposite is the case at higher temperatures. Therefore, the past history of the temperature determines the arrival of stock at the spawning grounds. The theory of Devold (1959), which provides an explanation of the fluctuation in the stock and of the year-to-year shifting of the spawning grounds of the Atlantic-Scandinavian herring, is partly based upon similar conclusions.

Table 1. Water temperatures during spawning of herring (*Clupea harengus*) in different areas. (Rearranged from a table by Jean (1956)).

Locality	Season (spring)	Temperature °C	Season (autumn)	Temperature °C	Authors
Norway	II – III	3.0 – 7.0			Buch (1885) Johansen (1924) Runnström (1941)
North Sea			VIII – XI	6.0 – 13.0 12.0 – 14.0	LeGall (1935) Johansen (1924)
Kattegat	I – VI	4.0 – 12.0			Johansen (1924) LeGall (1935)
			IX – X	11.0 – 13.0	Johansen (1924) LeGall (1935)
Baltic Sea	IV – VI	6.0 – 11.0			Altnöder (1929) LeGall (1935) Cieglewitz & Posadzki (1947)
			IX – X	11.0 – 14.0	Hessle (1925) Cieglewitz & Posadzki (1947)
English Channel	XII – II	6.0 – 12.0			Fage (1920) Johansen (1924)
Scotland	II – III	3.8 – 7.1			Fulton (1906) Wood (1936)
			VII – IX	11.0 – 12.0	Fulton (1906) Fage (1920) Johansen (1924) Wood (1936)
Barents Sea	II – IV	0.0 – 6.9			Rass (1936) Rass (1939) Manteufel & Marty (1939)
Iceland	Spring	5.0 – 9.0			Tåning (1936)
Faeroes	III – IV	ca. 3.0			Johansen (1921)
Grand Manan			Autumn	8.0 – 11.0	Bigelow & Schroeder (1953)
Cape Cod			Autumn	11.7 – 12.9	Bigelow & Schroeder (1953)
Newfoundland	Spring	8.0			Tibbo (1946)
Block Island Sound			Late summer	13.0 – 15.0	Merriman & Warfel (1948) Merriman & Sclar (1952)
Magdalen Islands	IV – V	3.8 – 4.5			Lauzier (1952)
Mean	Spring	6.5 ± 2.8	Autumn	11.2 ± 2.1	–

Jean (1956) has carried out a comprehensive study on the spring- and fall-spawning herring at Grande-Rivière, Bay of Chaleur, Quebec. His literature review on the problem of spawning and water temperature reads as follows:

»The correlation between water temperature and spawning of marine animals is generally recognized. Orton (1919) and more recently Hutchins (1947) have shown that several

Table 2. Optimum temperatures for fish in different areas.

Species	Locality	Optimum temperature range °C	Spawning temperature °C	Remarks	Author
Cod	Bear Island, Spitzbergen	2 – 4			Lee (1952, 1956)
»	Newfoundland	(3-) 5 – 7			Le Danois (1934)
»	» »	0.5 – 7			McKenzie 1934)
»	West Greenland	(2.5-) 3 – 4		Best catches with surface and bottom long lines	Rasmussen (1955)
»	Motovsky Bay		0.4 – 2		
»	Northern Norwegian waters		2.5 – 5		Pertseva (1939)
»	Skagerrack		4 – 6		
»	Newfoundland		3 – 5		
»	Newfoundland, spring	0 – 3			Thompson (1943)
»	» » summer	3.5 – 5.5			
»	Icelandic waters		> 6		Schmidt (1926)
»	Lofoten		3 – 6.5		Sund (1935)
»	Danish waters		3 – 7		Poulsen (1931)
»	Nova Scotia Banks, spring	–0.5 – 1.5			McKenzie (1934)
»	» » » summer	2.5 – 5.5			
»	Labrador waters	> 2		Poor catches if temp. < 1.5 or > 4.0	Rasmussen (1955)
»	Eastern Atlantic, winter	2 – 3			Lee (1952)
»	» » summer	3 – 5			
»	Western Atlantic	3 – 5			Le Danois (1932)
Haddock	» »	5 – 7			
Plaice	North Sea		4 – 7		Kändler (1955)
Shad	York River	7 – 15			Massman & Pacheco (1957)
Baltic herring	Gulf of Riga	8 – 12			Bērziņš (1949)
Baltic sprat	» » »	10 – 15			
Mackerel	North Atlantic		12 – 15		Allen (1897) Sette (1950)
»	» »		10 – 15	Salinity 26 – 33 ‰	Jensen (1955)
»	» »	12 - 14		Avoids temp. < 4	Dannevig (1955)
»Iwashi» sardine	Sea of Japan	12 – 16			Uda & Okamoto (1936)
» »	» » »		13 – 17 Optimum: 14 – 15.5		Uda (1959)
Pacific sardine	Off California		13 – 17 Optimum: 15 – 16		Ahlström (1959)
Pilchard	English Channel		9 – 16.5		Cushing (1957)
S. African pilchard	Off South West Africa		14.9 – 19.6		Mathews (1959)
Tuna	Kuroshio region	14 – 18		Favourable fishing	Kawana (1934)
		18 – 20		Best fishing	Uda (195

species of marine invertebrates spawn within narrow limits of temperature. RUNNSTRÖM (1927) correlated temperature requirements at spawning with geographical distribution of the flounder (*Pleuronectes platessa*). ALLEN (1897) and recently SETTE (1950) have shown that the mackerel (*Scomber scombrus*) spawns at temperatures ranging from 12° to 15° C. Spawning of this species takes place earlier in the southern than in the northern part of its range.

Water temperature may hasten or delay the onset of spawning of Atlantic herring as shown by LAUZIER (1952). He observed that mean water temperatures at Magdalen Islands, Gulf of St. Lawrence, from 1933 to 1950 were 0.3° C in April and 4.5 °C in May. During these years, the catches of spawning herring were less abundant in April than in May in a proportion of 1 to 18. In 1951, mean water temperatures at Magdalen Islands were 3.8° C in April and 6° C in May. In contrast with previous years, the catches of spawning herring were more abundant in April than in May in a proportion of 4.5 to 1. Spring spawning appears to have taken place earlier in 1951 because of temperatures higher than normal in April.

A review of the literature, however, shows that herring spawn over a wide range of temperatures.
. . . Table 1 . . . shows that water temperatures at which herring spawn range from 0° to 12° C in the spring and from 8° to 15° C in the fall.» – Actually, the mean spawning temperature for spring is 6.5 ± 2.8 and for autumn 11.2 ± 2.1 degrees centigrade. In table 2 a few water temperatures are given at which various other fish spawn in different localities.

The effect of water temperature on spawning has been studied in detail by various workers. MANKOWSKI (1950) stated that low temperatures during the spawning season delayed the spawning of Baltic cod, whilst higher temperatures hastened spawning. DRAGESUND (cf. DEVOLD 1959) has kept living Atlantic-Scandinavian herring in nets in shallow water. Thus, throughout the spring these fish were forced to stay in the cold surface water, with the result that they did not spawn until June when the temperature of their abnormal environment started to rise. This experiment shows that spawning can be delayed for three months by keeping the fish in water colder than the optimum.

The narrowness of the temperature range suitable for spawning, in a few cases different for different fish stocks of the same species (PERTSEVA 1939), affects the geographical distribution of spawning. For example, the cod spawn in Motovsky Bay three weeks later than near the Lofoten Islands and 1.5 to 2 months later than in the North Sea. Fish appear to respond to their oceanographic »climate» rather than to geographically fixed reference points during the spawning season (AHLSTRÖM 1959). Therefore, abnormal temperatures on the spawning ground during the spawning season force the fish to spawn in other areas than those to which they normally go for this purpose (SIMPSON 1953). Long-term temperature changes may therefore cause the periodic northward and/or southward displacements of spawning (and fishing) grounds. The conclusions of NIKOLAJEV (1958) on the behaviour of the Baltic herring are in accordance with these statements: »The abundance of the spring and autumn Baltic herrings seems to fluctuate within different ranges, the abundance of the spring herring increasing during cold-water periods (according to the winter regime) 1926 – 30 and decreasing during warm-water periods (1931 – 39 and 1951 – 57), the abundance of the autumn herring, on the contrary, increasing during warm-water and decreasing during cold-water periods. This fact seems to be consistent with the geographical distribution of these particular herrings and of all spring and autumn herring races in general. The spring herrings prevail in the subarctic waters of the Norwegian, Barents and White Seas as well as in the Northern Baltic whereas the autumn herrings mostly occur in the boreal waters of the North Sea and in the Southern Baltic. The main cause of these differences seems to lie in the fact that the biological peculiarities (particularly the spawning season) make for a better utilization of the feeding resources of colder waters by the spring herring and of warmer waters by the autumn herring.» (Cf. DEVOLD 1959).

The development of the eggs and larvae is undoubtedly the most critical period in the life history of fish, because this is when they are most strongly influenced, directly and indirectly, by physical conditions. Temperature directly influences the rate of development and, in conjunction with salinity, will determine the prevailing water density, thus affecting the buoyancy of the eggs. The length of time taken for the incubation of eggs, as well as the length of larval life, depends directly upon the temperature of the environment.

JEAN (1956) has surveyed the literature on the incubation period of Atlantic herring eggs at various temperatures, based partly upon laboratory experiments, partly upon observations in the sea. These data, from 21 different sources, are plotted in Figure 1. The probable form of the relationship between the water temperature and the incubation period is exponential, with an asymptote above zero. The best fitting curve is expressed by the equation

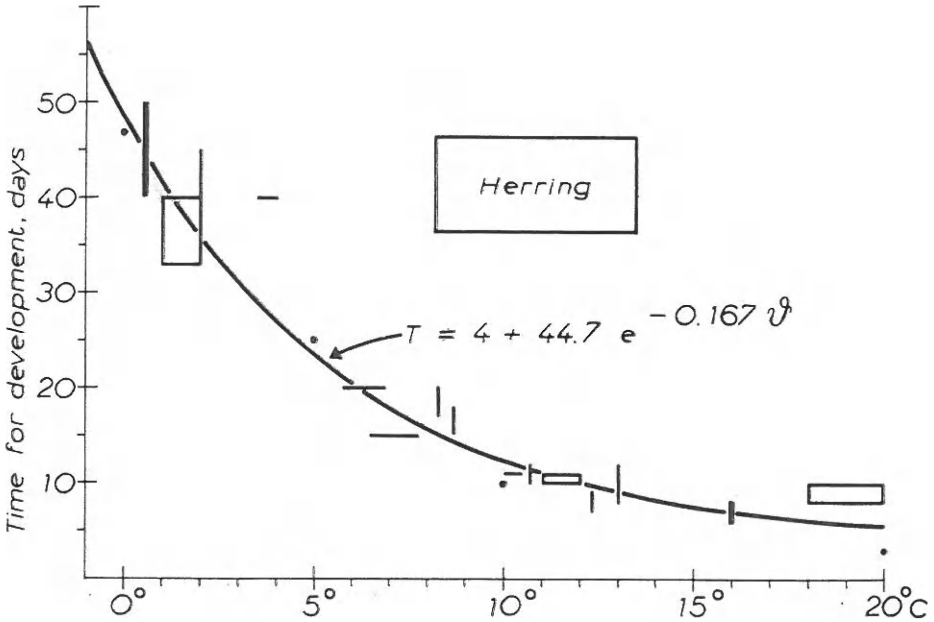

Fig. 1. Incubation period of herring eggs at various temperatures. Observations by HESSE (from GUNTER 1957) are indicated by heavy lines; other observations, collected from different sources by JEAN (1956), are indicated by thinner lines.

$$T = 4 + 44.7\,e^{-0.167\,\vartheta}. \qquad \text{(Herring)}$$

For the computation of this empirical equation the data of HESSE et al. (1937, from GUNTER 1957) were also used, according to which herring eggs develop in 40 – 50 days at 0.5° C and in 6 – 8 days at 16° C. The above equation indicates that the incubation period is about 49 days at 0° C, and is always 4 days or more regardless of the temperature.

Correspondingly, the incubation period, as a function of environmental temperature for cod eggs, based on data given by EARLL (1880) and DANNEVIG (1895), is as given in Fig. 2. In this case the best fitting curve is represented by the expression

$$T = 7 + 30.3\,e^{-0.215\,\vartheta}. \qquad \text{(Cod)}$$

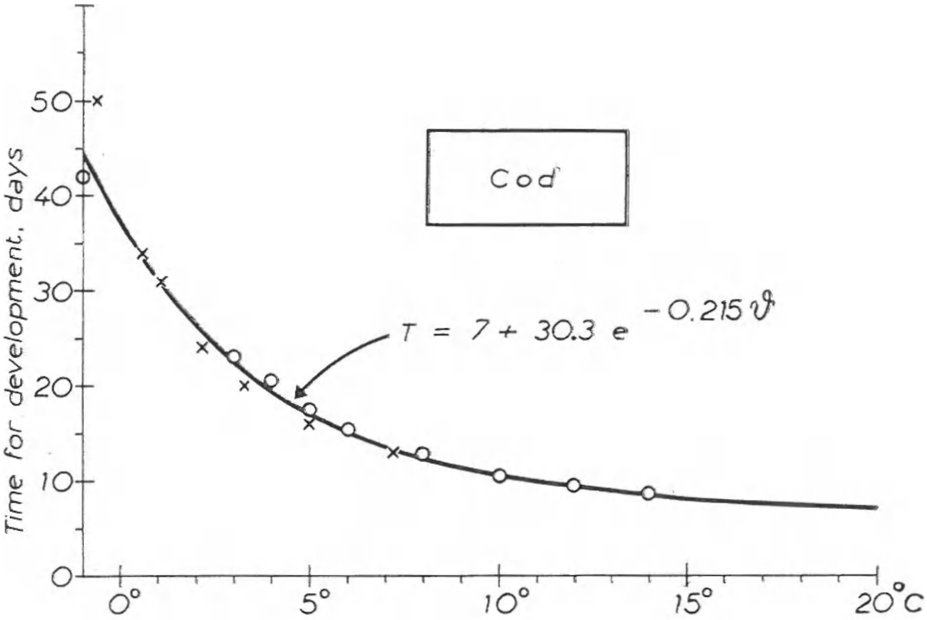

Fig. 2. Incubation period of cod eggs at various temperatures (x EARLL; o DANNEVIG.).

which means, among other things, that the incubation period for eggs is 37 days at 0° C, and is always 7 days or more regardless of the temperature. It is interesting to note that according to this treatment of the data, the incubation time for both herring and cod eggs is about 8.5 days if the water temperature is 13.5° C.

ITO (1958) gives data on the incubation time for sardine (*Sardinops melanosticta*) eggs. The best fitting curve is expressed by the equation.

$$T = 0.5 + 28.8\,e^{-0.159\,\vartheta}. \qquad \text{(Sardine)}$$

which means that the minimum incubation period for sardine eggs is approximately 0.5 days. At 10° C the period is 6.5 days. (Fig. 3.)

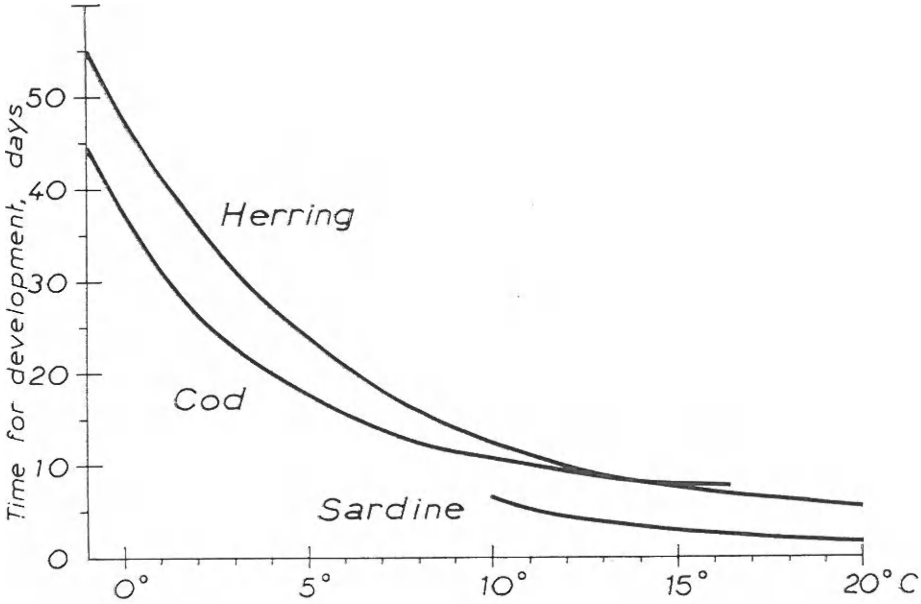

Fig. 3. Incubation periods of herring, cod and sardine eggs.

The prevailing sea water temperatures – and currents – during and after spawning are the most important factors determining the »brood strength» and survival of larvae of the commercially most important fish species (ROUNSEFALL 1930; UDA and HONDA 1934; KURITA 1959). This fact has been used in the prediction of the strength of coming year classes (CHASE 1955). In medium and higher latitudes, high temperatures coincide with rich year classes, and low temperatures with poor year classes (TÅNING 1951; HERMANN 1951).

Actually, there are several ways in which the temperature can influence the survival of larvae. The most important of these is probably its effect on the availability of food. It is evident that the availability of food suitable for larvae at the appropriate time is related to phytoplankton production, which in turn is closely related to the seasonal changes of temperature and to the amount of light (which normally shows a close correlation with the sea water temperature). Also, the abundance of zooplankton, important as food for the larvae, is related to (a) the abundance of phytoplankton, and (b) the spawning period of adult planktonic animals, which again is controlled by temperature. Many authors have reported that warmer water during and after spawning has resulted in better year classes of cod because of the consequent greater availability of plankton as food (WISE 1958). In general, too high or too low temperatures may put the development of larvae »out of phase», so that larval development occurs before or after the peak population of the proper plankton.

The following two cases indicate the significance of sea water temperature for the development of plankton. CRISP (1957) showed experimentally, with two species of Arctic barnacle, *Balanus balanoides* and *Balanus balanus*, that by maintaining individuals at too low or too high a temperature it was possible to cause breeding to take place at times of the year other than the normal breeding seasons. TANAKA (1955) showed by experiments that the time of the spawning migration of the porgy (*Pagrosomus major*) was controlled by the temperature and the number of daylight hours. The development of plankton in higher and medium latitudes is dependent on light, and the effect of light may be included in the »natural instinct», in that the feeding period of larvae normally coincides with the peak population of plankton.

It is worthy of mention that the influence of sea water temperature on the year class strength may also be exerted through competition, as suggested by MARR (1959): »The lack of spawning success off southern California is attributed to environmental conditions, specifically, to the below average temperature regime which has delayed sardine spawning off southern California by one or two months. It is proposed that under these conditions sardine larvae are unable to compete successfully with the anchovy, which has a lower temperature threshold.»

Finally, as a summary of the above observations, it may be said that

a) the following up of the temperature and its changes in the spawning grounds,

b) the following up of the temperature in the region later occupied by the larvae, with

c) the following up of the availability of food (plankton), and

d) a knowledge of the optimum temperature for survival of the larvae of a given fish stock would facilitate the prediction of the survival rate of the brood and the later strength of a given year class.

4. Influence of temperature on feeding, metabolism and growth

Rates of feeding, metabolism and growth are affected not only by the availability of food but also directly by the water temperature. At suboptimal temperatures feeding activity is usually reduced. (Indirectly the temperature affects feeding by affecting the abundance of the food, e.g. plankton.) It has been found that cod will not eat if the temperature is $< 1°$ C, the optimum for feeding varying between 2.2° and 15.5° C. NIKOLAJEV (according to a paper on the Baltic herring and cod by T. DEMENTJEVA read at the 1956 conference of the International Council for the Exploration of the Sea) counted from different catches the percentage of Baltic herring which had consumed food before being caught (Fig. 4). During the exceptionally mild winter of 1951 – 52, the herring continued to feed throughout the winter, which resulted in their substantial growth. During severe winters, and especially in 1953 – 54, the percentage of Baltic herring which ceased to feed dropped to zero for three to four months.

It has also been observed that abnormally high temperatures cause a decrease in feeding (KOMAROVA 1939).

Growth is directly dependent on metabolic rates. According to BRETT (1957), there is a temperature level at which the difference between active and resting metabolic rates is maximal. This is the maximum activity level of fish with optimum energy release. Therefore,

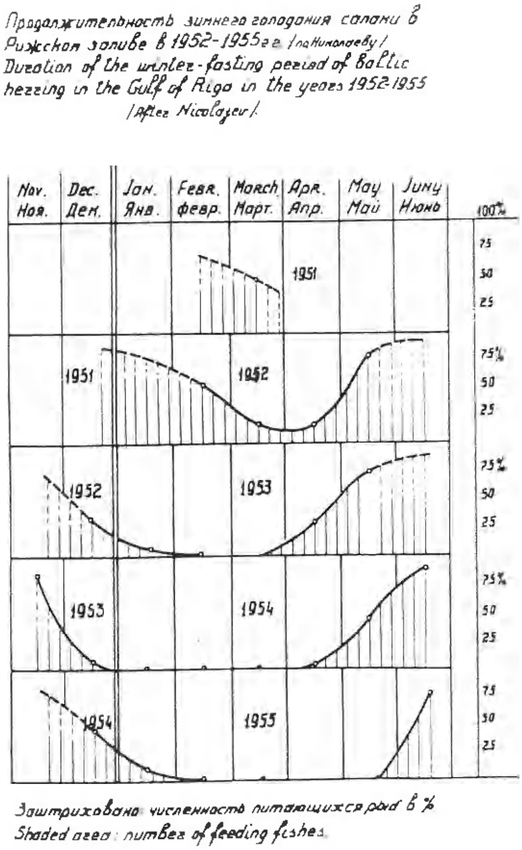

Fig. 4. Duration of the winter fasting period of Baltic herring in the Gulf of Riga in the years 1952 – 55 (according to NIKOLAJEV).

there is also an optimum temperature for optimum growth of a given acclimatized species, and the metabolic rates of this species are considerably influenced by temperature. However, the differences in the metabolic rates of acclimatized species or populations in warm and cold seas are relatively small. Although several fish species have a wide range of temperature tolerance, growth is usually optimal within a limited range of higher temperatures. KÄNDLER (1955) found that the growth of plaice is optimal at temperatures of 13 – 15° C; below 1° or 2° C it is completely arrested.

It is frequently claimed that fish grow larger and older at low temperatures, and that this is due to their lower metabolic rate and lower activity, or sometimes to the greater availability of food. TAYLOR (1958) showed that growth rate, life span and maximum size of cod is quantitatively related to annual mean sea surface temperature. WISE (1959) concluded that the large fish seek lower temperatures, and that there may be a physiological need in the larger fish for lower temperatures. This theory can be applied in the interpretation of the size and age distribution of species in the following way: the larger and older specimens migrate to the colder boundaries of the distribution area of the species, while the smaller specimens remain in the normal distribution area. Often these large specimens will not return to the normal spawning grounds and their spawning in the colder area is not successful. These old stocks could be fished more intensively than the »normal» stocks.

5. Temperature optima for adults and the influence of temperature on the abundance, migrations and shoaling of fish

Fish search for and select a certain optimum combination of physical and biological conditions in the environment. Nearly all fish stocks have specific optimum temperatures. (Some optimum temperatures reported for different species and areas were summarized in Table 2.) A thorough knowledge of these optimum temperatures is necessary for the prediction of fish concentrations. With such knowledge, predictions of temperature, either statistical or synoptic, can be used for predicting the seasonal abundance of a given stock of fish.

The problem is further complicated by the fact that the environmental requirements change during the various stages of growth. Furthermore, some investigations indicate that the temperature requirements of certain species also change seasonally (cf. DEVOLD 1959), at least in connection with spawning. And, moreover, the concentration of food is temperature dependent, which makes the determination of the »optimum temperature» for a fish exceedingly complicated in a few cases. In spite of this, the seasonal and year-to-year variations in thermal and other conditions will result in varying distribution and abundance on a given fishing ground. Actually, many fish make seasonal migrations towards the poles during the summer, and towards the equator in winter. It may be that these migrations are directly influenced by temperature, or indirectly by the effect of temperature on the abundance of food. Besides the seasonal migrations, the shoaling connected with spawning, feeding, etc., must be controlled, either directly or indirectly, by temperature.

The best fishing grounds and areas are frequently located on the boundary regions of two currents or in other areas of upwelling and divergence. UDA (1936) stated that the »Sanma» (*Cololabis saira*) stays in the areas between the boundaries of the Kuroshio and Oyashio Currents, and is always migrating towards the maximum gradient of surface temperature. According to UDA (1952), the best fishing area for tuna is in the contact zone of these same currents (at temperatures of 18 – 20° C). The same applies to Pacific sauri, sardine, mackerel and flying fish. Each of these species has a slightly different temperature preference. Similarly, GRAHAM (1957) stated that in the central North Pacific the catches of surface-swimming and possibly also of deep-swimming albacore were associated with the Polar Front and transition zone between Central Pacific and Subarctic waters. Surface catches were also associated with a seasonal latitudinal change in surface temperature, particularly about the isotherms 12.8 – 18.3° C. KAWANA (1934) and HIDA (1957) similarly reached the same conclusion that albacore tend to concentrate at certain surface isotherms (14 – 18° C, KAWANA op.cit.). Favourable catches of Japanese sardine on the southern grounds are made in the surface temperature range 12 – 16° C (UDA and OKAMOTO 1946).

DIETRICH, SAHRHAGE and SCHUBERT (1959) found that in the northern North Sea the concentration of herring may be influenced by four different phenomena in the distribution of temperature:

1) In summer and autumn the herring is concentrated in the core of the cold bottom water. (The fishery workers of Japan and Norway have independently found out that the cold water pockets in the boundary regions have a profound influence on the migrations of certain pelagic fish which tend to aggregate in these pockets.)

2) The lower the temperature of this cold water, the longer is the duration of herring concentration.

3) The geographical position of this concentration fluctuates with the displacement of the centre of the cold water mass.

4) The daily vertical movements of the herring schools are influenced (indirectly and directly) by the structure of the thermocline.

The depth of the pelagic schools depends largely on the vertical temperature structure. It is known, for example, that pelagic fish swim deeper when the surface waters are warm. POSTUMA (1957) has indicated that the depth of the herring schools at night depends on the vertical extension of the mixed surface layer, since the herring do not penetrate far into this layer. The pattern of the diurnal vertical migration of herring must be affected both directly and indirectly, through the concentration of food at the thermocline. Similarly, BĒRZIŅŠ (1949) has shown that the pelagic fish in the Gulf of Riga (at night) avoid extremely warm and extremely cold water. In July and August most sprat (*Clupea sprattus balticus* Schneider) are caught in the temperature range 10 – 15° C, while most of the small Baltic herring are caught at the temperature 8 – 12° C.

GALTSOFF (1924) and PEKTAS (1954) have related the seasonal migrations of mackerel in the Black Sea to the temperature. The seasonal, temperature-controlled migrations of mackerel in the North Sea were described by DANNEVIG (1955), who pointed out the fact, already known to fishermen, that the mackerel in North European waters disappear from the surface when the water gets colder, and appear again in the spring when the water starts to warm up. In the higher latitudes, the mackerel stay at a depth of several hundred metres during the winter. The migration to the surface starts in the spring when the bottom water grows colder. After a long, severe winter the mackerel therefore migrate to the surface earlier than after a mild winter, when the temperature of the bottom water is relatively high. Mackerel seem to avoid water which has a temperature lower than 4 – 5° C. (Similarly, JACKMAN and STEVEN (1955) correlated the arrival and departure of the mackerel to the sea surface temperature at Torbay, and also to the establishment and breakdown of the summer thermocline.)

LEE (1952, 1956 and 1959) has shown that paying catches of cod, in Bear Island waters, were not taken in water with a temperature below 2° C except in July to September, when the cod sometimes entered very cold water in order to feed on the capolin and krill. In May to June and in October to December, good catches of cod were made on the Bear Island Bank, when the temperature of the bottom water was 2 – 4° C, along the boundary between the warm Atlantic water and the cold Arctic water; the cod were sometimes found in the pockets of warm water surrounded by water below 2° C.

RASMUSSEN (1955) found that in Labrador waters the best catches of cod with long line in the surface waters were made when the temperature was 3 – 4° C, and that satisfactory catches could sometimes also be made when the temperature was 2.5 – 3° C. The best catches with the bottom long lines were made at temperatures of 2.1 – 2.5° C. If the

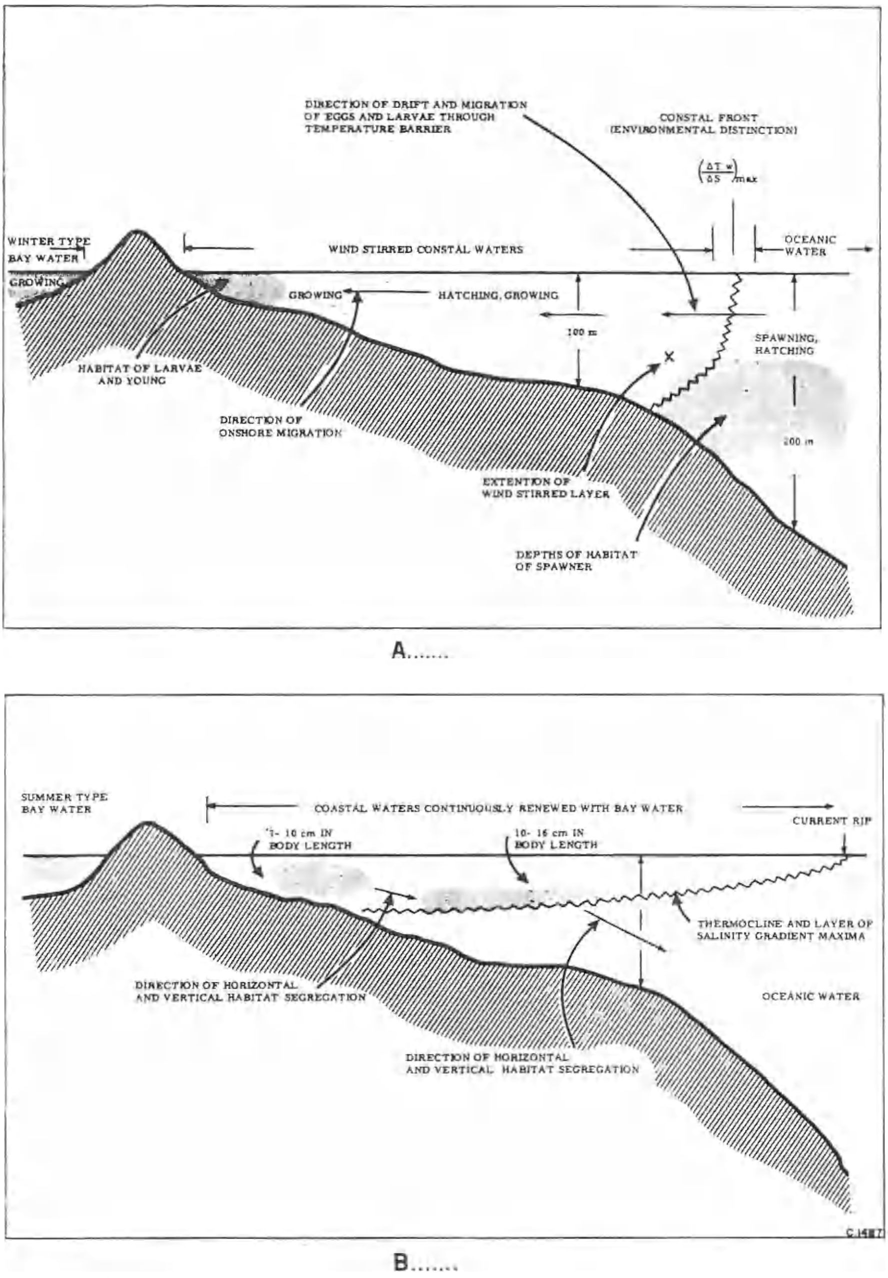

Fig. 5. Schematic representation of the offshore-onshore movements of the Japanese sardine (*Sardinia melanosticta*) in the coastal waters of western Japan (according to TSUJITA 1957). (A. . . winter season; B . . . summer season.)

bottom temperatures were below 1.5° or over 4.0° C, the catches were considerably smaller. McKenzie (1934 and 1936) indicates that most of the cod on the Nova Scotia Bank are caught in water at temperatures of 0.5 – 7° C. Le Danois (1934) claims that at temperatures of 3–5° C cod are very abundant, and at temperatures of 5–7°C haddock are plentiful. Further information on the behaviour of cod in relation to temperature is given by Hachey, Herman and Baily (1954) among others. Dietrich, Sahrhage and Schubert (1959) concluded that a correlation exists between the concentration of haddock and the temperature in the region of the Dogger Bank as soon as the total number of fish in this area and the differences in temperature reach certain levels.

Sullivan and Fisher (1953) have found that in autumn and in the beginning of winter the fish select progressively lower temperatures, the change being slow in autumn but rather rapid in the early winter. Then, in spring, independently of changes in water temperature, the fish seek higher temperatures. The finding of Thompson (1943) that catches of cod, in relation to temperature, vary with the season near Newfoundland, is in accordance with this observation. Seasonal temperature-controlled migrations of Japanese sardine are illustrated schematically in Figure 5 (Tsujita 1957).

Thus, whatever the actual causes, the fluctuations in the catches of many pelagic species are »controlled» by temperature (see Uda and Okamoto 1936; Nakai 1959). The relative distribution of catchable stocks are correlated with temperature (Radovich 1959). Several attempts have therefore been made to correlate the sea water temperature and/or density with the annual catch of fish, for instance with the commercial catch of »iwashi» (sardine, anchovy and round herring) in the Inland Sea of Japan. In addition, Uda and Honda (1934) concluded that the duration of the fishing season for »buri» (*Seriola quinqueradiata*) in the waters around Japan is longer when the temperature of March is lower than that of January, and also when the temperature rises more slowly than usual. Uda and Watanabe (1938) assume that the passage of cyclonic storms causes the lowering of sea surface temperature and the southward extension of the Oyashio Current, resulting in a rapid southward shift of the fishing areas of skipper and bonito.

As mentioned in the introduction, the behaviour of fish is not infrequently influenced by environmental factors other than temperature, but even in these cases the temperature may serve as a most useful indicator. This is illustrated by the observations of Davies (1957), who found that off the west coast of South Africa in general, but excluding Saldanha Bay, the maximum occurrence of juvenile pilchards (*Sardinops ocellata*) coincided with the minimum temperatures recorded during the summer months. It was also apparent that a relationship existed between the abundance of juvenile pilchard and wind: In spring and summer, when juvenile pilchard were most abundant, southerly winds were most prevalent. In autumn and winter, when southerly winds were far less frequent, juvenile pilchard were present in small numbers only. The seasonal variation in the abundance of juvenile pilchard also showed a direct relationship with the seasonal variation in the abundance of edible plankton.

It appears from the observations presented in this section that many species tend to concentrate in certain isotherms and that current boundaries and areas with sharp horizontal temperature gradients often form the limits to the distribution of certain species.

Furthermore, aggregations of fish may occur at these limits as well as in the »water pockets» close to them, as so clearly demonstrated by the Bergen school of fishery scientists. As another example it may be mentioned that the Japanese offshore salmon fishery in the Bering Sea is confined within narrow temperature limits; the fishermen and research vessels keep a continuous check on the changes in sea surface temperature, in cooperation with the Japanese Meteorological Agency, thus providing a basis for the oceanographers on board the factory ships to make appropriate synopses and forecasts of sea temperature conditions, which are then communicated to the fishing fleet.

In order to be able to predict the presence of fish plentiful enough for profitable fishing in a given area,

1) the optimum temperatures (and other optimum environmental factors) of all economically significant species must be known,

2) a sufficient number of frequent hydrographical and meteorological observations must be made to provide information on the location of critical surface isotherms and, furthermore, on the areas of sharp surface temperature gradients, where water pockets are formed by meandering eddies of the currents, and

3) the changes in the hydrographical conditions must be predicted.

6. Lethal temperatures and mass mortalities caused by too low or too high temperatures

The lowest and highest temperatures at which a fish may survive depend upon its previous acclimatization. Therefore, sudden changes of temperature are normally much more dangerous to fish than slower changes during which they have time to become acclimatized.

DOUDOROFF's (1942) experiments showed that fish normally living in water of 12° to 25° C were killed by temperatures well above freezing point. He (1957) found that temperatures as high as 5° or even 10° C proved fatal to the species studied after acclimatization to 20° C. MATHEWS (1959) stated that mass mortalities can be caused by a change of as little as 5° C in less than a few days. HAYASAKA (1934) reported that in the Pescadores Islands, certain fish which live in shallow warm seas were killed in the winter of 1933/34, when the air temperature suddenly dropped below 10° C and stayed so for several days. GALLOWAY (1941) has recorded extensive mortality of fish in the coastal areas of Florida when the minimum temperature was as high as 14° C. From these cases it can be concluded that sudden drastic changes of temperature are lethal.

On the other hand, SIMPSON (1953) has found that temperatures slightly under 0° C do not injure the cod or plaice of the North Sea. According to SIMPSON (op.cit.), W. C. SMITH found that 43 per cent of plaice survived in the hatchery when the water temperature was below 0° C. In his experiences at Espegrend, LEIVESTAD (personal communication by V. SJÖBLOM) has shown that bottom fish (of the genus *Cottus*) survive at freezing temperatures.

MEUWIS and HEUTS (1957) have studied the effect of temperature on the respiratory movements of carp. The results showed that the upper lethal temperature was lower for the older and heavier carp than for the younger, smaller fish. The younger fish showed little change in a temperature range of 15 – 35° C.

7. Long-term temperature changes and their influence on the distribution of species

Several workers have studied the correlation between long-term temperature changes and changes in the distribution of species. In spite of the high degree of statistical correlation, the causal explanation must, in general, be more complicated. MEYER and KALLE (1950) have analyzed the situation in 1938, in which a close correlation can be shown between the long-term warming of the Baltic waters and the increase of the cod catches. Their causal explanation can be summarized as follows: the warming of the Baltic waters was the result of an intensification of the atmospheric circulation which also resulted in the penetration of less diluted, more saline Kattegat water into the western and southern basins of the Baltic Sea. This penetrating water, being heavier than normal, displaced the stagnant bottom water of the basins, with resulting reutilization of the phosphates and other nutrients stored there. This, in turn, led to a period of increased fertility over wide areas of the Baltic Sea. At the same time the deep waters were, of course, enriched with oxygen, which, together with the rich phytoplankton, led to the heavy cod catches of the following years.

LEE (1956) concluded that the effect of climatic fluctuations upon the adult cod in the Barents Sea is probably only slight. He has put forward the hypothesis that the increase in fish stocks in the north has been mainly due to such changes in the environmental conditions as have increased the survival of the eggs and larvae of the cod. TÅNING (1953) summarized the probable ways in which a long-term temperature rise can influence the distribution of fish (in the Northern Hemisphere):

a) spawning is diminished at its southern limit and increased at its northern limit,
b) an increase in bottom water temperature can produce changes in spawning grounds,
c) new nursery and feeding grounds become available in the north,
d) an increase in the amount of food is brought about by the rise in temperature in higher latitudes and changes occur in currents and in the amount of nutrient salts present,
e) the growth period is prolonged, and
f) the limit at which larvae can survive is shifted further north.

Thus, if, instead of the direct apparent correlation, the more complicated but causally sound correlations are studied, in a few cases more significant factors can be found which explain the synchronism of the long-term temperature trends and changes in the fish distributions.

Several cases show that statistical correlation studies may give useful results. RODEWALD (1955) discussed the heavy Greenland cod catches in recent years occurring simultaneously with the general increase of temperature in the North Atlantic, and believed that the small decrease of temperature of the past few years did not indicate a general return of the cold conditions prevalent before 1920, since this decrease was to be considered a small fluctuation only. He also showed that the small catches of cod on the west Greenland Banks in July – August are related to the low temperatures of the Kap Farwel Current, which reaches the Banks during this season.

UDA and OKAMOTO (1936), observing the improvement in the sardine fishing in the sea of Japan in the south during the winter and spring, and in the north during the summer, concluded that the fluctuation in the yield of sardine is related to long-term changes in temperature. UDA (1952) concluded that the cause of the northern displacement of the main sardine spawning ground off Nagasaki is the decrease of the coastal water temperature along the coast of Japan in recent years; the fluctuation in the yield of sardine runs parallel to that of tuna, but inversely to the fluctuations of herring, squid, Pacific sauri, and cod.

8. Present and future possibilities for finding fish concentrations by »thermometric methods» and for prediction of abundance

Predictions of the survival of larvae and the strength of the coming year-classes have been made with some success in the past, on the basis of data on sea temperature and other environmental factors. Some of these possibilities have been discussed by CARRUTHERS (1956). The main limitation of these methods depends upon the multitude of local and special factors involved. Therefore, no general rules for making these predictions can be given; the factors involved must be evaluated separately for each given locality and stock.

Nevertheless, it is obvious that great use can be made of the relations existing between the concentrations of different commercially important fish and the temperature, in locating fish concentrations. Temperature is the environmental factor most easily measured and likewise the most important one, influencing the behaviour of fish in the different ways discussed above. However, since many other factors may be involved in the particular behaviour of a species, predictions cannot always be expected to be correct. A very fair chance of better catches may be expected from such predictions, provided that the following conditions are fulfilled:

1) The behaviour of a given species at various temperatures must be known (including optimum temperature and spawning temperature).

2) The present distribution of temperature must be known and the future course of its distribution must be predicted.

3) In addition, it is necessary to assume that the horizontal (and/or vertical) temperature gradients are not too weak.

The great horizontal temperature gradients in the sea occur in the regions of divergences and convergences of currents. These areas are rich in pelagic fish. Therefore, the prediction of the movement of these zones, with the meandering and eddying of water masses at their boundaries, is of great importance for the fisheries. This is also true of the location of whaling areas (HANZAWA, OKABAYASHI, YOSHIDA and MURAMO 1951).

Many species are caught in greater quantities during their aggregation for spawning. As observed above, the arrival of spawning stocks as well as fluctuations in area and time of spawning, can be predicted relatively accurately, if both the past and present history of the temperature in the sea and the specific thermal requirements of the species are known.

In order to be able to map the sea temperature distribution in detail in a short period (such as five days or a week), systematic hydrographic observations, supplemented by some meteorological observations, are necessary. In the most important fishing areas of the world this goal is attainable if and when certain organizational measures can be applied.

REFERENCES

AHLSTRÖM, E. H., 1959: Synopsis on the biology of the Pacific sardine (Sardinops caerulea) – Scient. Meet. Biol. Sardines, Rome, 1959.

ALLEN, E. J., 1897: Reports on the present state of knowledge with regard to the habits and migrations of the mackerel (Scomber scombrus). – Journ. Mar. Biol. Ass. U. K. 5, 1 – 40.

ALLEN, F. E., 1955: Identity of breeding temperature in southern and northern hemisphere species of Mytilus (Lamellibranchia). – Pacif. Sci. 9, 107 – 109.

BÉRZINS, B., 1949: Über Temperaturbedingte Tierwanderungen in der Ostsee. – Oikos 1, 29 – 33.

BIGELOW, H. B. and W. C. SCHROEDER, 1953: Fishes of the Gulf of Maine. – Fish. Bull. U.S. Fish Wildl. Serv. 74, 88 – 100.

BRETT, J. R., 1957: Salmon research and hydroelectric power development. – Bull. Fish. Res. Bd. Canada 114, 1 – 26.

BUCH, S. A., 1885: Spawning of spring herring near Norway. – Fish. Bull., U.S. Comm. Fish. 5, 297 – 300.

BULL, H. O., 1952: An evaluation of our knowledge of fish behaviour in relation to hydrography. – Rapp. Proc.-Verb. ICES 131, 8 – 23.

CARRUTHERS, J. N., 1956: Fish, fisheries and environmental factors. – Oceanus 4, 14 – 20.

CHASE, J., 1955: Winds and temperatures in relation to the breedstrength of Georges Bank haddock. – Journ. Cons. ICES 21, 17 – 24.

CIEGLEWITZ, W. and K. POSADZKI, 1947: Comparative studies on the spring and autumn spawning herring of the Bay of Danzig. – Ann. Biol. ICES 2, 159 – 165.

CRISP, D. J. 1957: Effect of low temperature on the breeding of marine animals. – Nature 179 (4570), 1138 – 1139.

CUSHING, D. H., 1957: The number of pilchards in the Channel. – Fish. Invest., London Ser. II, 21, 1 – 27.

DANNEVIG, A., 1955: Mackerel and sea temperature. Measurements – 21 April to 15 May 1952. Praktiske Fiskeforsøk, 1952. – Årsber. Norges Fisk. (5), 64 – 67.

DANNEVIG, H., 1895: The influence of temperature on the development of the eggs of fishes. – Annual Rep. Fish. Bd. Scotland 1894. 13 (3) (5), 147 – 152.

DAVIES, D. H., 1957: Young fish survey, 1955 – 1956. The South African pilchard (Sardinops ocellata) and maasbanker (Trachurus trachurus). – Comm. Industr. 16, 81 – 115.

DEVOLD, F., 1951: Herring trip with »G. O. Sars» in Norwegian Sea 5/7 – 24/8, 1950. Praktiske Fiskeforsøk, 1950. – Årsber. Norges Fisk. (5), 110 – 119.

–»– 1959: Otto Petterssons teori om de skandinaviske sildeperioder sett i sammenheng med de senere års undersøkelser over den atlanto-skandinaviske sild. — Naturen, Bergens Mus. 2, 83 – 92.

DIETRICH, G., D. SAHRHAGE and K. SCHUBERT, 1959: The localization of fish concentrations by thermometric methods. Modern fishing gear of the world. Fishing News Ltd. – London, pp. 453 – 461.

DOUDOROFF, H. P., 1942: The resistance and acclimatization of marine fishes to temperature changes, I. Experiments with Girella nigricans (Ayres). – Biol. Bull., Woods Hole (2), 219 – 244.

EARLL, R. E., 1880: A report on the history and present conditions of the shore cod fisheries of Cape Ann, Massachusetts, together with notes on the natural and artificial propagation of the species. – Rep. U. S. Fish. Comm. 1878, 6, 685 – 740.

FAGE, L., 1920: Engraulidae, Clupeidae. – Rep. Danish Oceanogr. Exped. Mediterr. and Adj. Seas, 2. Biol. A 9, 1 – 140.

FULTON, T. W., 1906: On the growth and age of the herring (Clupea harengus). – 24th Annual Rep. Fish. Bd. Scotland, Part III., Scient. Invest. 12, 293 – 342.

GALLOWAY, J. C., 1941: Lethal effect of the cold winter of 1939 – 1940 on marine fishes at Key West, Florida. – Copeia (2), 118 – 119.

GALTSOFF, P. S., 1924: Seasonal migrations of mackerel in the Black Sea. – Ecology 5, 1 – 5.

GRAHAM, J. J., 1957: Central North Pacific albacore surveys, May to November, 1955. – U.S. Fish Wildl. Serv., Spec. Scient. Rep. 212, 1 – 32.

GUNTER, G., 1957: Temperature. In: Treatise on marine ecology and paleoecology. Vol. 1. Ecology. – Mem. Geol. Soc. Amer. 67, 159 – 184.

HACHEY, H. B., F. HERMANN and W. B. BAILEY, 1954: The waters of the ICNAF Convention area. – Annual Proc. ICNAF (4), 67 – 102.

HANZAWA, M., K. OKABAYASHI, K. YOSHIDA and R. MARUMO, 1951: Report on sea and weather observations on the Antarctic whaling ground, 1950 – 1951. – Oceanogr. Mag. 3, 107 – 137.

HAYASAKA, I., 1934: On the fatal effect of cold weather upon certain fishes of the sea around the islands of Hoko (the Pescadores Islands). A paleontological point of view. – Taikohu Imp. Univ. Mem. 13 (2); (Geology No. 9), 5 – 12.

HESSLE, C., 1925: The herrings along the Baltic coast of Sweden. – Publ. Circ. ICES. 89, 1 – 55.

HERMANN, F., 1951: Hydrographic conditions off the West Coast of Greenland, 1950. (With remarks on the influence of temperature on cod year-classes). – Ann. Biol. ICES 7, 21 – 24.

HIDA, T. S., 1957: Chaetognaths and pteropods as biological indicators in the North Pacific. – U.S. Fish Wildl. Serv., Spec. Scient. Rep. 215, 1 – 13.

HUTCHINS, L. W., 1947: The bases for temperature zonation in geographical distribution. – Ecol. Monogr. 17 (3), 325 – 335.

ITO, S., 1958: On the relation between water temperature and the incubation time of sardine (Sardinops melanosticta). – Ann. Rep. Jap. Sea Reg. Fish. Res. Lab. (4), 25 – 31.

JACKMAN, L. A. J. and G. A. STEVEN, 1955: Temperatures and mackerel movements in the inshore waters of Torbay, Devonshire. – Journ. Cons. ICES 21: 1, 65 – 71.

JEAN, Y., 1956: A study of spring and fall spawning herring (Clupea harengus L.) at Grande-Rivière, Bay of Chaleur, Québec. – Contr. Dept. Fish. 49, 1 – 76.

JENSEN, A. J. C., 1955: Account of the present knowledge of the reaction of the mackerel to environmental factors. – U. N. Resource Conf. Rome.

JOHANSEN, A. C., 1921: On the summer-spawning herring (Clupea harengus L.) of Iceland. – Medd. Komm. Havundersøg., Ser. Fisk. 6: 3, 1 – 40.

–,– 1924: On the summer- and autumn-spawning herrings of the North Sea. – Ibid. 7: 5, 1 – 119.

–,– 1924: On the summer- and autumn-spawning herring of the North Sea. — Ibid. 7: 5, 1—119.

KÄNDLER, R., 1955: An account of the knowledge concerning the response of the plaice to environmental factors. – U. N. Resource Conf., Rome.

KAWANA, T., 1934: On the relations between the oceanographical conditions and tuna fishing. (In Japanese). – Journ. Imp. Fish. Inst. 31, 1 – 80.

KOMAROVA, T. V., 1939: Feeding of the long rough dab in the Barents Sea in connection with food resources. – Trans. Inst. Mar. Fish. Oceanogr. U.S.S.R. 4, 298 – 320.

KURITA, S., 1959: Causes of fluctuations in the sardine population off Japan. – Scient. Meet. Biol. Sardines, Rome, 1959.

LAEVASTU, T., 1960: Factors affecting the temperature of the surface layer of the sea. — Soc. Sci. Fenn., Comm. Phys.-Math. XXV:1, 136 pp.

LAUZIER, L., 1952: Recent water temperatures along the Canadian Atlantic coast. – Progr. Rep. Atl. Biol. Sta. 53, 5 – 7.

LE DANOIS, E., 1934: History of the investigations made at Newfoundland. – Proc. North Amer. Counc. Fish. Invest. 1, 35 – 56.

LEE, A. T., 1952: The influence of hydrography on the Bear Island cod fishery. – Rapp. Proc.-Verb. ICES 131, 74 – 102.

–,– 1956: British fishery research in the Barents sea. – Polar Rec. 8: 53, 109 – 117.

–,– 1959: The influence of environmental factors on the Arcto-Norwegian cod stocks. – Prepr. Int. Oceanogr. Congr., New York, 243 – 245.

LEGALL, J., 1935: Le hareng Clupea harengus Linnée. I. Les populations de l'Atlantique Nord-Est. – Ann. Inst. Oceanogr. Monaco 15, 1 – 125.

LYMAN, J., 1958: Requirements in military oceanography. – (Second Symposium on Basic and Applied Science in the Navy, San Diego, Calif. March 1958. Mimeo. 8 pp.)

MANKOWSKI, W., 1950: The influence of thermal conditions on the spawning of fish. – Bull. Inst. Pêches Marit., Gdynia 5, 65 – 70.

MANTEUFEL, B. P., and J. J. MARTY, 1939: The study of the spawning of the Murman herring. – Trans. Knipovich Polar Scient. Inst. 4, 41 – 94.

MARR, J. C., 1959: The causes of major variations in the catches of Pacific sardine (Sardinops caerulea, Girard) – Scient. Meet. Biol. Sardines, Rome, 1959.

MASSMANN, W. H. and A. L. PACHEIO, 1957: Shad catches and water temperatures in Virginia. – Journ. Wildl. Mgmt. 21, 351 – 352.

MATHEWS, J. P. 1959: Synopses on the biology of the South West African pilchard (Sardinops ocellata, Pappe). – Scient. Meet. Biol. Sardines, Rome, 1959.

MCKENZIE, R. A., 1934: The relation of the cod to water temperatures. – Canad. Fisherm. 21, 11 – 14.

–,– 1936: Cod and water temperatures. – Progr. Rep. Atlantic Biol. Sta. 17, 11 – 12.

MERRIMAN, D. and R. SCLAR, 1952: The pelagic fish eggs and larvae of Block Island Sound. – Bull. Bingham Oceanogr. Coll. 13, 165 – 220.

MERRIMAN, D. and H. E. WARFEL, 1948: Studies on the marine resources of southern New England. VII. Analysis of a fish population. – Ibid. 11: 4/5, 131 – 146.

Meuwis, A. L., and M. J. Heuts, 1957: Temperature dependence of breathing rate in carp. – Biol. Bull, Woods Hole, 112, 97 – 107. – Water Poll. Abstr. 30: 7.

Meyer, P. F. and F. Kalle, 1950: Die biologische Umstimmung in der Ostsee in den letzten Jahrzehnten, eine Folge hydrographischer Wasserumschichtungen? – Arch. Fischereiwiss. 2: 1/2, 1 – 9.

Nakai, Z, 1959: Fluctuations in abundance and availability of sardine populations caused by abiotic factors. – Scient. Meet. Biol. Sardines, Rome, 1959.

Nikolajev, I. I., 1958: Some factors determining fluctuations in the abundance of Baltic herring and Atlanto-Scandian herring. (In Russian with English Abstract.) – Trans. Inst. Mar. Fish. Oceanogr. U.S.S.R. 34, 154 – 177.

Orton, J. H., 1919: Sea-temperature, breeding and distribution in marine animals. – Journ. Mar. Biol. Ass. U. K. 12, 339 – 366.

Pektas, N., 1954: Uskumrularin muhtemel muhaceret sebepleri ve bu kenuda muhit suhunetinin rolü. (The probable cause of migration of Black Sea mackerel and the part played by temperature). (In Turkish). – Hidrobiologi Mecmuasi, Istanbul. Ser. A 2, 113 – 121.

Pertseva, T. A., 1939: Spawning, eggs and fry of fish in Motovsky Bay. – Trans. Inst. Mar. Fish. Oceanogr. U.S.S.R. 4, 412 – 470.

Postuma, K. H., 1957: The vertical migration of feeding herring in relation to light and the vertical temperature gradient. – ICES, Herring Committee 1 – 8.

Poulsen, E. M., 1931: Biological investigations upon the cod in Danish waters. – Medd. Komm. Havundersøg. Fisk. 9: 1, 1 – 150.

—»— 1944: On the fluctuations in the size of the stock of cod in the waters within the Skaw during recent years. – Rep. Dan. Biol. Sta. 46, 1 – 36.

Radovich, J., 1959: Some causes of fluctuations in catches of the Pacific sardine (Sardinops caerulea, Girard. – Scient. Meet. Biol. Sardines, Rome, 1959.

Rasmussen, B., 1952: Sea temperatures and the cod fishery. – Ann. Biol. ICES 8, 30 – 32.

—»— 1955: Norwegian research report for 1954. Note on the composition of the catch by Norwegian long-liners off West Greenland. – Annual Proc. ICNAF 5, 43 – 49.

Rass, T. S., 1936: Spawning, eggs and fry of the food-fishes of the Barents Sea. Breeding and development of fish in subarctic. – Int. Rev. Hydrobiol. 33, 250 – 270.

—»— 1939: On the life-history of the Murman herring. (In Russian with English summary). – Trans. Knipovich Polar Scient. Inst. 6, 93 – 164.

Rodewald, M., 1955: Klima und Wetter der Fischereigebiete West- und Südgrönland. (Climate and weather of the fishery areas of west and south Greenland). – Amtl. Veröff. Seewetteramtes Hamburg, 98 pp.

Rounsefell, G. A., 1930: The existence and cause of dominant year classes in the Alaska herring. – Contr. Mar. Biol., Stanford Univ. 260 – 270.

Runnström, S., 1927: Über die Thermopathie der Fortpflanzung und Entwicklung mariner Tiere in Beziehung zu ihrer geographischen Verbreitung. – Bergens Mus. Aarb. 1927 2, 1 – 67.

—»— 1941: Racial analysis of the herring in Norwegian waters. – Rep. Norw. Fish. Invest. 6: 7, 6 – 110.

Schmidt, J., 1926: The frequency of young cod etc. on the north and east coasts of Iceland during a period of years, preceded by a general survey of the life-history of the Iceland cod. – Rapp. Proc.-Verb. ICES 39, 139 – 148.

—»— 1931: Racial investigations X. The Atlantic cod (Cadus callarias L.) and local races of the same. – Comptes Rend. Lab. Carlsberg 18: 6, 1 – 72.

Sette, O. E., 1950: Biology of the Atlantic mackerel (Scomber scombrus) of North America. Part II. Migrations and habits. – Fish. Bull. U.S. Fish Wildl. Serv. 49, 251 – 358.

Shapiro, S., 1950: The Japanese long-line fishing for tunas. – Comm. Fish. Rev. 12: 4, 1 – 26.

Simpson, A. C., 1953: Some observations on the mortality of fish and the distribution of plankton in the Southern North Sea during the cold winter 1946 – 1947. – Journ. Cons. ICES 19, 150 – 177.

Sullivan, C. M. and R. C. Fisher, 1953: Seasonal fluctuations in the selected temperature of speckled trout, (Salvenius fontinalis). – Journ. Fish. Res. Bd. Canada 10, 187 – 195.

Sullivan, C. M., 1954: Temperature reception and responses in fish. – Ibid. 11: 2, 153 – 170. – Water Poll. Abstr. 30: 7.

Sund, O., 1935: Echo sounding in fishery research. – Nature 135 (3423), 953.

Sverdrup, H. U., M. W. Johnson and R. H. Fleming, 1942: The oceans, their physics, chemistry and general biology. Prentice-Hall. – New-York, 1087 pp.

Tait, T. B., 1952: Hydrography in relation to fisheries. Edward Arnold and Co. – London, 106 pp.

Tanaka, K., 1955: On the influence of hours of sunshine upon the maximum group of the caught porgy. – Jap. Journ. Ichtyol. 4, 40 – 44.

Tåning, A. V., 1936: Herring larvae in Icelandic waters 1924 – 1934. – Rapp. Proc.-Verb. ICES 99: 6, 1 – 20.

—»— 1951: North-Western area. Introduction. – Ann. Biol. ICES. 7: 8.

—»— 1953: Annual proccedings, ICNAF. (Articles on long-term temperature changes and fisheries). – Annual Proc. ICNAF 3. 1952 – 1953.

TAYLOR, C. C., **1958**: Cod growth and temperature. – Journ. Cons. ICES **23**, **366 – 370**.

THOMPSON, H., **1943**: A biological and economic study of cod (Gadus callarias L.) in the Newfoundland area. – Res. Bull. Div. Fish. Resources Newfoundland, **14**.

TSUJITA, T., **1957**: The fisheries oceanography of the East China Sea and Tsuchima Strait. **1**. The oceanographic structure and the ecological character of the fishing grounds. – Bull. Seikai Reg. Fish. Res. Lab. **13**, **1 – 47**.

UDA, M., **1936**: Fishing centre of »Sanma» (Cololabis saira Breevert), correlated with the head of Oyashio cold current. (In Japanese with English summary). – Bull. Jap. Soc. Scient. Fish. **5**, **236 – 238**.

–»– **1952**: On the relation between the variation of the important fisheries conditions and the oceanographical conditions in the adjacent waters of Japan 1. – Journ. Tokyo Univ. Fish. **38**, **363 – 389**.

–»– **1959**: The fluctuation of the sardine fishery in the oriental waters. – Scient. Meet. Biol. Sardines, Rome, **1959**.

UDA, M. and K. HONDA, **1934**: The catch of keddle nets in two fishing grounds on the coast of Nagasaki Prefecture and Izu Pensinsula. (In Japanese with English abstract). – Bull. Jap. Soc. Scient. Fish. **2**, **253 – 271**.

UDA, M. and G. OKAMOTO, **1936**: Effect of oceanographic conditions on »Iwashi» (sardine) fishing in the Japan Sea. (In Japanese with English abstract). – Journ. Imp. Fish. Exper. Sta. **7**, **19 – 49**.

UDA, M. and N. WATANABE, **1938**: Autumn fishing of skipper and bonito influenced by the rapid hydrographic change after the passage of cyclones. (In Japanese with English abstract). – Bull. Jap. Soc. Scient. Fish. **6**, **240 – 242**.

WISE, J. P., **1958**: Cod and hydrography; a review. – U. S. Fish Wildl. Serv., Spec. Scient. Rep. **245**, **1 – 16**.

–»– **1959**: Emigration of cod (Gadus morhua L.). – Prepr. Int. Oceanogr. Congr., New York, **358 – 359**.

WOOD, H., **1936**: Race investigations of the herring population of Scottish waters. – Fisheries, Scotl., Scient. Invest. **3**, **1 – 52**.

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