SECTION

F

F-1

POSSIBLE EFFECTS OF OXYGEN LACK ON SHOALING FISH

By

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ABSTRACT

This paper suggests that a critical shortage of oxygen may be the cause of the so-called vertical "swim" of dense herring shoals.

It is a well known fact in the herring fishery that herring shoals sometimes rise suddenly from the bottom layers to the surface. The vertical "swim", mainly observed in dense spawning shoals, is assumed to be due to a panic caused by predators chasing the herring. Other causes might be tidal effects, the narrowing of the shoal while approaching shallow water, or sudden internal stimuli. Besides these factors, decrease of oxygen below a critical level may be considered. In contrast to conditions for freshwater fish the oxygen supply for marine fish is normally sufficient. In very dense aggregations of fish with a high metabolic rate, however, a shortage of O_2 may occur. A hypothesis may be produced to explain the swim as a result of decreasing O_2 supply in a densely-packed shoal of herring. As long as the shoal is moving through the water and as long as the tidal currents cause some turbulence the O_2 content of the water occupied by the shoal will always remain high by continuous renewal.

Critical reduction of O_2 within the shoal may occur under the following conditions:
(a) during the slack period when turbulence is at a minimum
(b) in calm weather
(c) while the shoal is not moving, *e.g.* while it is concentrated on the spawning ground.

In addition to this reduction in exchange of water, an increase of shoal density or of the metabolic rate, or both, of the single fish due to external and internal stimuli will accelerate the reduction in O_2 inside the shoal.

The reduction of O_2 by the respiratory activity of the shoal may be estimated as follows:
(1) Weight of herring 150 g
(2) (a) O_2 consumption 90 mg O_2/kg/hr
therefore
(b) O_2 consumption per herring 13.5 mg O_2/hr
(3) (a) space occupied by a single herring assumed as about ten times its volume of 1500 ml,
therefore
(b) volume of water available 1350 ml per fish
(4) (a) O_2 saturation in seawater 9.6 mg O_2/l. (Salinity 35 /oo, temperature, 8°C)
therefore
(b) O_2 available to herring in 1350 ml is 12.96 mg.
(5) (a) minimum level of O_2 content for unrestricted respiration 3.5 mg O_2/liter, *i.e.* 4.73 mg O_2 in 1350 ml.
(6) No replacement of O_2 within the shoal.

Each of the statements in this balance sheet may now be discussed.

(1) The average weight of herring in a shoal varies considerably within and between the different races but an individual weight of 150 g is reasonable for adult North Sea herring.

However,

(2) data on the metabolic rate of herring are not available. The value given was derived from measurements by Sundnes (1959) on gadoid fish. A cod of 1,750 g total weight had an O_2 consumption

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of 50 mg O_2/kg/hr, and a coalfish of 1,020 g had an average consumption of 67 mg O_2/kg/hr. For herring, with its much smaller body size and rather high activity, the value of 90 mg/kg/hr should be regarded as an underestimate. Several measurements by Fry (1957) and other workers suggest that for salmonids of comparable size and under similar temperature conditions, values of 150-200 mg O_2/kg/hr are reasonable.

(3) Not much is known so far about the water volume per herring within the shoal because measurements of the volume of a herring shoal and the number of fish in this shoal are very difficult. The individual swimming space, *i.e.*, volume of the shoal divided by the number of fish in the shoal, is not constant. Observations in tanks show that fish close up if they are irritated and scatter while feeding. In the open sea an increase in shoal density may occur due to stimulation by gear or predators or during spawning.

(4) A temperature of 8°C will apply for the northern spawning grounds of the North Sea herring. It is an overestimate for Atlanto-Scandian spring spawners but an underestimate for the herring spawning in the central and southern North Sea and the English Channel and for some groups of Baltic herring. At higher temperature the O_2 saturation is reduced while the metabolic rate is increased. In addition the O_2 content of the bottom water is slightly lower than that of the upper layers.

(5) The critical level of the respiratory demand of herring is not known. But compared with other fish *e.g.* gadoids and salmonids (Sundnes, 1957 and Job 1955) 3.5 mg O_2/liter seems reasonable.

(6) The prerequisites for this assumption were listed earlier.

Using the above figures the O_2 supply available per herring for unrestricted respiration will be 8.23 mg O_2, *i.e.* the difference between the values for O_2 in (4b) and in (5a) above. The duration of unrestricted respiration is given by this amount of O_2 available and the respiratory rate of herring (2b).

$$8.23/13.5 \text{ hr} = 36.5 \text{ min.}$$

Thus, under the circumstances assumed in these calculations, critical shortage of O_2 in the shoal will occur after about half an hour. This figure should be taken as an upper estimate. If O_2 consumption of the stimulated herring is higher than assumed, or if the water temperature is above 8°C, the time will be much shorter. When herring approach the critical level they possibly show a panic-like behaviour and move up to the surface to search for aerated water.

Tank experiments with shoals of juvenile herring are planned to study the influence of reduced O_2 on shoaling behaviour. Measurements on the reduction of O_2 by herring shoals are also needed and should be conducted in the sea and in aquaria. New instruments for continuous recording of oxygen under sea conditions may facilitate those measurements.

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F-2

EFFECT OF CHANGE OF LIGHT INTENSITY ON FISH

By

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CONTENTS

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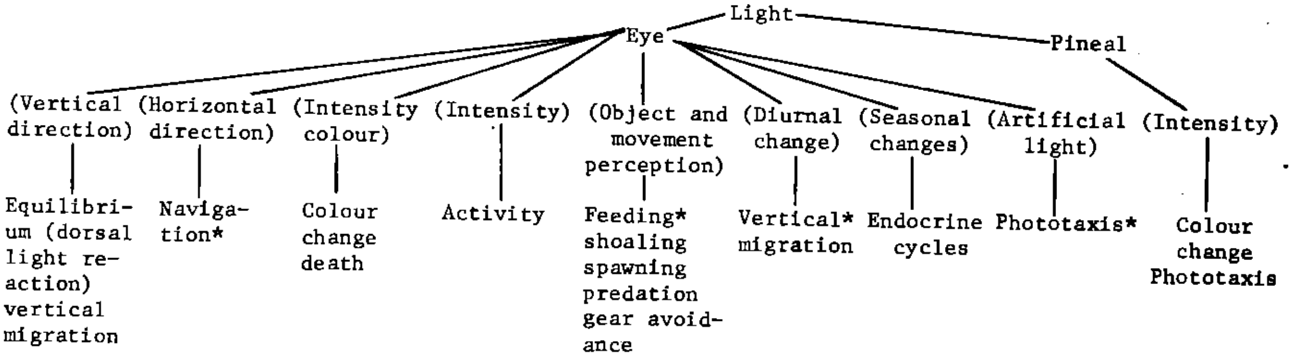
INTRODUCTION

Light may be considered as providing the most useful sensory information for fish. Due to its speed it gives the earliest possible warning of the environment at a distance, and its directional properties are also of great value in the perception of form and movement and in orientation. Diurnal and seasonal changes in light coordinate patterns of behaviour and physiology within a fish species. It is possible that the total integrated effect of light over an extended period may also be of importance.

The effects of light on fish may be shown by the following diagram:



This paper reviews some of the work done on the importance of light for different behaviour patterns (*) and especially refers to work done in recent years at the Marine Laboratory, Aberdeen.

CHARACTERISTICS OF LIGHT IN THE SEA

A brief outline of this subject will be given based on papers by Jerlov (1951, 1963).

1. Changes in Intensity

The intensity of light depends on time of day, cloud cover and the altitude of the sun, especially on a clear day. Surface reflection varies, in some cases only amounting to 1-3%, where the surface is calm. Reflection may be increased by wave action and absorption at the surface, by a turbid layer may be considerable. Below the surface light is attenuated due to absorption and scattering. Scattering will be low in clear oceanic water and high salinity is often associated with low particle content. High particle content will greatly affect attenuation; for instance, the blue component of daylight was reduced to 1% of the surface value in 8 m in Woods Hole Harbor, in 32 m in the deep basin of the Gulf of Maine, in 100 m in average oceanic conditions and only in 149 m in the Sargasso Sea (Clarke, 1936). The general extinction of light in various types of water is shown in Fig. 1. At night or in very deep water the light intensity may be more affected by bioluminescence than by light from the surface.

2. Changes in Colour

The colour of light changes with depth due mainly to absorption, scattering being less selective. The maximum penetration is by light of 460-490 mμ (blue) in oceanic water, but is at somewhat longer wavelengths in coastal water, see Fig. 2, (Jerlov, 1951; Atkins and Poole, 1958; Kampa, 1961). This is partly due to the presence of yellow substance (Kalle, 1961) which absorbs light of shorter wavelength. Red light is absorbed very rapidly; for example light of 600 mμ may be reduced to 2% of the surface value within 20 m. Ultra-violet light down to a wavelength of 230-240 mμ may be transmitted fairly well in clear water (Armstrong and Boalch, 1961; Jerlov, 1950). Light of 310 mμ for instance, was found to be absorbed only at the rate of 14%/m and of 375 mμ at 5%/m, compared with 3%/m for blue light. Absorption of ultra-violet light may be much greater in coastal water (for example 90%/m for light of about 310 mμ (?) in the Skagerrak) and may be substantial at 350 mμ when phytoplankton blooms are present.

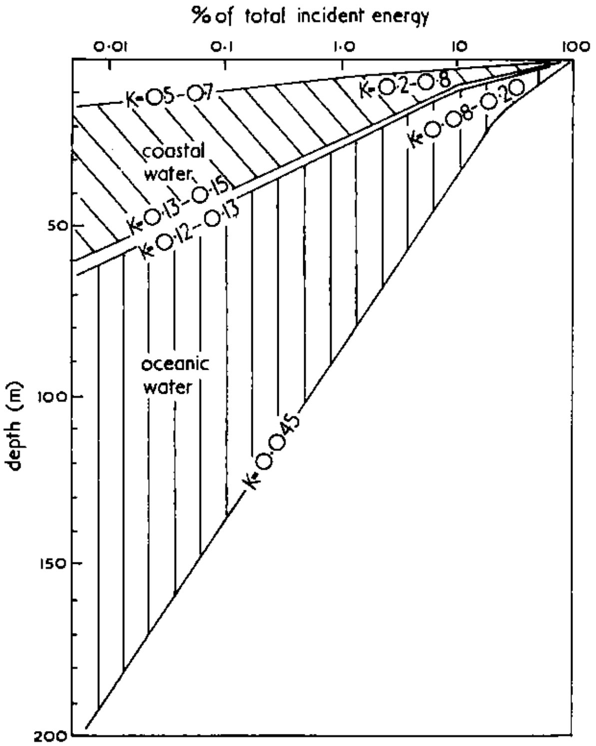
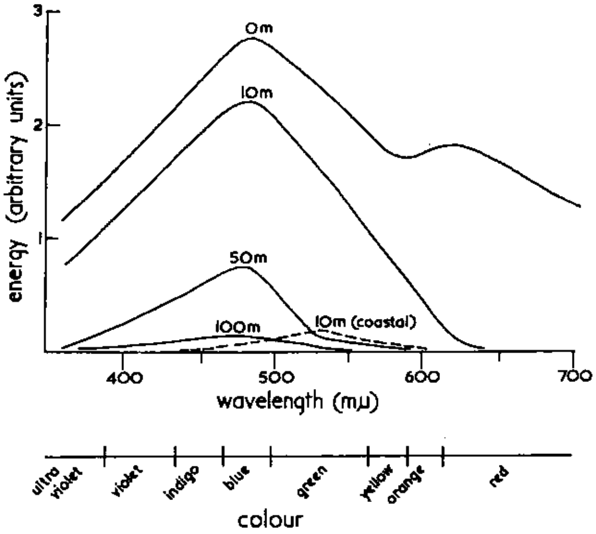


Fig. 1. Extinction of light at different depths in different types of water. (K is extinction coefficient in the relationship $K = 2.3 (\log I_z - \log I_z + 1)$, I being the intensity of a given wavelength at depth z and z + 1) (adapted from Jerlov, 1951).



Spectral absorption of sea water at 0, 10, 50 and 100 m off Bermuda (from Jerlov, 1951) with comparable curve for typical coastal water at 10 m (from Sverdrup *et al*, 1946).

It is of interest that luminescent organisms appear to produce light with a spectral peak at about 470 mμ (Clarke and Denton, 1962).

3. Angular Distribution

The angular distribution of light could be important for orientation of animals. The direction of highest light intensity is partly controlled by the altitude and azimuth of the sun, refraction tending to offset extreme obliquity. Theoretically the maximum obliquity would be about 48° to the vertical, this being the angle of refraction at the critical angle of incidence, but surface effects and scattering reduce obliquity, which becomes less extreme with depth. However, Atkins and Poole (1958) found an average obliquity of 30-40° from the vertical in the English Channel which was not very much affected by depth and altitude of the sun. The average ratio of light intensity measured vertically to the maximum value was 1:1.25. Jerlov (1951) and Sasaki, Okami, Watanabe and Oshiba (1958) found a dependence between the angle of maximum light intensity and the direction of the sun. This obliquity was lost gradually with depth, Jerlov estimating an equilibrium of distribution with vertical light predominant at 300 m in clearest ocean water. The upwelling light amounted to 1-4% of the downward light and had a peak of spectral composition at about 450 mμ. Sasaki *et al.* (1958) measured the extent of the horizontal light component and found that even at 80 m some directionality remained, related to the azimuth and altitude of the sun.

Clarke and Denton (1962) mentioned work on polarisation of light in the sea which showed that it diminished rapidly in the first 10-40 m. It seems possible it would be sufficient to permit azimuthal orientation of animals which can perceive polarised light.

4. Relationship to Fish Behaviour

In relation to fish vision, only few data of light intensity at different depths are available for the ICNAF area though more work has been done in the NE Atlantic. Estimates of light intensity at different depths using known average surface values and measurements of turbidity from Secchi disc readings (as taken in ICNAF NORWESTLANT Surveys) are not really satisfactory, because higher turbidity readings at the surface are likely to cause calculations of bottom light intensities which are much too low. Joseph (1961) estimated the turbidity at different depths in the North Atlantic using a transparency meter with a red light source. His extinction coefficients are related to water of very high clarity and do not permit calculations of light intensity at different depths very easily.

Information on fish vision is usually based on light intensity measurements in lux. The following values of lux are given for various light conditions at the surface:

													lux
10^{-7}	10^{-6}	10^{-5}	10^{-4}	10^{-3}	10^{-2}	10^{-1}	10^{0}	10^{1}	10^{2}	10^{3}	10^{4}	10^{5}	
				overcast night	clear new moon summer	full moon		dusk dawn		dull day		zenith sun	

In the wide variety of latitudes found in the North Atlantic there may be great variations in "night" and "day" values of light intensity. For instance during the summer Arctic "nights" the light may not fall below 10^3-10^4 lux (Digby, 1960).

Because the absorption of red light by water gives a spectral composition of light below 5 m not dissimilar from the spectral sensitivity of the human eye, especially when dark-adapted, lux values may be approximately equated with total energy values (Ångstrom, 1936).

LIGHT PERCEPTION

1. Vision

Vision in fish and its numerous adaptations to different environments has been reviewed recently by Sverdrup *et al.* (1946), Brett (1957), Polyak (1957) and Nicol (1963). The brief account in this paper is based on these four publications. The work on marine commercial species is inadequate and is mainly anatomical.

Generally speaking, the fish eye is not dissimilar in structure from the human eye. The retina contains both rods and cones, but accommodation is brought about by movement of the whole lens towards or away from the retina. The arrangement of the cones in many marine species has recently been reviewed comprehensively by Engstrom (1963). The adaptations of the lens to the marine environment and the optical system in fish are discussed by Clarke and Denton (1962). Teleosts are generally considered to be myopic (Brett, 1957). There is little pupillary movement and adaptation to light or dark results from migration of retinal pigment or of the visual cells. In elasmobranchs a reflecting layer, the tapetum, is found at the back of the retina.

Vision in high light intensities is due to the cones and in low light intensities to the rods. The rods summate giving added sensitivity but poor acuity. A fovea seems to be uncommon in fish, though there are often areas of the retina in which the density of cones is greatly increased, giving a higher acuity (Tamura, 1957*a*). The optic nerve decussates completely. The structure of the brain reflects the main sensory basis of the life of the fish. Thus, Evans (1935) correlated the brain structure of gadoids with their mode of life. The "visual" feeders such as cod, haddock, whiting, saithe, pollock and ling, had enlarged optic and small olfactory, lobes, while the three-bearded rockling had rather small optic, but large olfactory, lobes related to its mode of feeding. In the same way Blaxter and Holliday (1958) noted that the herring, which is also a visual feeder, had large optic lobes. Polyak (1957) and Tamura (1957*a*) discussed the anatomical basis and role of binocular vision in fish and its importance for the localisation of prey and predators. Some fish have a projecting cornea and siting grooves in the dermal bones in front of the orbit to improve the overlap of the visual field of the two eyes.

2. Colour Perception

This is generally accepted as being a function of the cones. So far no teleosts have been shown *not* to have colour vision. Walls (1942) considered that a duplex retina, containing rods and cones, was a reasonable indication of the presence of colour perception. The absence of cones in elasmobranchs suggests that they cannot perceive colour.

The lenses of diurnal and surface oceanic fish appear to absorb ultraviolet light, but in nocturnal and deep sea fish the lens may transmit light down to 310 mμ. As mentioned in the section on light in the sea, ultraviolet light may be transmitted quite well by oceanic water, but not inshore. This light may, therefore, be of use to some species. Craig and Baxter (1952) reported what might have been a reaction of fish to artificial ultraviolet light and Breder (1959) stated that *Jenkinsia* was photopositive to ultraviolet light. Care must be taken in this type of experiment to exclude the possible effects of longer wavelength fluorescence, which may also occur.

3. Optimum Light

The optimum light for the performance of behaviour patterns has not been studied much. Tamura, Mitarai and Sugita (1957) measured the minimum light intensity for the maximum cone response, using a micro-electrode on the retina, and found values of 64-175 lux for *Sparus*, 175 lux for *Cyprinus*, 800+ lux for *Lateolabrax*.

4. Intensity Perception

4.1 As the light decreases dark adaptation takes place and photopic (cone) vision changes to scotopic (rod) vision. There is usually a "Purkinje shift" in the spectral sensitivity of the eye, the maximum sensitivity shifting to shorter wavelengths.

Thus Borisov and Protasov (1960)[2] gave the following values:

	Maximum sensitivity in mμ	
	Light adapted	Dark adapted
Cod	550	504
Haddock	565	520
Saury	580	510
Catfish	545	470
Plaice	580	525
Star-like skate	500	500
Anchovy	560	500
Horse mackerel	555	505
Red mullet	590	505
Grey mullet	557	500

This shift has been shown by electrophysiological means, the response by the retina to lights of different colours being recorded on an electro-retinogram. (It should be stressed that this is not necessarily concerned with colour vision. The visual cells are more, or less, sensitive to different wavelengths; this may not result in subjective colour discrimination, but only that the colour to which the cells are most sensitive will appear brightest.) It should be noted that no shift was found in skate, which has no cones. There is very little other evidence for a "Purkinje shift" due to a lack of data on spectral sensitivity of fish when light-adapted. There are more data on scotopic spectral sensitivity, however, in freshwater fish, but few on marine fish. Blaxter (1964), using various behaviour techniques, found a maximum at 510-520 mμ in dark-adapted *Clupea harengus* and Blaxter and Little (unpublished results) maxima around 500 mμ for *Gadus merlangus* and *Limanda limanda*, though the spectral sensitivity curves were very plateau-like at the blue-green end of the spectrum. It should be stressed that the spectral sensitivity determined by behaviour techniques (such as feeding in different coloured lights) may, in a sense, be subjective. In other words fish may cease to feed in red light of low intensity, for instance, although they can still see the food. A more objective measure of spectral sensitivity might be found by an electro-physiological technique, for instance by electrodes placed on the retina or optic nerve, but even this is not evidence of a "central" perception of light.

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[2] "Some aspects of light perception in fish and selective light sources" I.C.E.S. Comp. Fish Committee. Paper 139, 1960.

4.2 More data are to be found on the absorption spectra of the retinal pigments, which are often in close agreement with the spectral sensitivity obtained by other means. In general, dark-adapted fish have a peak absorption at about 500 mμ (due to the pigment rhodopsin), dark-adapted freshwater fish at about 530 mμ (due to porphyropsin) and dark-adapted deep water fish at 485 mμ (due to chrysopsin). It should be noted that these correspond well with the spectral make-up of light in the water at the depths these fish are found. Thus the fish are most sensitive to the colour of light which is predominating in their environment. Those species which change their environment may or may not change their visual pigment. Thus Atlantic salmon retain porphyropsin throughout their life; whereas the eel acquires a pigment similar to deep sea fish before migrating into deep water.

The importance of vitamin A, which is concerned in the photochemical cycle of rhodopsin, in the visual sensitivity of fish, was shown by Kampa (1953) who found in *Gillichthys* that a diet free of vitamin A resulted in a loss of sensitivity.

4.3 The change from light to dark adaptation may be judged from a study of behaviour patterns and especially from the "photo-mechanical" movements in the retina. In the light-adapted state the sensitive rods are invested by pigment and the cones contracted away from the pigment. In the dark the pigment contracts, leaving the rods free, and the cones lengthen. The light intensities at which this change occurs in various species are shown in Table 1.

TABLE 1. LIGHT INTENSITIES AT WHICH EYES CHANGE FROM THE LIGHT-ADAPTED TO DARK-ADAPTED STATE, BASED ON PHOTO-MECHANICAL CHANGES IN THE RETINA.

Species	Light intensity for light to dark adaptation (lux)	Author
Atherina mochon pontica	$10^{1} - 10^{0}$	Protasov *et al.*, 1960.
Sargus annularis	$10^{-1} - 10^{-2}$	
Engraulis encrasicholus	$10^{0} - 10^{-1}$	
Clupea harengus	$10^{1} - 10^{0}$	Jones and Blaxter, unpubl.
Lateolabrax japonicus	$4 \times 10^{-2} - 10^{-2}$	Tamura, 1957*b*.
Cyprinus sp.	$5 \times 10^{-4} - 6 \times 10^{-5}$	
Oncorhynchus spp	$10^{1} - 10^{-1}$	Ali, 1959.
Salmo salar	$10^{0} - 10^{-2}$	Ali, 1961.
Leuciscus rutilus	$10^{-3} - 10^{-4}$	Engström and Rosstorp, 1963.

Except for *Cyprinus* and *Leuciscus* sp. the values in Table 1 are similar to the light intensity at dusk and dawn.

The "photo-mechanical" changes are fairly slow, varying from 20 to 70 min in different species (Nicol, 1963). Usually light adaptation is faster than dark adaptation. When fish are placed in darkness after being at a high light intensity there may be a latent period (Ali, 1962). Ali (1959) has suggested that the light intensity at dusk may decrease at a greater speed than the process of dark adaptation in the retina, thus giving an especially vulnerable period of night-blindness just after dusk. If this were so in other species, it might mean that fish capture would be most advantageous at this time. It is possible, also, that fish descending fast in turbid water might also undergo such a "blind" period.

The control of the "photo-mechanical" changes seems to be unknown. Only rarely have any signs of a diurnal rhythm (in constant experimental conditions) been found and it seems that the changes in light themselves mediate the adaptation by nervous or hormonal stimuli.

4.4 The structure of the retina may sometimes hint at the habitat and light conditions occupied by a species. This is especially true for species living in low light intensities. For instance, Ali and Hanyu (1963) studied the retinae of fish off the Labrador coast. The cod, *Gadus callarias*, had many cones and a well-developed pigment epithelium, suggesting eyes that could function at high light intensities and yet be efficient under diurnally changing illumination.

Sebastes species, however, often found at 300 m or more, had many rods and a degenerating pigment epithelium, suggesting life at greater depths. Interesting differences in the size and density of the cones were apparent in two specimens of *Sebastes marinus mentella*, one found at 270 m and the other at 540 m. The cones were larger and denser in the fish nearer the surface. Differences in the retinal of *Sebastes* spp. found at varying depths was also reported by Wunder (1958).

4.5 Vision in dark-adapted fish will cease at the absolute rod threshold. This is not easy to measure except by electro-physiological methods, because behaviour techniques may only give the subjective level. In other words a fish may still be able to perceive light even though its behaviour patterns in low light intensities have ceased. Presumably conditioned response techniques could be used to determine the absolute threshold though this has not been done. Clarke (1936) quoted a threshold value based on a behaviour technique of 1.5 × 10^{-6} μW/cm^2 (about 3 x 10^{-6} lux) for *Lepomis*, a pond fish, which suggests fish can detect light at least 10^{-10} or less that of full sunlight. Thus fish like *Lepomis* might be able to detect light (but not necessarily see an object) ranging from 430 m in the Sargasso Sea (depth 4500 m) to only 75 m in water of a similar turbidity to that found in Woods Hole Harbour. According to Clarke and Denton (1962) some fish may well have a threshold as good as, or better than, the human eye (3 × 10^{-8} μW/cm^2 at the pupil, or equivalent to about 6 × 10^{-8} lux). It is possible that deep sea fish which possess better light collecting properties in the eye (a large lens in relation to the whole eye), a very transparent lens and very dense retinal pigment, and because of certain other neurophysiological considerations, may have a sensitivity of 10-100 times that of the human eye. This might mean that deep sea fish could detect light for a while each day down to nearly 900 m, or perhaps to 1,000 m, in exceptionally clear water with an extinction coefficient between 0.03 and 0.04. In coastal water with an extinction coefficient of 0.13, the threshold would be reached at 250 m. However, the light intensities at great depths are sometimes enhanced by luminescent organisms. It has been found that flashes may give off more light than that penetrating from the sky, even as high as 10^{-2} μW/cm^2, enabling fish to locate each other and their prey at sub-threshold overall intensities.

BEHAVIOUR PATTERNS

1. General

Many behaviour patterns will depend on form perception which will not be possible at light values near the rod threshold. The sharpness and contrast of objects underwater is frequently much impaired even at high light intensities. However, such patterns as phototaxis may depend only on the perception of light down to the threshold. In some behaviour there may be a gradual changeover of the dominant stimuli from visual ones at high light intensities to olfactory or other stimuli in darkness. There are some reports of a decrease in activity at low light intensities. This could be mediated by the pseudobranch (Holliday and Parry, 1962) which may be an endocrine organ controlled by the choroid gland at the back of the eye.

2. Feeding

The importance of light for a high rate of feeding in some species has been observed by a number of workers. Some other species may feed equally well by day and night (Girsa, 1961) if food is readily available, while others still may reduce feeding by day, because their food becomes more difficult to catch (*Corvina*, *Silurus*, ling).

The range of light intensity at which various daylight feeders cease to feed is given in Table 2.

These values may be compared with those for the change from light to dark adaptation. From this it appears that feeding becomes much reduced in dark-adapted fish, presumably due to the loss of acuity. However, some feeding may still be possible when the food is silhouetted against the light. That is why in experiments with light from the side (Table 2) rather lower values were found.

Feeding in deep sea fish, where it is visually controlled, must almost certainly be by the detection of phosphorescence which produces flashes of 10^{-7} to 10^{-2} μW/cm^2 (about 2 × 10^{-7} to 2 × 10^{-2} lux), (Clarke and Denton, 1962). The large mouths of deep sea fish may not only allow large food organisms to be taken on rare occasions, but may also assist the taking of food where location of the prey and the efficiency of snapping are poor.

An optimum light intensity for feeding was found in herring ranging from 100 to 1,000 lux (Blaxter and Holliday, 1958).

TABLE 2. RANGE OF LIGHT INTENSITY OVER WHICH "VISUAL" FEEDERS CEASE TO FEED.

Species	Range of light intensity (lux)	Remarks	Author
Cod	10^{0} - 10^{-2}	some residual feeding in dark	Girsa, 1961
Boreogadus saida) *Alburnus alburnus*) *Trachurus trachurus*)	10^{0} - 10^{-2}		ditto
Trachurus) *Leucaspius*)	10^{1} - 10^{-1}		Protasov *et al.*, 1960
Clupea harengus	10^{1} - 10^{-1}	light from above, juvenile fish	reviewed in Blaxter and Holliday, 1963
" "	c.10^{-2}	light from the side, juvenile fish	Blaxter, 1964*a*[3]
" "	10^{0} - 10^{-1}	light from above, larvae	Blaxter, 1964*b*[4]
Gadus virens	- 10^{-3}	blue light from the side	Blaxter unpbl.
Gadus merlangus	- 10^{-4} - 10^{-5}	ditto	Blaxter & Little unpubl.
Limanda limanda	- 10^{-3} - 10^{-4}	ditto	ditto
Phoxinus phoxinus	10^{-3} - 10^{-4}	some feeding in dark	Jones, 1956
Oncorhynchus kisutch	10^{0} - 10^{-3}		Brett and Groot, 1963
Oncorhynchus spp.	10^{1} - 10^{-4}	varied in different species	Ali, 1959

3. Schooling

Schooling is used here in the sense of a group of fish which are polarized or orientated to one another as a result of mutual interaction. Much of the work on schooling has been reviewed by Breder (1959). In the main schools appear to break up in the dark, though the fish may remain as a group, perhaps kept aggregated (but not necessarily polarized) by other stimuli, as well as by a decrease in activity.

The literature on the importance of light for shoaling has been reviewed by Loukashkin and Grant (1959) and Shaw (1961). The results of work where the light intensity was measured when shoaling ceased are given in Table 3.

There are some instances of fish schooling without visual cues. Blinded *Anchoviella* (Moulton, 1960) will school with intact fish as long as they are moving sufficiently rapidly. Shlaifer (1942) showed a dispersion of the mackerel *Pneumatophorus grex* in darkness, but nevertheless some polarization was still evident. Jones (1962), for instance, reported that groups of herring in the southern North Sea remained at least partially intact (as observed by echo-sounder) at night, but this and other reports of groups of various species remaining together by night as observed on echo-trace records cannot be considered as evidence for polarization, but only for aggregation. Nor can reported instances of "schooling" in the dark be used as evidence for polarization by non-visual means unless they are accompanied by a definition of schooling and measurements of light intensity.

Perhaps the best evidence for apparent schooling at night by clupeids are photographs of *Clupea harengus* polarized near the sea bed during darkness (Craig and Priestley, 1961). Whether the fish were reacting to each other or to some common external stimulus is uncertain. A mass rheotropism is considered to be impossible without visual or tactile cues. Clearly the analysing and defining of schooling behaviour becomes difficult if fish can polarize by a common reaction to external stimuli other than each other.

4. Spawning

This is not often directly observed in marine fish. Holliday (1958) reported that herring in

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[3] in Journal of Experimental Biology (in press)

[4] "The feeding of herring larvae and their ecology in relation to feeding" in CalCOFI Report of Symposium on "Larval Fish Biology" held in 1963 (in press)

TABLE 3. RANGE OF LIGHT INTENSITY OVER WHICH SCHOOLING CEASES.

Species	Range of light intensity (lux)	Remarks	Author
Clupea harengus	10^{-2} - 10^{-3}	8 m^3 aquarium	See Blaxter & Holliday (1963)
" "	10° - 10^{-1}	225 m^3 aquarium	ditto
Sardinops caerulea	$< 10^{-1}$	aquarium	Loukashkin & Grant (1959)
Alburnus alburnus) *Atherina*) *"Anchovy"*)	$< 10^{-1}$		Girsa (1961)
Engraulis encrasicholus) *Atherina mochon pontica*)	10^{1} - 10^{-1}		Protasov *et al* (1960)
Hepsitia stipes) *Bathystoma rimator*)	5 x 10^{-1}		Steven (1959)
Oncorhynchus spp.	10^{-3}		Ali (1959)
Phoxinus phoxinus	10^{-2} - 10^{-3}		Jones (1956)
Menidia	10° - 10^{-1}		Shaw (1961)

captivity ceased to spawn in darkness, the pattern of the bottom and the presence of the opposite sex being important stimuli. Brawn (1961) found that cod spawned in very dim light, but did not observe whether they continued to spawn in complete darkness. Doubtless the importance of light varies in different species, depending on the role of vision in courtship, display and pairing.

Spawning may so affect fish that their reactions to other stimuli become weaker. Thus, Mohr (1964) found that spawning *Clupea harengus* were much less reactive to a mid-water trawl than non-spawning fish.

5. Avoidance of predators

The study of predation in marine fish has received very little attention from research workers. The effectiveness of predation in light and dark will depend on the searching activity of the predator and its success in taking food, as well as on the perceptibility and availability of food organisms. Girsa (1961) found that some predators tended to be more active in low light intensities and caught their prey by means other than sight. Shoaling prey species may be less active by night, perhaps making them easier to catch, but they may also be more dispersed, making them more difficult to locate. Bioluminescence, while showing the presence of organisms, may also act as a warning to, or elicit fright reactions from, predators. At very low light intensities, where the detection of objects may only be by silhouette against light from above, the avoidance of predators is probably an easier process than the taking of prey.

6. Avoidance of Fishing Gear

6.1 The importance of sight in the avoidance of nets and the scaring effect of different colours has been reviewed by Mohr (1960) and Blaxter and Holliday (1963). Blaxter *et al.* (1964) reported that herring started to swim into stationary nets (which they avoided in daylight) at 10^{-3} - 10^{-4} lux in a small tank and 10^{-2} - 10^{-3} lux in a big tank. The use of drift nets made of polyamide fibres of low visibility has resulted in improvement of catches in a number of species. Blaxter *et al.* (1964) also studied the reaction of *Clupea harengus*, various gadoid fish and flatfish to moving nets in tanks, and found that the reaction distance and extent of herding depended on their conspicuousness. At light intensities below 0.5 - 0.05 lux herding dropped substantially and at lower intensities only a residual degree of herding was left, due mainly to tactile stimulation. In experiments at sea photographs were taken of fish in front of the ground rope of a trawl and confirmed, especially in herring, the reduction in orientation to the ground rope and herding by night.

It is of interest that in elasmobranchs, where sight seems to be of less importance than in many teleosts, the reaction to nets may be poor.

6.2 Artificial barriers have been used to control fish. For example, curtains of air bubbles may be used to guide schools of *Clupea harengus* (Smith, 1961) and a moving barrier composed of chains to deflect salmonids (Brett and Groot, 1963). Visual stimulation seems to be necessary in these reactions.

6.3 Recently diurnal differences in catch by bottom trawl have been reported as relevant to the estimation of population abundance (*e.g.* reviews by Woodhead, this symposium and Parrish *et al.*, 1963[5]). Woodhead found mainly higher catches by day in plaice, cod, haddock and coalfish, but not with soles. Parrish *et al.* reported higher catches by night in flatfish (including plaice), whiting and sometimes haddock and in general in species fished in Faroese waters. Woodhead gave the possible reasons for the differences in catch, which are certainly not consistent from area to area, or season to season, within a species. There may be differences in diurnal cycles of swimming activity and feeding or differences of physiological condition. Where night catches are lower there is good evidence that vertical migration away from the bottom is occurring. Where day catches are lower it seems possible that avoidance of the trawl is taking place (Blaxter *et al.*, 1964). It is possible though that the trawl tends to pass over flatfish by day, and that they leave the bottom by night and become more vulnerable.

7. Attraction to Light and Activity

7.1 Attraction (to artificial light). Phototaxis would appear to be mainly under nervous control. Phototaxis and preference for different lights has been reviewed by Breder (1959). The use of artificial lights to attract fish, reviewed in general by Schärfe (1953), and on clupeids by Blaxter and Holliday (1963), provides artificial stimuli for fish which may well cause abnormal behaviour patterns. Various explanations such as curiosity, feeding, positive phototaxis, hypnosis and following an optimum light intensity have been put forward to explain light attraction. Verheijen (1958) considered it was due to a mass disorientation, such as found in birds and insects attracted to lights at night. In this case the lamp would need to act as a point source and the explanation appears unlikely for attraction in turbid water, or where the fish remain at a distance from the light. Russian workers consider the attraction to be due to a conditioned response brought about by the association of light with feeding. This could be tested experimentally.

Blaxter and Parrish (1958) attracted fish to underwater lights and found that whiting collected at a distance from the lamp where the intensity was about 10^{-1} lux and herring and sprats aggregated near the lamp at 10^3-10^4 lux.

7.2 Activity. This subject has been considered by Woodhead in this symposium and will not be referred to further here.

LIGHT IN ORIENTATION

1. General

Light can control both vertical and horizontal orientation in fish as well as allowing for the more intimate orientation required for capturing food, shoaling and rheotropism.

2. Diurnal Vertical Migration

A rise towards the surface by night has been observed in a number of marine species, especially clupeids, by echo-sounder. It may also be shown from results of decreased catch of fish near the bottom during the night. The subject has been reviewed generally by Hela and Laevastu (1962) and is also discussed by Woodhead in this symposium. In particular Richardson (1952) related the downward movement of shoals in the North Sea to light intensity, but it was apparent that they were found in a light intensity at night which was much lower than the "preferred" day intensity. Postuma (1957)[6] showed that herring in the North Sea tended to remain in light intensities below 1 lux and Chestnoy (1961) that the depth of herring shoals could be correlated with isolux lines. However, Brawn (1960) could find no relationship between mean solar radiation and the depth of shoals of immature herring in Passamaquoddy Bay. What is probably the dominant influence of light in most cases may be modified by other factors such as temperature gradients.

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[5] "Diurnal variations in size and composition of trawl catches". ICES Abundance Symposium Paper 34.

[6] "The vertical migration of feeding herring in relation to light and vertical temperature gradient". ICES Herring Committee 1957.

Studies on vertical movements and distribution of gadoids such as cod, haddock, hake and coalfish (Woodhead, this symposium 1963) have not been related to light intensity to the same extent. However, Woodhead cited an interesting paper by Konstantinov showing that there was little or no sign of vertical migration in Arctic cod in the months of January and July when there was a minimal variation in light intensity, but there was vertical movement in spring and autumn when the greatest variation in light intensity occurred.

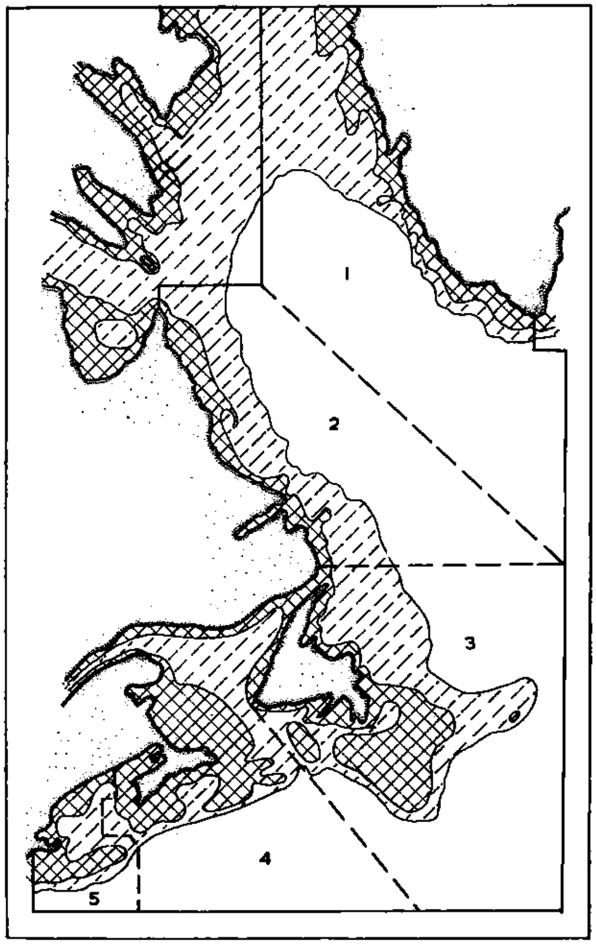

Fig. 3. The ICNAF area showing tentatively:

a. in cross hatching, the area within which diurnal changes in light intensity should occur on the bottom sufficient to bring about changes in light and dark adaptation of fish (on the assumption that the light will reach at least 10^{-1} lux on the bottom at some time during the day, the extinction coefficient being 0.13).
b. in broken hatching, the additional area within which the light will at least reach the absolute threshold on the bottom at some time during the day (based on an absolute threshold of 10^{-10} lux and an extinction coefficient of 0.045).

Diurnal vertical movements have often been correlated with the need to follow food organisms towards the surface at night. There is some evidence that feeding activity may be most intensive at dusk and dawn. It is interesting to speculate whether these periods are more favourable (in terms of light intensity) for predation or for escape from predators, or whether movements to the surface prevent the "night blindness" which fish might undergo if the light intensity falls too rapidly in the evening.

3. Sun Orientation

In an earlier section the directional nature of light in the sea was considered, a horizontal component being found to depths of 80 m or more. Light may be oblique to much greater depths with the greatest intensity in the direction of the sun's azimuth. Experimental work on freshwater fish (*Lepomis*, salmonids) has shown that they have the *ability* to navigate by the sun and that they possess a clock system which allows them to compensate for changes in azimuth bearing, depending on the time of day, longitude, and season (Hasler 1960; Hasler and Schwassmann, 1960; Brett and Groot, 1963). Saila and Shappy (1963) analysed the migration of Pacific salmon to the American coast and concluded that only a very rough ability to orientate by the sun is necessary, plus a great deal of searching; too good an orientation would result in displacement by currents. Some other species undertake considerable migrations (eel, tunny) but it is not certain to what extent homing is involved. It seems doubtful whether the type of overall movement North and East described by Wise (1959) in the cod off the East American coast would require sun navigation. In fact while sun navigation has been shown *experimentally* to exist in some species it is not known to what extent the faculty is utilised by these fish.

The existence of polarized light in the sea and its directional properties have also been considered earlier. Although the effect of polarized light on fish is not known, it is interesting that Stewart (1962) reported an adipose eyelid in a large number of families of fish. He found that it was birefringent in *Clupea pallasii* with different degrees of transmission depending on the plane of polarization of the incident light. The possible role of this in orientation is intriguing.

LIGHT AS A RHYTHMICAL STIMULUS

Both diurnal, lunar and seasonal periodicity play a part in the life of fish. Wynne-Edwards (1962) has developed the idea that the numerical density of animals may be regulated at certain times, for instance during a nightly vertical migration. This could be considered in relation to fish. There is sometimes considerable lunar periodicity in catches of clupeids. Seasonal changes of light may affect the reproductive cycle (Holliday, this symposium). They may even control the temperature tolerance of some species (Hoar, 1956) making them more resistant to high temperature in summer and low temperature in winter.

CONCLUSIONS

Despite the abundant evidence of the importance of light in the biology of fish, it is often one of the more neglected of the physical conditions which are recorded. It is intended to produce before long charts showing diurnal changes of light conditions in different areas of the sea bed in Scottish waters throughout the year. If possible only the light which is "useful" to the fish should be measured. Thus, the light meter should have the same spectral response as that of the fish eye. As a first attempt to show the possible value of further light intensity measurements, for instance in the ICNAF area, Fig. 3 has been drawn. It shows the areas where the diurnal variation in light intensity is probably sufficient for light and dark adaptation to take place during each period of 24 hr and the somewhat more extensive area, within which the light, at least during part of the day, reaches the absolute threshold for dark-adapted fish when surface illumination is at a maximum.

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F-3

THE SIGNIFICANCE OF ENVIRONMENT/ENDOCRINE STUDIES TO THE INVESTIGATION AND EXPLOITATION OF FISH STOCKS

By

F.G.T. Holliday[1]

ABSTRACT

In any investigation of an exploited fish stock prominent among the factors considered are those concerned with a) location and b) the maintenance of the stock. Relevant data come from studies of migratory behaviour, activity levels, growth rates, maturation and spawning cycles, and estimates of natural mortality at various stages in the life history of the fish.

Almost all of these aspects of fish biology are associated with variations in the levels of circulating hormones. The fish react to a series of internal stimuli which in turn are geared to changes in single, or combinations of variables in the external environment such as day length, temperature and salinity.

Measurements of seasonal changes in the levels of endocrine activity are an important step towards the accurate prediction of the availability and accessibility of stocks.

INTRODUCTION

There have been many reviews of the relationships existing between specific factors, or combinations of factors, in the environment and the activity of endocrine glands in fish. Although experimental studies of the activity of endocrine glands have been made on only a few species, and these mostly estuarine or freshwater fish, the consistency of the results obtained is an indication of the existence of a fairly uniform pattern of endocrine activity and reactivity to the environment. The close link between day length, pituitary activity and gonad maturation is now so well established that Pickford & Atz (1957) were able to state that "with one possible exception...it has never been demonstrated that light fails to effect the reproductive system of fishes". It would now be surprising if an endocrine control system were discovered that did not conform in a general way to the pattern that has so far been found.

It is not the primary intention of this contribution to repeat information which can be found in many well known and comprehensive reviews such as Dodd (1960), Fontaine (1954), Hoar (1953, 1957), Pickford and Atz (1957). In particular Pickford and Atz devote a section of their book specifically to review 'The effects of the external environment on the gonadotrophic activities of the pituitary of fishes.' The main emphasis here will be on the relevance of environment/endocrine studies to fisheries problems, and to consider the position such investigations might take in a fisheries research programme.

As was pointed out by Kesteven (1958) fishery science ultimately deals in problems of fish behaviour, which in turn is the external expression of a particular physiological state. The secretions of the endocrine glands result in profound variations in this state; a change in the level of a circulating hormone is effectively a change in the internal environment of the fish.

Figure 1 shows, in schematic form, the principle endocrine organs in fish, their secretions and target organs. The scheme is much simplified and does not indicate several important factors, one being the inherent rhythm of certain endocrine activities which although normally reinforced by the environment have been shown to be independent of it. Bullough (1941) demonstrated the presence of a reproductive rhythm in *Phoxinus* which persisted under constant environmental

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conditions. An organism may be responsive to specific factors in its environment or blood only if these impinge on target organs in a state capable of response. The gonads of an immature or spent fish may be refractory to environmental and pituitary influences that at a different time would result in the onset of maturation (*e.g.* Harrington, 1957).

ENDOCRINES AND THE COMPONENTS OF A FISHERY

At the joint scientific meeting of ICNAF, ICES and FAO on 'Fishing effort, the effect of fishing on resources and the selectivity of fishing gear' (Lisbon, 1957), certain of the concepts, elements and properties relating to fishing effort and mortality were defined. As was pointed out in this report, each characteristic represents the end result of a long chain of cause and effect, with the organism and the environment interacting together. The properties of a fish stock which make it potentially useful to a fishery are

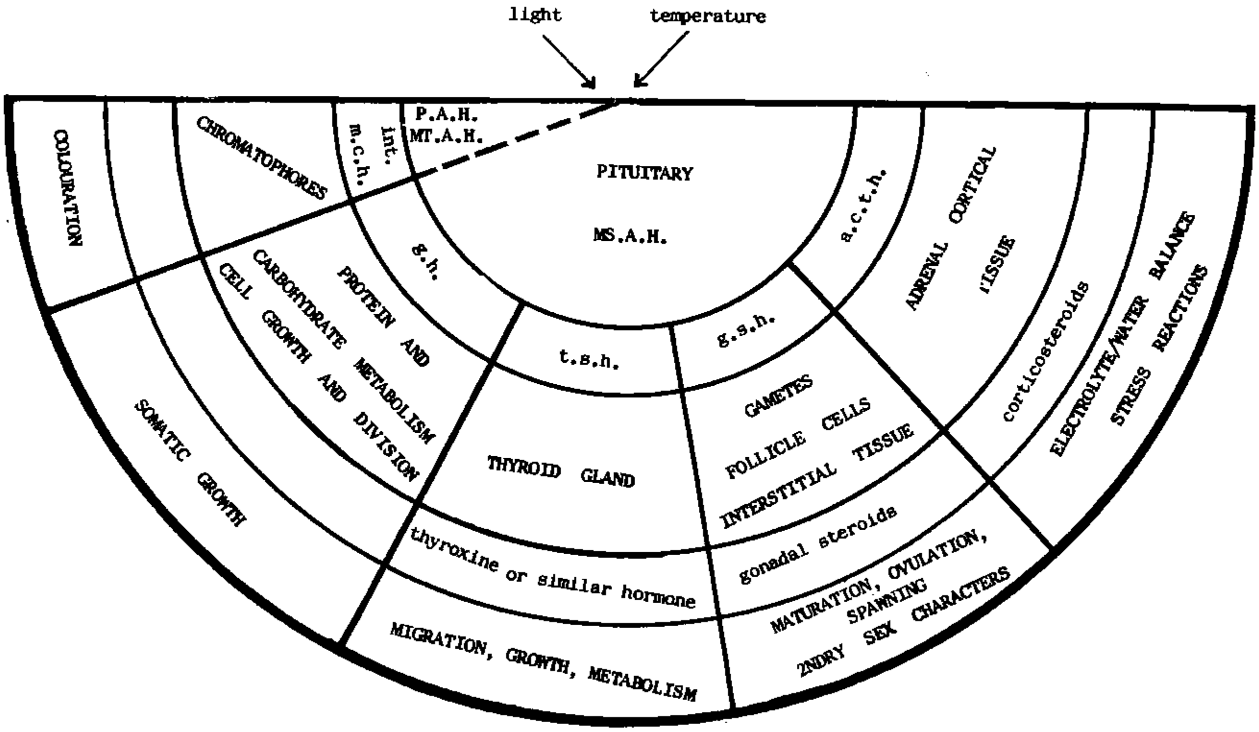

Fig. 1. The principal endocrine glands, hormones and target organs or processes in teleosts. Each radial segment represents a functionally linked sequence of events.

Key: Stimulating factors in lower case. Target organs or processes in capitals. P.A.H. Proadenohypophysis; M.S.A.H.-Mesoadenohypophysis; M.T.A.H.-Metaadenohypophysis (Regions of pituitary gland). int.-Intermedin. m.c.h.-melanophore contracting hormone. g.h.-growth hormone. t.s.h.-thyroid stimulating hormone. g.s.h.-gonad stimulating hormone. a.c.t.h.-adrenocorticotropic hormone.

1. Location and Availability
2. Magnitude and Structure
3. Distribution and Accessibility
4. Vulnerability to the fishing force exerted on it.

It is interesting to consider the relevance of endocrine studies to these characteristics.

Location and Availability.

A species is available to a fishery by reason of its presence in a known area at a specific time. Any force, internal or external, which makes fish migrate into or holds them on such an area is a factor to be considered in relation to location and availability.

The influence of the thyroid gland on migratory activity was discussed by Hoar (1953) and by Woodhead (1959*a*). The latter obtained good circumstantial evidence for this influence in *Gadus morhua* of the Barents Sea. Thyroid gland activity, as estimated from the height of the follicular cells, was greatest during the spawning migration. Buchmann (1940) found increased thyroid activity in the herring, associated with spawning. Woodhead (1959*b*) demonstrated that the changes in the cod thyroid were not due to gonad activity alone. She found increased thyroid activity in immature cod during an overwintering migration in the Barents Sea. Migration of these fish continued for as long as the thyroid gland remained active.

Hoar and his co-workers (Hoar, 1955; Hoar *et al.*, 1952; Hoar *et al.*, 1955) in investigations on young salmon obtained experimental evidence for the association between high levels of locomotor activity and the presence in the water of thyroxine. Conversely, decreased activity levels were found if the thyroid was inhibited by immersing the fish in thiourea. Baggerman (1959, 1960) found that treatment with thyroxine induced a change in the salinity preference of *Gasterosteus* and young *Oncorhynchus;* this change was associated with the onset of the breeding migration. There are many other instances of increased thyroid activity associated with migrations (Fontaine and Callamand, 1943 on the eel; Fontaine *et al.*, 1948 on the salmon). What is still not clear is the link between the environment and the initiation of thyroid activity. Baggerman (1957), in the light of her own and other work, suggested that in cases where external conditions were able to induce a change in salinity preference (associated with migration) then this was the result of increased production of thyrotropic hormone from the pituitary. This production was closely associated in *Gasterosteus* with increasing day length and rising temperature in the spring.

Reproductory drives would appear to motivate migratory behaviour in many marine teleosts. It is on the predictable regulatory of the reproductive cycle that many fisheries are based.

There have been a relatively large number of experiments to demonstrate the effects of light, temperature, water conditions etc. on the reproduction of fishes easily kept in the aquarium (Pickford and Atz, 1957). For many of these species the critical levels and sequences of illumination and temperature necessary to control reproduction have been established. Most experiments support the view that these external factors influence reproduction by way of the production of pituitary gonadotropin. One fact of particular significance emphasised by Pickford and Atz is that light can affect the pituitary - gonad system by means other than the eye, perhaps via the pineal organ or other area of the fish brain responding to light transmitted through the thin bones of the skull. Hoar's (1961) analysis of the andocrine control of the complex behaviour patterns involved in reproduction in *Gasterosteus* illustrates the potential value that lies in such investigations.

The factors that influence and control the timing of maturation and spawning in commercially important fishes are virtually unknown. The maturation of the gonads is made up of a number of phases; Holliday (1960*a*) and Iles (1964) suggest that in the herring these stages differ in duration and control. The early stages (to about stage III-IV) appear to be influenced primarily by the availability of suitable food, whereas the later stages are under pituitary control and may, by analogy with other fish, be responsive to daylength and temperature. Naumov (1956) correlated the maturity stage of herring with water temperature, solar radiation etc., but while it was clear that different stages were associated with different environmental conditions, it was not possible to identify a particular initiating or controlling factor. The picture is complicated by the fact that the gonads of male and female herring mature at different rates when under the same environmental conditions (Holliday, 1963; Iles 1964). There is a seasonal variation in gonadotropic activity of the pituitary in herring, a peak of maximum potency being found at spawning. It is not known what factors initiate spawning. The process is two-part; first ovulation occurs, *i.e.* the release of the egg from the follicle, then after a variable time interval that might be as long as seven days, the gametes are shed. Control of the two phases is almost certainly by different mechanisms, and although these mechamisms are presumably the same within a species the environmental releasing agents are not so specific. Different groups of *Clupea harengus* may mature and spawn under very different conditions at different places and times of the year. These groups are apparently showing different responses to the same stimuli, as they often share a common environment (Blaxter, 1958). Dragesund (1960) suggested that a sharp rise in temperature induced spawning in *Clupea harengus;* Outram (1951) suggested that a sudden decrease in salinity stimulated *Clupea pallasii* to spawn. Holliday (1960*b*) could find no direct effect on the spawning of *Clupea harengus* of either temperature or salinity changes. Ovulation in the herring is under pituitary control, but it is not known what stimulus is required for the release of the appropriate hormone from this gland. Direct visual factors (the amount of light, the nature of the substrate) appear to release egg deposition. Barr (1963 *a, b, c*) demonstrated that maturation of the gonads in plaice (*Pleuronectes platessa*) was controlled by the pituitary. He also obtained evidence that egg deposition in this fish was dependent on pituitary activity.

The spawning of the herring is a mass process (see review by Blaxter and Holliday 1963). On the other hand Brawn (1961 *a, b*) has shown that aggregation and spawning in cod is preceded by complex aggressive and nuptial behaviour. Aggressive behaviour between individuals leads to dispersal, and Brawn correlated a high incidence of aggression with a decrease in catch. It is possible that these behaviour patterns in cod are under the hormonal control of the steroids formed in the gonads of this fish (Gottfried *et al.*, 1962).

Magnitude and Structure.

The recruitment of fish as a result of growth and migration, and the loss of fish by death or emigration are major factors in determining the magnitude and structure of the available stock. The part played by endocrine secretions in migration has been considered, and applies to movements into and from a given area. Growth rate and recruitment are closely linked. The control of growth in fish by a pituitary hormone is well established (Pickford and Atz, 1957 review the literature) and clearly the measurement of the production and release of growth hormone is relevant to the study of growth patterns in the sea, especially as the annual rings on scales and otoliths are influenced by this hormone. Unfortunately the relationships, if any, between the environment and the production of growth hormone are not known. Swift and Pickford (1962) showed that the onset of rapid growth in May of *Perca fluviatilis* was accompanied by a sharp rise in pituitary growth hormone at this time, demonstrating that there is a seasonal variation in the production of this hormone.

Losses by way of natural mortality are difficult to measure, and little is known of the factors contributing to this process. Mass mortality as a result of spawning is known in the Pacific salmon (*Oncorhynchus*), and on a smaller scale similar deaths may take place in the sea. Barr (1963*a*) and Holliday (1958) found that after spawning, plaice and herring are exhausted, in poor condition and probably at this time incapable of withstanding stress.

A good deal of work has been done on the changes in the level of blood corticosteroids and tissue structure of *Oncorhynchus* during its spawning migration (Idler *et al.*, 1958; Robertson and Wexler, 1960). A large increase in the levels of adrenal steroid hormones was found in the blood, and histological studies showed that prior to death the salmon showed symptoms comparable with Cushing's syndrome in man *i.e.* hyperplasia of adrenal cortical tissue, degenerative changes in the pituitary and pathological changes in other organs. The influence of the environment on the production of these hormones is not clear. The pituitary gland (usually the mediator of environmental factors) certainly influences corticosteroid production, (Pickford and Atz, 1957). Rasquin and Rosenbloom (1954) demonstrated the effects of keeping fish in total darkness, when hypertrophy of adrenal tissue was followed by its atrophy. Return to the light could reverse the early stages of these stress responses. Cold shock was also found to induce adrenal cortical changes (Rasquin, 1951). Fontaine and Hatey (1953) found that response to pituitary corticotropin could be varied by a change in temperature.

Distribution and Accessibility.

The same endocrine factors which influence the availability of a species to a fishery will also operate in a general way with regard to distribution and accessibility to the fishing gear. Whether or not a fish lies within the range of operation of a particular gear depends on its position within the fishing area. A drive which results in the localisation of the fish in relation to substrate or a point in depth will to some extent determine its accessibility.

Some components of the complex pattern of diurnal vertical migrations found in pelagic fish such as clupeids may well be due to diurnal differences in the metabolism. There are indications (Holliday and Parry, 1962; Blaxter and Holliday 1963) that the pseudobranch gland, by regulating the availability of oxygen to the tissues, may control the general level of activity of the fish.

It is interesting that Copeland (1952) found that the pseudobranch also controlled gas secretion into the swim-bladder - a factor which is of importance in vertical migration. The pseudobranch is linked with the eye by a common blood supply, and light may in this way control diurnal differences in pseudobranch activity and hence metabolism and vertical migration.

In describing the reproductive behaviour of cod, Brawn (1961*a*) suggested that succeeding phases in the pattern of reproductive behaviour would tend to stratify the fish. There was a downward movement of non-aggressive males, immature fish of both sexes and spent females. There was an upward movement of spawning males and females with spawning in the surface waters.

Vulnerability to fishing force.

Vulnerability is defined as the degree to which an organism is open to attack by a specific force or process. Clearly an animal is most vulnerable to a force designed to exploit its innate or acquired behaviour patterns; for example a particular bait might appeal to a specific appetite or a series of nets might be interposed in a known migration route. Of special relevance to these problems are studies of sensory physiology and behavioural motivation. The effects of endocrines on sensory physiology is not well understood. Apart from inducing patterns of innate behaviour at the time of reproduction, sex hormones may alter acquired behaviour patterns. Vanderplank (1938) found that treatment of rudd (*Leuciscus leuciscus*) with oestrone inhibited conditioned responses to light.

As far as motivation is concerned, cyclical changes in metabolism resulting from hormone action may underlie changes in feeding drives and reactivity to lures and nets. A change in the threshold for the release of escape reactions, or a change in sensory thresholds may alter the vulnerability of fish. Mohr (1963) found that following ovulation herring were less responsive to the approach of a trawl and more easily captured. Skadovskii (1939 *a* and *b*) showed an increase in phototactic responses of *Gambusia* and *Rhodeus* immersed in dilute solutions of chorionic gonadotropin.

THE POSITION OF ENVIRONMENT/ENDOCRINE STUDIES IN A RESEARCH PROGRAMME.

Environmental surveys.

The fundamental study of endocrine control of physiological systems and the initiating and regulating effects of the environment is one that must be based primarily on laboratory experiments. Environmental surveys can provide valuable background data for these experiments. Any attempt to induce or interpret changes in fish kept in aquaria must have relevance to the range of conditions in which the fish normally live. The demonstration of sensitivity to unphysiological doses of hormones or unnatural levels of external stimuli is of value only in so far as it demonstrates the presence of systems which have a potential to respond. On the other hand, environmental surveys alone generally do not demonstrate true cause and effect relationships between the organism and any specific environmental factor. Useful pointers may be obtained if a year or season presents an abnormal factor; Sahrhage (1954) found that in 1952, when sea temperatures in December were 2°C below normal the herring of the southern North Sea were not ripe, whereas in December 1953 when sea temperatures were 2°-3°C above normal the majority of the herring sampled were ripe. The usefulness of such data is limited by the fact that other unmeasured factors in the environment may have interposed between the fish and the temperature stimulus.

Laboratory experiments.

To determine the primary relationships existing between the environment and target organs in fish it is necessary to study the effects of varying a single factor or specific combination of factors while all others are held constant. Not only should the environment be strictly controlled, but the experimental fish should be of uniform physiological background. Only in long term aquarium experiments can these conditions be met. However, as already pointed out, these experiments should be designed and interpreted in the light of measurements of the environment and endocrine activity in the sea.

Endocrine activity measurements in fish caught at sea.

Useful indices of activity can be obtained from the histological appearance of the cells of the gland *e.g.* cell height in the thyroid or ratios of different types of cells in the pituitary. Assay of the glands either chemically or, more often, by a bio-assay technique have been used to determine seasonal variations of potency *e.g.* Gerbil'skii (1940). The most reliable, but also the most difficult technically, of measurements would be the level of circulating hormones in the blood. Changes in target organs *e.g.* the gonads may be indirect indicators of endocrine activity. The sensitivity of the fish to injected hormones may be used to indicate its physiological condition. Gerbil'skii (1951, 1953) used sensitivity to pituitary injections as a criterion for differentiating the spawning races of *Aciperser*.

CONCLUSIONS

In discussing a programme of organized research Parrish (1956) drew attention to some of the physiological problems associated with fisheries biology, but suggested that at the time many could be regarded as largely academic and not essential to the accomplishment of a rational fishery. However as environmental investigations in relation to fisheries problems are almost invariably interpreted in the light of the actual or expected responses of the fish, direct measurements of the fishes' capacity to respond should be available to complement these studies.

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F-4

EFFECT OF ABIOTIC FACTORS IN YOUNG STAGES OF MARINE FISH *

By

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CONTENTS

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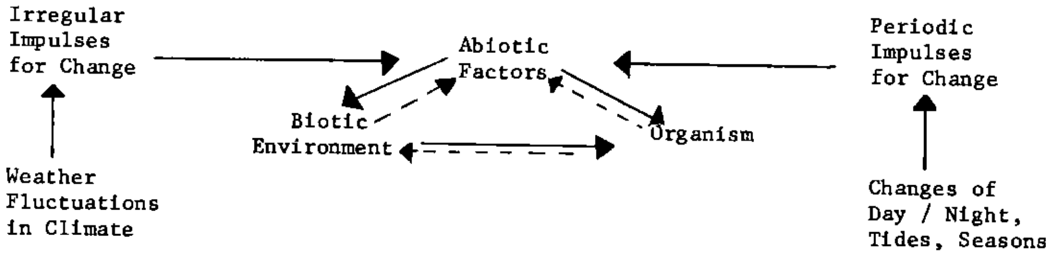
* This paper is dedicated to Prof. Dr R. Kändler on the occasion of his 65th birthday.

INTRODUCTION

The relationship between an organism and its biotic and abiotic environment and the causes which lead to a change in environmental conditions can be roughly schematized as follows:



As the above scheme shows, there should be distinguished between the *direct* effect of environmental factors on the specific organisms, and the *indirect* effect via the biotic environment. Moreover it seems to be useful to distinguish between two further possible effects,

(a) direct effect of a rather *constant* abiotic environmental factor
(b) direct effect through *changes* in the existing abiotic environmental conditions.

ad (a): In this connection the following facts are of special interest: the mode of action of the environmental factor on the organism; the ranges of tolerances and of optimum development of the species concerned.

ad (b): The effect of changing abiotic environmental conditions on fish eggs and larvae to a great extent depends on the speed and the range of change. It may be taken for sure that organisms have a resistance to periodic and unperiodic changes *normally* occurring in their biotop.

Among the abiotic environmental factors the following seem to be of special influence on fish eggs and larvae:

temperature
salt content
content of dissolved oxygen
light
currents
waves

In the following a review is given on investigations on the effect of abiotic factors in young stages of marine fish with special references to experimental results.

1. TEMPERATURE

1.1 General Remarks

The development of eggs and larvae is influenced to a high degree by water temperature. Many investigations have shown that the position of the spawning place, the beginning and duration of spawning depend on the water temperature. Furthermore, the intensity of spawning is closely related to the temperature, as indicated by Poulsen (1936) for the autumn-spawning herring of the Belt Sea and the Western Baltic. There is, however, less information on the effects these factors have on the success of fertilization and the survival rate of eggs and larvae.

Extremely low temperature in winter may lead to a late beginning of spawning for spring-spawners. In this way it becomes more probable that eggs and larvae develop during a period of rapidly increasing water temperatures. Qasim (1956) indicated that in such a case larvae of northern fish will be affected by too high water temperatures. On the other hand, the rich fauna caused by rapidly increasing water temperatures is favourable for the development of larvae.

1.2 Experiments on the Effect of Temperature on Egg Development

1.2.1 Time of Incubation

Recent investigations have shown that in many species there is no straight-line relation between temperature and time of incubation (Krüger, 1961; Barlow, 1961; Blaxter and Hempel, 1961; Lillelund, 1961; Hempel, 1962).

As the time to hatching is shorter at higher temperatures, the time during which hatching takes place in areas of rising water temperatures becomes shorter than the spawning period. For example, Lillelund (1961) computed for *Osmerus eperlanus* a mean spawning period of 29 days, whereas the difference between first and last hatching date of larvae was only 14 days.

1.2.2 Limits of Tolerance

Intensive investigations on the limits of tolerance during the time of incubation of eggs of *Salmo gairdneri* were made by Hamdorf (1960). These showed that the upper lethal temperature increased as the embryos develop. Immediately after fertilization, upper lethal temperatures were 14° to 15°C, and in later stages 20° to 24°C. This relation was confirmed by Lillelund (1961) for *Osmerus eperlanus*.

During breeding experiments, the rate of survival of cod eggs decreased at low water temperatures near the lower tolerance limit (Dannevig and Hansen, 1952). It is not known to what degree lethal temperatures during egg development are influenced by acclimatization of the eggs.

1.2.3 Size of Larvae at Hatching

The size at hatching to some extent depends on the temperature. In spite of a few contradictory results the size at hatching in general seems to decrease with increasing breeding temperatures. Thus, at low temperatures larvae hatch at a later stage, with smaller yolk supply, than at higher temperatures (Gray, 1928; Lindroth, 1946; Hamdorf, 1961; Blaxter and Hempel, 1961; Lillelund, 1961; Hempel, 1962).

1.2.4 Meristic Characteristics

There are several studies on the relation between temperature and the number of vertebrae (or myomeres) (among others, Tester, 1938; Tåning, 1952; Hempel, 1953; Blaxter, 1957; Lillelund, 1961). According to these studies there is a correlation between the number of vertebrae and the breeding temperature, differing from species to species.

1.2.5 Change of Temperature during Breeding

Such experiments have been carried through by Dannevig and Hansen (1952) with eggs of Norwegian cod, showing that the changes in temperature from 2° to 10°C. caused a high egg mortality. Temperature shocks at a sensitive period may influence the number of myomeres and vertebrae (Tåning, 1952; Hempel and Blaxter, 1961).

1.3 Experiments on the Relation between the Development of Larvae and Young Fish and Temperature

1.3.1 Absorption of Yolk Sac

According to the higher speed of metabolism at higher temperatures, the duration of the yolk sac stage (until absorption of yolk sac) decreases with increasing temperature. On this, thorough investigations have been made by Blaxter and Hempel (1963) on larvae of *Clupea harengus*.

1.3.2 Limits of Tolerance

The range of temperature tolerated by organisms depends to a high degree on the acclimation temperature, as some investigations have shown (Doudoroff, 1946; Fry *et al.*, 1942; Fry *et al.*, 1946; Brett, 1952, 1956; McCauley, 1958; Bishai, 1960; Blaxter, 1960). To what extent an organism is capable of tolerating extreme temperatures by acclimation may vary between different species. With decreasing water temperatures, near the lower limit of tolerance, the survival rate decreases in the form of a sigmoid curve. Furthermore, Brett observed that lowering of the temperature towards the lethal level caused a rapid death of part of the sample. Some larvae, however, survived for several hours, but died then slowly. Brett assumes that lethal temperatures have a shocking effect on the central nervous system for most of the organisms, whereas those surviving the shock will die from an increasing osmotic discrepancy.

Contrary to the results of experiments on species from temperate areas, Kuthaligam (1959) found that larvae of 10 marine tropic species tolerated only a very narrow range of temperature.

Other investigations indicated that young stages of fish tolerated a smaller range of temperature than adult fish, and marine fish smaller than fresh water fish.

1.4 Investigations at Sea

1.4.1 Horizontal and Vertical Distribution

In many species there is a close relation between the abundance of eggs and larvae in the horizontal distribution and the course of isothermal lines. (Literature especially Rapp. Proc. Verb. (150) ICES/ICNAF Redfish Symposium 1961 and this Symposium Section A.)

This distribution may originate from the preference of a certain water temperature by the parent fish during spawning, as it is shown for the larvae of red fish, or from temperature-induced migrations of the larvae. As an example, the behaviour of larvae and young fish of the Baltic Herring may be mentioned here. As elucidated by Lisivnenko (1958), in October, when the temperature in the coastal regions falls to 8° to 9°C., all the fry of the spring spawners migrate to deep waters. Together with the larvae of the autumn spawning herring they return to coastal waters when the temperature has risen to 7° to 8°C. in spring of the following year. With the water temperature rising to 14° to 15°C. in summer, young fish again migrate to deep waters.

In many species the vertical distribution is also strongly correlated with temperature. In this connection, recent investigations by Miller *et al.* (1936) are of special interest. These authors found over 80% of the haddock larvae within the confines of the thermocline.

1.4.2 Limits of Tolerance

Under special circumstances it may be possible that the boundaries of currents will change in such a way that in the mixed water area eggs and larvae are affected by extreme temperature and die.

2. SALINITY

Investigations on the tolerance of eggs and larvae to salinity have been carried out in the following species:

from the Baltic:	*Platichthys flesus* *Pleuronectes platessa* *Limanda limanda* *Scophthalmus maximus* *Gadus morhua* *Clupea sprattus* (Strodtmann, 1918)
from the Canadian Coast:	*Clupea pallasii* (McMynn and Hoar, 1953)
Others:	*Clupea harengus* Population from the Firth of Clyde, (Holliday and Blaxter, 1961) *Osmerus eperlanus eperlanus* (Lillelund, 1961) *Clupea pallasii* Okho Herring (Kurata 1959, Galkina 1962)

2.1 Experiments on the Influence of Salinity on Egg Development

These investigations showed in general that fertilization and development of eggs was possible in a wider salinity range than occurring in nature. However, within the wide limits of tolerance there was a narrower range of salinity with an optimum hatching rate. As pointed out by Strodtmann, pelagic eggs brought into lower salinity will at first sink down. In a medium salinity the eggs may adapt themselves by reducing their specific weight. As experiments by McMynn and Hoar, and those by Lillelund, showed, the salinity tolerance increases during incubation. While early embryological stages of *Osmerus eperlanus* tolerated a salinity of 8 ^{o}/oo, the late stages (eyed stage) could be exposed without danger to a salinity as high as 24 $^{o}/oo$. Only immediately before hatching, the upper lethal tolerance decreased to 8 $^{o}/oo$. This tolerance decrease in the last phase of incubation seems to be a consequence of changing permeability of the egg membrane. As with the temperature, salinity influences the number of myomeres. (Hempel and Blaxter, 1961). The influence on the number of myomeres is not uniform throughout the total range of tolerance. The effect of salinity on the number of myomeres seems to be more marked in especially high and/or low salinity. There are no consistent results on the dependence of the larvae size at hatching on salinity during incubation. While Blaxter and Hempel (1961) and Hempel (1962) found extreme salinity conditions causing smaller larvae, Galkina in her experiments arrived at just opposite results. (Galkina, 1962).

2.2 Experiments on the Influence of Salinity on Larval Development

After hatching, the salinity tolerance of sardine larvae increased rapidly (Lasker and Theilacker, 1962). In a medium salinity range the salinity will have no influence on the life span of non-fed larvae, as is indicated for larvae of *Clupea harengus* by Blaxter and Hempel (1963), and for *Osmerus eperlanus* by Lillelund (1961). The larvae also have a good adaptability to a wide salinity range. Corresponding with the wide range of tolerance to salinity of herring larvae, Bückmann *et al.* (1953) could state no preference for a special salinity by the larvae of this species. There is no conformity in the results of investigations on the question of whether the tolerance to salinity will change during later life history or not. In Shelbourne's (1957) experiments the larvae of *Pleuronectes platessa* were more sensitive to salinity than the adult fish, whereas Holliday and Blaxter came to opposite results with *Clupea harengus*.

3. CONTENT OF DISSOLVED OXYGEN

The O_2 consumption was investigated for eggs and larvae of many species, especially of fresh water fish. (Among others: Juday and Wagner, 1909; Wells, 1913; Lindroth, 1942; Jones, 1952.) Especially thorough studies on the effect of O_2 content of water on fish eggs have been made by Alderdice, Wicket and Brett (1958) with *Oncorhynchus keta*, as well as by Hamdorf (1961) with *Salmo gairdneri*. Experiments of these authors have shown that low O_2 concentrations at the beginning of incubation lead to disturbance in the development of embryos. A low O_2 concentration in early embryological stages causes a longer incubation period and in later stages a shortening of incubation time. Hamdorf also dealt with the special question of the dependence of growth on O_2 content. According to his investigations, the body weight at hatching decreased with decreasing O_2 content (in his experiments from 28 to approximately 5 mg). Moreover, the growth rate of embryos as well as of larvae was influenced by the O_2 concentration. Parallel to the growth of embryos there was a rise in O_2 consumption. Hatching occured as soon as the O_2 concentration in the breeding water became insufficient for covering the minimum O_2 requirements of the embryo. During the growth of larvae, the additional O_2 consumption was proportional to the addition in weight of larvae. It was of interest here that young fish that developed in low O_2 concentrations during embryological and larval stages, and were afterwards brought into normal O_2 conditions, reached -after absorption of yolk sac- the same sizes as the control-fish. The effects of low O_2 concentration on larvae and young fish of some species of salmonids have been studied by Bishai (1962), who found that the sensitivity of the fry to low O_2 content of the water decreased with age. The fry was able to avoid low O_2 concentrations by trial and error. These observations by Bishai are in agreement with results of experiments by Shepard (1955) with fry and fingerlings of *Salvelinus fontinalis*. According to Shepard, larvae and young fish are able to acclimate to low O_2 concentrations, thus reducing the lethal limits.

4. LIGHT

4.1 Experiments on the Effect of Light on Fish Eggs and Larvae

There is little information on the extent to which marine fish eggs and larvae will be affected by light. Blaxter (1956) found in *Clupea harengus* a higher rate of hatching in the dark than in the lighted tank. Corresponding observations were made by Dannevig and Hansen (1952) in breeding experiments with eggs of plaice. However, with cod eggs the best success of hatching was found in tanks near the window. A characteristic example of the sensitivity to light are the eggs of numerous species of salmonides. Recent investigations by Hamdorf (1960) have shown that the different spectral regions have different effects on egg development. The lowest survival rate resulted in the spectral region around 420 mu/. As the degree of sensitivity at this wave-length depends on the intensity of the yellow to red egg pigments, Hamdorf believes that these pigments have the function of protection pigments. As Hamdorf could further show, the sensitivity to light increases until the heart starts beating, after which it decreases rapidly. This process can be understood, as Hamdorf points out, if it is assumed that the radiation destroys the lactoflavin which is of special importance for the respiration of early embryological stages. A sudden lightening of herring eggs ready for hatching after a period in the dark effected spontaneous hatching. In further rearing experiments by Hempel, he found that larvae continuously kept in the dark had a longer life span than those kept at normal day/night conditions.

4.2 Behaviour of Larvae to Light

Immediately after hatching, larvae differ in their reactions to light from species to species. Later they prefer water depths with specific light conditions. Correspondingly, larvae of many species make daily vertical migrations. (Johannsen, 1925; Russel, 1926; Silliman, 1943; and others.) As the larvae of many species take food only in light (Blaxter and Hempel, 1961), it may be assumed that the daily vertical migrations of these larvae are a direct reaction to changing light intensity rather than following the movements of the nutrition horizon. Different quantities of larvae in day and night catches may be caused by the fact that at daylight larvae can better escape plankton nets (Bridger, 1956). Concerning experiments with fish larvae it is of interest that the mortality rate of larvae will be higher in transparent than in opaque tanks, as stated by Bückmann *et al.* (1953) for herring larvae.

5. CURRENTS

5.1 Effect of Currents on Eggs and Larvae

The position of the spawning places of many species of fish is influenced by currents. As an example, investigations by Poulsen (1930) on the spawning intensity of cod in the Belt Sea may be given. The question to what extent current eddies affect the horizontal and vertical distribution of eggs in the marine, also after spawning time, is discussed by Laevastu (1961). By a change of the normal boundaries of currents, eggs and larvae in the mixed area may be exposed to a rapid change in abiotic environmental factors, as Colton (1959) indicated in his investigations in the area of Georges Bank.

More often, however, currents cause a slow drift of eggs and larvae from the original spawning place to other marine areas. In this connection the following observations are of special interest:

The northern drift of cod eggs along the Norwegian coast to the area of the Bear Islands - Spitzbergen Banks and the Barents Sea. (Rollefsen, 1930; Wiborg, 1957).

The inflow of larvae of different species from the North Sea to the Western Baltic (Poulsen, 1934, 1935).

The drift of planktonic stages of many marine species from spawning places to the North-East Atlantic (Fraser, 1958).

The drift of herring larvae by off-coastal winds from the Norwegian coast to deeper areas with poor nutrition (Hjort, 1926).

The drift of haddock larvae from Georges Bank seawards over the edge of the Shelf (Walford, 1938; Chase, 1955; Colton and Temple, 1961).

Consequent to driftings, a change in biotic and abiotic environmental factors will occur for eggs and larvae, offering more or less favourable conditions for development.

5.2 Behaviour of Larvae to Currents

The respective results for fresh water fish do not apply to marine fish because of the completely different current conditions in fresh water areas. Of interest in relation to the behaviour of larvae of marine fish are the observations of Creutzberg (1958, 1959), as well as experiments by Bishai (1960). According to Creutzberg it is possible that elvers (*Anguilla vulgaris*) use the tides for coastward transportation. Bishai found positive rheotaxis in larvae of *Clupea harengus* and *Cyclopterus lumpus*. Larvae of herring began to drift in the tanks only at current speeds higher than 0.58 m/sec.

6. WAVES

It is well known for many species of fresh water fish that eggs are very sensitive to vibration during the first 24 hr of incubation. According to investigations on pressure resistance of eggs of cod and plaice, Rollefsen (1930) and Devold (1935) pointed out that it seems to be probable that eggs of marine fish will be destroyed and burst mechanically by breakers during rough weather. Galkina (1957) investigated the dependence of mechanical resistance of different egg stages of the Okhotsk herring on salinity. The experiments indicated that with increasing salinity also the resistance to mechanical pressure increased. The effect of wave action on fish eggs in coastal waters may therefore be lower than in the open sea.

7. CONCLUSION

7.1 In the foregoing some important results of experimental research on the effect of some abiotic factors on fish eggs and larvae have been summarized. It was not so much intended to give a complete bibliographic review, but to present a large number of different forms of effect. In order to avoid false interpretation, the following points of view should be taken into account:

(a) Special environmental conditions in the experiments.
(b) The isolated consideration of single factors.

ad (a): One of the special environmental factors in the experiments is the limited size of aquariums. This factor might be of more significance in experiments with fish larvae than with eggs. While studying the effect of the biotop volume on metabolism and growth of young trout, Willer and Schnigenberg (1927) coined the term "Raumfaktor" (factor of biotop volume). Also the distance of the test animals from each other has to be taken into account. Two further "artificial" conditions in many experiments are the insufficient depth of water and the unnatural gas content (Henley, 1951). Also the currents produced in experiments are never as laminar as the great marine currents.

ad (b): The character of an experiment requires to limit investigations to the variation of one factor only, leaving the others as constant as possible. In the majority of experiments — also in the aforementioned ones — only the effect of one factor has been studied at a time. In nature, the observed effects mostly result from a combination of several variable factors. The effect of each of these factors may, by parallel actions of other abiotic factors, be intensified, or weakened or, in special cases, even neutralized. There are little experimental investigations on the effects of such combined factors. Kinne (1956, 1960) investigated the 'Temperature/Salinity' relation on *Cyprinodon maculatus*. At relatively low temperatures (15°, 20°C.) the growth of young fish is best in fresh water, whereas at higher temperatures (25°, 30°, 33°C.) best results were found in water of 35 to 55 ‰. Moreover, the intensity of food intake and of conversion efficiency depends on the temperature/salinity relation. Kinne supposes that in the temperature/salinity relation the density of the water—as a function of temperature and salinity—plays a role.

7.2 Investigations on the effects of abiotic factors on fish eggs and larvae may contribute to a better understanding of the following three problems which, during the last years, have become of increasing interest:

(a) Long-term changes in the abundance of fish populations;
(b) Critical periods during the first months of life;
(c) Dependence of annual fluctuations on the environmental conditions of the O-group.

ad (a): A phenomenon frequently studied during the last decades is the rapid reduction in the stocks of some species of marine food fish, as
the Norwegian herring,
the Plymouth herring,
the sardine Sardinops melanostica in the Japan Sea,
the *Sardinops caerula* of the American West Coast.

Parallel to the reduction in stocks, a more or less obvious change in the reproduction behaviour was observed, as indicated by an alteration in spawning dates as well as spawning places. There was good reason to assume that these long-term changes in the stocks were caused by long-term changes of hydrographical conditions. As investigations in the Baltic have shown, there is a remarkable increase in the stocks of sprat, plaice and, especially, cod. According to Kändler (1949) it may be assumed that the long-term change in abundance may be due to an increasing inflow of water with relatively high salinity into the Baltic during the last three decades. The better hydrographical conditions have led to an increase in the plankton and, thus, to better conditions for the fry. The example of the Baltic indicates that long-term changes in the abundance of fish stocks most probably are part of a complex in which a great number of abiotic and biotic factors are working together, influencing the life cycle of the species concerned.

ad (b): For several species there is evidence for an especially high mortality rate (critical phase) in certain developmental stages from the incubation of the egg to the end of the first months of life. Such high mortality periods have been found, among others,
— in egg stages III and IV of the Baltic herring (Toom, 1962);
— from hatching of larvae to absorption of yolk sac in the Californian sardine (Ahlström, 1954; Farris, 1960) and in the Japanese sardine (Nikai *et al.*, 1955);
— for the span immediately after absorption of the yolk sac and after reaching a length of 16-20 mm in herring larvae (Blaxter and Hempel, 1961);
— 30 to 40 days after hatching in the Atlantic mackerel (Marr, 1956);
— and in the same species for the total first months of life (Sette, 1943).

The given examples have shown that the model of Hjort (1926), who postulated a critical phase immediately after hatching, is not always realized. It is more evident that critical phases may occur in several species and, possibly, in the same species in different developmental stages. The aforementioned results on wide tolerance to abiotic factors in young stages of fish — with the exception of some egg stages with special sensitivity — do not give any hint to critical phases being caused by direct effects of abiotic environmental factors. It is more probable, as pointed out especially by Shelbourne (1957) and Harris (1960), that periods of high mortality are chiefly due to biotic factors, as predators and lack of nourishment. Thus, the effect of the abiotic factors has to be seen more as an indirect one in connection with critical phases.

ad (c): There are many indications that the abundance of a year-class is determined by the combined effects of biotic and abiotic factors during the first months of life. As, in the end, the biotic factors — especially the food supply for the fry — depend to a high degree on the abiotic conditions, the key for the fluctuations of year-classes may well be seen in abiotic conditions from fertilization of the eggs to the end of the "fry stage". As hydrographical conditions before the spawning time influence the begin, position and intensity of spawning, the span during which the abundance of the year-class is determined by abiotic factors may start even before spawning. Some scientists have made attempts to find correlations between the abundance of year-classes and abiotic factors (especially temperature and wind) in the respective breeding area. (Veley, 1950, 1951; Carruthers and Parrish, 1951; Carruthers, Lawford and Veley, 1951; Rae, 1957). Although the correlations represented were not always obvious, it was suggested that the studied abiotic factors play an important part in the determination of the abundance of a year-class. It seems to be possible, however, that in some years their effect may be neutralized by other factors.

In order to examine the coaction of several factors, Wiborg gathered and tabulated for a number of years certain factors that might have been of influence on the abundance of year-class of the Norwegian cod. Wiborg assumed that the following factors caused a rich year-class:

long spawning period;
late hatching or late spawning;
northern drift of eggs and larvae;
northward shifting of the spawning center.

While Wiborg marked the factors by plus or minus only, Lillelund (1961) has gone a step farther. He found in smelt that the abundance of year-class of the population concerned is influenced by the following four factors:

mean volume of water of the river Elbe during spawning time;
mean water temperature
(a) 0. to 13. day after mean date of hatching,
(b) 14. to 27. day after mean date of hatching;
duration of spawning time.

Furthermore there had been indications that the effect of one factor in some year was neutralized by the effect of one of the other factors. In order to quantify the effect of abiotic factors on the abundance of year-classes in relation to the different intensity of the factors concerned, Lillelund set up a graduated scheme of valuation for each of these factors as demonstrated in Table 1.

The table shows that Lillelund assumed a non-straight correlation between temperature and its effect on larvae. This hypothesis based on the fact that, on one hand, plankton development in the

TABLE 1. SCHEME OF VALUATION OF SOME ENVIRONMENTAL FACTORS ON THE ABUNDANCE OF YEAR-CLASSES

		$10\ m^3/sec$	Valuation
I.	Mean outflow of water during spawning time (at water gauge Darsau/ Elbe)	50- 59	— (= minus 2)
		60- 69	-
		70- 79	+
		80- 89	++
		90- 99	+++
		100-109	++++
		110-119	+++++
		120-129	++++++
		130	+++++++
		°C	Valuation
II.	Mean water temperature 0.-13. day after mean date of hatching	9.5	—
		9.5-10.4	-
		10.5-11.4	+
		11.5-12.4	++
		12.5-13.4	++++
		13.5-14.4	++++++++
		14.5-15.4	++++
		15.5-16.4	++
		16.5-17.4	+
		°C	Valuation
III.	Mean water temperature 14.-27. day after mean date of hatching	10.5	-
		10.5-11.4	+
		11.5-12.4	++
		12.5-13.4	+++
		13.5-14.4	+++
		14.5-15.4	+++
		15.5-16.4	+++
		16.5-17.4	++
		17.5-18.4	+
IV.	Duration of spawning time/less than 22 days		-

river Elbe does not start at temperatures lower than 10°C, on the other hand, as indicated by experiments at high temperatures the duration of the yolk sac stage is extremely short. There is a good correlation between the abundance of year-classes of smelt and the scopes calculated on the basis of the scheme and the hydrographical and biological data available for 12 years.

Of course this can only be regarded as an attempt to quantify the effects of combined factors on the abundance of year-class. As it was necessary for the mathematically formulated population dynamics to start with a number of assumptions and to approach the individual parameters only gradually in later years, it will be necessary to correct the scoring of environmental effects by and by on the basis of latest data available. I would not fail to state that, similar to the population dynamics, there will be required a good deal of optimism to come to an evaluation - by using either the above way or another - of the complex effect of abiotic factors on fish eggs and larvae.

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F-5

FECUNDITY AND EGG SIZE IN RELATION TO THE ENVIRONMENT *

By

G. Hempel[1]

ABSTRACT

Information about how fish react in their reproduction to changes in the environment is rather scarce. Some possible direct and indirect environmental effects are discussed, mainly by using data on herring. Direct effects on the number and the weight of eggs at spawning seem to be restricted. Indirect influences of food supply and temperature will affect the reproduction by changes in growth rate, in maturation rate, migratory pattern, mixing of neighbouring populations and the resulting time and place of spawning. This may have considerable effect on the total number of eggs produced by the population and on the average yolk-content of the egg. The dry-weight of the eggs affects the duration of the yolk-sac stage, the size of the young larvae and their searching effort. This will be positively related to survival rate.

INTRODUCTION

Until now not much is known about the influence of the environment on the reproduction of marine fish. The main purpose of this paper is to stress the need for more extensive and detailed studies in this field. Both the number and the size of the eggs produced by a female of a given age may vary with the environmental conditions. The absolute number of recruits for the fishable stock will depend on the number of eggs spawned as long as no density-dependent compensatory mortality occurs. The egg size has a direct influence on the early life history and the survival rate of the larvae, as recently shown for herring (Blaxter and Hempel, 1963).

TERMS

The term number of eggs refers to the total number of eggs spawned by a female within a season. Usually it is estimated from the number of ripening eggs in a female under the assumption that no eggs are resorbed or additionally produced afterwards until spawning. "Egg weight" is the average dry weight of the ripe, transparent eggs. "Total egg mass" is the term for the product of the average number and weight of eggs for a given age and size group of fish at spawning. At stage VI, weighings of the total egg mass are not reliable, some eggs may be shed beforehand and others may not have finished the intake of organic matter.

DIFFERENCES IN NUMBER OF EGGS

Information on the number of eggs is available for several species of marine fish, but with special emphasis on plaice and herring. In herring the number of eggs per female normally increases faster than the weight of the fish. This is most pronounced for the increase in number of eggs produced at the second spawning compared with the low number at the first spawning. A direct influence of age (or related to this the number of spawning seasons) on the number of eggs in herring was noticed by several authors (Antipova, 1928; Liamin, 1956; Probatov and Friedland, 1957; Baxter, 1959; Anokhina, 1963; Polder and Zijlstra, 1959; Krivobok, 1961). In fish of the same size and age, the number of eggs is higher in those which spawn for the second time compared with first time spawners. Exceptions to this rule may be found in those herring which live under unfavourable feeding conditions. The first time spawners amongst the herring of the Onega Bay of the White Sea produce more eggs than the second-time spawners of the same size. Here the feeding period after the first spawning is not long enough (part of the short season of unfavourable feeding conditions is used for spawning), for a high egg production to take place.

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* This paper is dedicated to Prof. Dr R. Kändler on the occasion of his 65th birthday.

Direct influences of the environment on the number of eggs in a female seem to exist in a number of species. Scott (1962) showed for rainbow trout that egg number but not egg size varies with the physiological condition and the feeding of the mother fish. Bagenal (1957) described changes from year to year in the number of eggs produced by a female of a given size in *Hippoglossoides platessoides*. According to Polder and Zijlstra (1959) the Doggerbank herring produced about 20% more eggs in 1957 than herring of similar size and age in the period 1954 to 1956. No attempt was made by the authors to attribute the high production of eggs in 1957 to any specific environmental factor or to an admixture of herring with higher egg numbers (*e.g.* Buchan herring). Anokhina (1960) related the number of eggs produced by Baltic herring to the fat content of the mother. She reported higher egg numbers in fat fish than in lean fish. This held for comparison between fish of different fat content caught within one season, as well as for a comparison between different seasons where the average fat content differed from year to year. The differences in fat content were attributed to differences in food supply and overwintering conditions. Hodder (this symposium) tried to explain the low fecundity of Grand Bank haddock in 1959 by environmental effects as temperature and especially feeding conditions. Unfavourable conditions two years in advance and/or during the few months immediately preceding spawning may reduce fecundity, the same may hold for good feeding conditions about one year before spawning, *i.e.* during a period while they grow and occupy the surface area of the lamellae.

Indirect effects of the environment on the number of eggs might be expected because of the relationship of the number of eggs to total age, weight and age at first maturity. The effect by changing the growth rate in fish (and so affecting the age at first maturity) has been described for herring by various authors. Anokhina (1963) ascribed changes in the egg number in 4- and 5-year-old herring of the White Sea to changes in growth rate which were related to feeding conditions, *e.g.* in 1958 the food supply and the overwintering conditions were better than in 1957, in consequence the fish grew faster and produced more eggs relative to their age (but not to their body size). The most striking indirect effect of this kind was described by Bibov (1960) as a result of the very fast growth shown by Baltic herring which were transplanted as fry into the Aral Sea. Bridger (1959) analysed the changes in egg number in relation to age which took place in Downs herring in 1950-55. He attributed the higher average number of eggs in herring of the age-groups 4 to 7 to both the increase in growth and in maturation. As suggested by Cushing and Burd (1956) these fish "speeded up" growth and first maturity by one year due to unfavourable feeding conditions. Similar indirect effects of the environment on the spawning potential of the stock are to be expected in other marine fish.

THE WEIGHT OF EGGS

Data of the size of eggs in relation to age, size and condition factor of the mother are scarcer than those on the number of eggs. In the course of their work on the number of eggs in different herring populations, Farran (1938), Baxter (1958), Bridger (1959) and others, refer to racial differences in the size of eggs. This has been carried further in more detailed studies by Hempel and Blaxter (1963) with special emphasis to changes of egg size during the life history of the fish.

Recruit spawners produce eggs which are about 10% lighter than those of the older fish. From the second spawning onwards the egg weight does not depend on the age of the fish, except possibly in very old fish. In Norwegian herring of 12 years of age and more, some indications of a decrease in egg size were found.

The variability in egg volume (calculated from the diameter of the fixed ripe egg) is considerable in some groups of herring. The ratio between the smallest and the largest egg in a sample of 100 eggs was in most cases from 1:1.3 to 1:2.0. In samples of Baltic and Doggerbank herring higher variability was found. Whether this variability in volume reflects a variability in the content of organic matter or just differences in the water content must be checked by weighings of individual eggs.

Anokhina (1960) found higher coefficients of variance in the diameter of eggs in lean herring than in fat herring. Nikolski (1962) tried to explain this finding as due to insufficient nourishment of those eggs in lean herring, which were distant from the main blood vessels. Only in well fed herring are the nutrients sufficient to reach all eggs. Anokhina (1960) assumed that high variability in egg size permitted at least some larvae (those from the biggest eggs) to survive in poor years. Preliminary investigations on 50 North Sea (Downs) herring (Hempel, unpublished) failed to show a relationship between the fat content of the mother and the mean value and variance of egg size. The average fat content of the eggs was also found to be independent of the maternal fat content. Further investigations in this field are urgently needed in order to get an understanding of the effect of the condition of the mother on the quality of the eggs. In this connection, two facts should be considered: The eggs of most species of marine fish have very low fat contents. Protein rather than fat is the main constituent of the yolk and seems to be used both for conversion into larval substance and for metabolism. High "condition" of the mother taken as the relative fat content or the weight/length relationship does not necessarily mean that the female is in her prime for reproduction, especially the storage of fat, which might be due to unbalanced feeding.

TIME OF SPAWNING

Shifts in spawning time due to changes in the temperature regime are often described but they are rarely related to changes in fecundity. Only Krivobok (1961) made a careful study on the changes in number of eggs in coastal herring spawning in summer in the White Sea. He compared herring of uniform length (17 cm) which, however, differed considerably in age. In the course of the six week's season, he found a shift in the average age of the fish from 4.9 to 5.4 years, fast growing young fish with low fecundity arriving first on the spawning ground, followed by older fish. The number of ripe eggs increased in each age-group by 45 to 65%. The gutted weight of the fish caught at the end of the season (end of June) was almost the same as in the early spawners, although the average weight of the gonads was 14.8 g instead of 4.2 g. The number of eggs differs from female to female but it is fixed before feeding starts in spring. The rate of maturation depends on the number of eggs laid down (and their final size?) and on the supply of food. Temperature affecting the ratio between growth and basic metabolism will have a very strong influence on the survival rate of the larvae. It would therefore be worthwhile to check how far differences in food supply may affect the time of spawning. The relationship between the number and size of the eggs and spawning time and its dependence upon the environment require extensive and careful studies.

DISCUSSION

Direct effects of environmental factors on egg number and egg size seem to be rather limited compared with effects on growth. When considering the effect of changes in the environment on reproduction we are mainly left with the indirect influences which affect the reproduction of the stock by changes in the growth rate, the rate of maturation, age structure and possibly by shifts in spawning time and spawning place. Changes in the total fecundity of the population and the average fecundity of individual fish may also be caused by mixing of different groups of herring, which differ in their total egg mass at a given age or in the ratio between egg size and egg number. Racial differences in number of eggs are described for various species of fish. Sometimes differences are quite striking between neighbouring populations; in North Sea herring the egg weight of Downs herring is three to four times as high as that of Buchan herring (Hempel and Blaxter, 1963).

As shown by Baxter (1957), however, the number of eggs in Buchan herring is far higher than in Downs herring. The total mass of eggs produced by a female 27 cm is, however, higher in Downs herring than in Buchan herring (7.3 g dry-matter against 5.0 g). This difference in total production per season might be interpreted as a result of differences in spawning time, giving the Downs herring the opportunity of using the whole season of high plankton abundance for feeding, while in Buchan herring the feeding period is cut down by early spawning. Dogger herring whose time and place of spawning occurs between the spawning of Buchan and Downs herring show intermediate values.

If the migratory pattern or the spawning time of one of these groups shifts due to environmental factors, a considerable mixing of the populations may take place, causing changes in the reproduction and in the fitness of the larvae which are originally pre-adapted to other areas and seasons.

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F-6A

SEASONAL CHANGES IN THE PHYSIOLOGY OF THE BARENTS SEA COD, *GADUS MORHUA* L., IN RELATION TO ITS ENVIRONMENT

I. ENDOCRINE CHANGES PARTICULARLY AFFECTING MIGRATION AND MATURATION

By

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and

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CONTENTS

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ABSTRACT

Changes in their internal environment directly affect the reactions of fish to the external environment; the activities of the system of endocrine glands co-ordinate many of these internal changes. This paper considers quantitative changes in the activity of three glands in the Barents Sea cod, the thyroid, gonads and interrenals, and attempts to assess their physiological role in maturation and migration.

A seasonal cycle of thyroid activity was demonstrated in adult and in immature cod. In adults, the thyroid became active at the start of the spawning migration, and activity continued until the fish reached the spawning grounds; the duration of thyroid activity coincided with migration. In immature cod the gland was active throughout the period of their overwintering migration. Adult cod were ripening during their spawning migration, so that the activities of the gonadal and thyroid hormones could not be separated, but there was no gonadal activity in immature fish, and it appeared that the activity of the thyroid gland alone would support a lengthy migration.

The southerly overwintering migration of some large immature cod extends to within a short distance of the adult spawning grounds. Thyroid activity in these fish continued over a longer period than in immature fish overwintering around Bear Island, corresponding to the increased duration of their winter migration. It is suggested that in immature cod migration continued as long as the thyroid remained active.

Histological changes in the cod ovary during maturation are described, and a dual mechanism to relate fecundity closely to the growth achieved by the fish is discussed. Problems of oestrogen secretion in the ovary are outlined and reasons given for considering that oestrogen secretion occurs in the latter part of the maturation cycle, during the period of vitellogenesis. The histology of the maturing testis, and seasonal variations in the activity of the interstitial cells, secreting male hormone, are also described. The interstitial tissue became active in November-December, reaching maximum activity just prior to spawning. It appears that in the cod gonadal hormones are secreted in the latter part of the migration period, several weeks after the onset of migratory activity. Though thyroid hormones appear to play the dominant role in migration, their effects may later be augmented by sex steroids.

Activity in the interrenal gland began in November, continuing until June; by July the interrenal had returned to the summer resting condition. The role of adrenal cortical hormones in fish is discussed, and from the present results it is concluded that interrenal activity in adult and immature cod may be associated with the winter period of poor feeding, and, in the adults, with the physiological demands of gonadal maturation during this time.

The external factors regulating maturation and migration in the Barents Sea cod are considered. These cycles are initiated at the autumnal equinox and it is suggested that photoperiod may be critical; it seems unlikely that they are initiated by temperature changes.

INTRODUCTION

Fish must continually adjust and acclimatize their metabolic processes and their activity in relation to changes in environmental conditions. Seasonal variations in environmental factors may be great; thus, in the Arctic seas, food may only be available in quantity for a limited period of rapid growth and development, and conditions for good larval survival may only be achieved by reproduction in a restricted area and over a relatively short period of time in each year. It is reasonable to expect that in such circumstances the physiological responses of the fish would be of a highly adaptive character.

While this Environmental Symposium was largely devoted to considering some of the results of these internal reactions to external environmental variables, seasonal changes in the response of the fish itself were discussed; in this context it is not out of place to draw attention to the reactions of the fish to changes occurring within its own "internal environment". Thus, although successful spawning may depend on the correct behavioural reactions to environmental stimuli in the vicinity of the spawning area, it is also dependent upon precisely timed physiological changes controlling growth, maturation and migration, which may have occurred over several months prior to the spawning event. The activities of the system of endocrine glands are intimately concerned in the regulation and co-ordination of these physiological reactions, but relatively little detailed information is available concerning these alterations of the internal environment in even the commonest demersal fishes.

This paper considers some results of a study of the physiological reactions of the Arcto-Norwegian cod to its environment, and the nature of seasonal changes in these reactions; in particular we have tried to make quantitative measurements of the activity of different glands of the endocrine system in order to assess their role in modifying the reactions of this fish. This study is still far from complete but some aspects concerning migration and maturation are discussed below, and the reactions of cod to low temperatures are considered separately in Part II of the paper.

THYROID ACTIVITY AND MIGRATION

1. Introduction

In many species of migratory fish, gonadal maturation and migration occur simultaneously and initially it was thought that gonadal hormones might be essential for the induction of migration. However, amongst juvenile salmon migrating seawards, were fish with quiescent and with developing gonads, while others had regressing gonads after participating in the adult spawning (Fontaine, 1954, 1956). Migratory behaviour has been observed in sterile male hybrid Anabantid fish (Forselius, 1957) and in sterile male salmonids (Fabricius, quoted in Forselius, 1957) indicating that gonadal activity was not an essential requisite for migration. In these fish, and in adult migrating salmon, *Salmo salar* L. and *Oncorhynchus* spp., and in eels, *Anguilla vulgaris*, evidence of increased thyroid activity at the time of migration has been obtained (Fontaine, 1954; Hoar, 1953, 1955; Olivereau, 1954). These observations, and the more recent studies of Honma and his associates on other salmonid fishes (Honma, 1959*a*, *b*; Honma and Tamura, 1963) have suggested that it is probable that the thyroid gland has an important role in controlling migration. However, the evidence obtained from these studies was not conclusive since these species encounter changes in the salinity of their environment during migration, and salinity changes alone have been shown to stimulate thyroid activity in non-migratory fish (Olivereau, 1954).

The Barents Sea cod appeared to be a particularly suitable species for a study of the hormonal factors regulating migration, because of the great length of its spawning migration, the adults often travelling distances of up to 800 miles to their spawning grounds, without the complication of a change in osmotic medium. The migrations of the Barents Sea cod have been described in detail (Maslov, 1944, 1960; Saetersdal, 1956; Konstantinov, 1957; Trout, 1957). Throughout the summer months the cod are found on shallow-water feeding grounds in the north-eastern and central areas of the Barents Sea. In late September, as the gonads begin to ripen, the adult fish leave the feeding areas and migrate to their spawning grounds inside the Lofoten Islands on the north Norwegian coast. The main spawning season is from mid-February to the end of March. After spawning, the spent cod return again to the Barents Sea feeding areas.

The immature cod are found on the shallow-water feeding grounds during the summer months, June to September. In autumn these fish migrate into deeper waters around the edges of the shelf, where they remain throughout the winter until, in the late spring, they return to the feeding areas. This migration is repeated each year until the fish mature.

2. Thyroid activity in the Barents Sea cod

Changes in thyroid activity have been studied in adult cod migrating to their spawning grounds, and in immature cod moving to overwintering areas.

In the cod, as in the majority of teleosts, the thyroid gland consists of numerous discrete thyroid follicles, lying in the connective tissue around the ventral aorta (Fig. 1). The thyroid tissue was removed, fixed in Bouin's fluid, embedded, sectioned and stained with Heidenhain's Azan stain. A quantitative estimate of thyroid activity was obtained from measurements of the follicular cell height, and the results of these readings were confirmed by the staining reaction of the colloid. In resting glands the follicular cells were low, and stretched around the stored colloid, which had a dense laminated appearance and stained deep red. The follicular cells in active glands were high and columnar, whilst the colloid stained blue, and appeared granular.

Using these criteria, the thyroid gland of adult cod was found to be inactive throughout the spring and summer months, from April to September, when the follicular cell height was low and the follicles were packed with stored colloid. Secretory activity commenced in late September, and

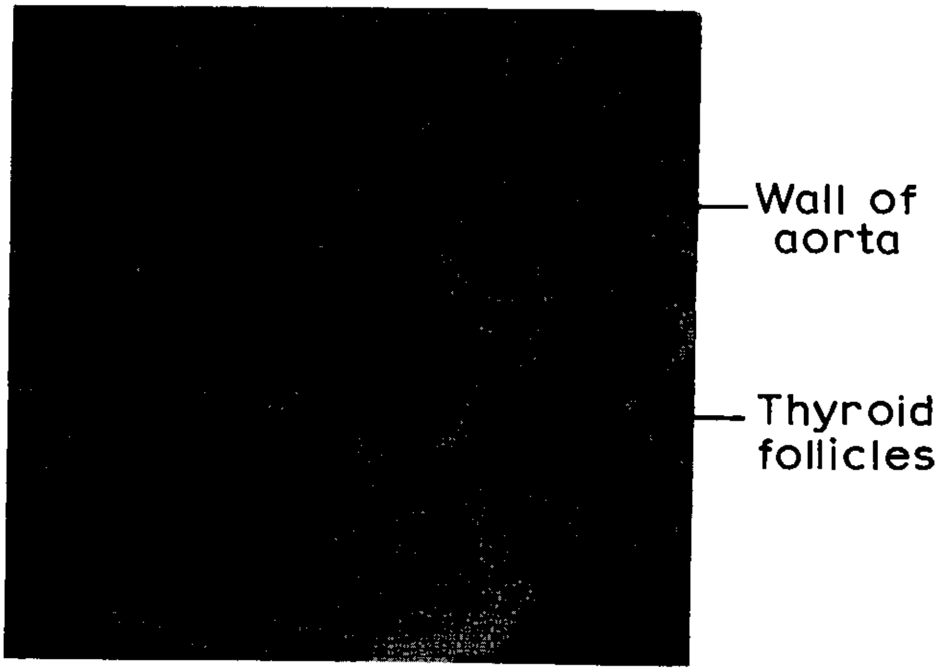

Fig. 1. Photomicrograph of distribution of thyroid follicles around aorta in cod.

increased throughout the winter months; the colloid appeared granular, was rapidly resorbed, and was often invaded by leucocytes. Maximum cell height was reached in January, prior to spawning. The activity of the gland was less in fish caught in March at spawning time. In spent fish, the gland had re-entered the resting condition (Fig. 2).

There was also a seasonal cycle of thyroid activity in the immature cod migrating to their overwintering areas. The thyroid became active in late September, as in the adult fish, but the maximum cell height was reached in December, after which follicular cell height decreased, returning to the resting stage by March (Fig. 2). The magnitude of the seasonal changes in thyroid activity in immature cod was less than in the adults (Woodhead, 1959*a*).

These results suggested that thyroid activity might be related to migration in the Barents Sea cod, since the gland became active at the start of the migration in both the adult and immature fish; in the adults, the thyroid remained active until March, when the fish reached the Lofoten Island spawning grounds, but in immature cod thyroid activity had begun to fall by January, when most of the fish were completing their migration to the overwintering grounds. The period of thyroid activity therefore coincided with the duration of the spawning migration of the adult fish, and with the overwintering migration of the immature fish.

In the adult cod the gonads were also ripening throughout the spawning migration, so that activities of gonadal and thyroid hormones could not be separated, but gonads were inactive, of course, in the migrating immature fish, suggesting that the activity of the thyroid alone might stimulate and support an extensive migration.

3. The prolonged migration of large immature cod

It has been shown that the extent of the overwintering migration of the immature cod tends to increase as the fish become older, so that some of the largest immature cod may migrate to the Norwegian coast, within a short distance of the adult spawning grounds; this extended winter migration has been called a "dummy run" (Trout, 1957). The relationship between thyroid activity and migration was further demonstrated from a study of the thyroids of immature cod collected at stations near Bear Island and on the Norwegian coast, during early spring. In comparing thyroid activity in immature

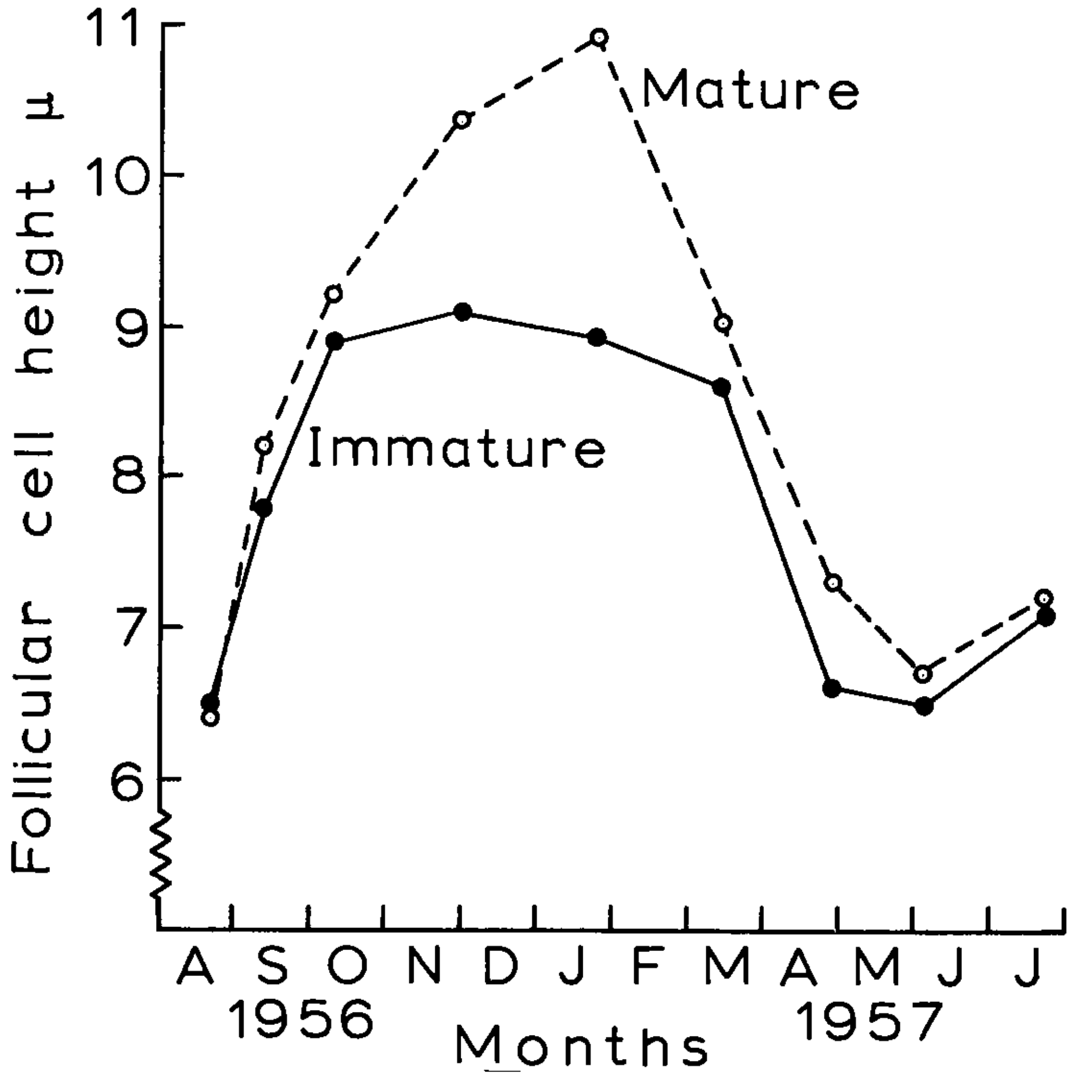

Fig. 2. Seasonal cycle of thyroid activity in Barents Sea cod, expressed in terms of follicular cell height.
N.B. An *increase* in follicular cell height indicates increasing activity.

Svalbard cod which had moved to their overwintering grounds around Bear Island with those of "dummy run" immature fish caught on the Norway coast, the otoliths of the cod were read to ensure that only fish which had migrated from the Svalbard region were used. (The cod from the north-western and south-eastern parts of the Barents Sea, and from the Norwegian coastal stock, can be distinguished by characteristic otolith types (Trout, 1957; Mankevich, 1960).) Generally, the "dummy run" immatures migrating to the Norway coast are large fish, so that it might be objected that any differences in thyroid activity were due to differences in size; there was no evidence of a direct relationship between size and thyroid activity in the cod, but to meet this objection fish of the same size range from each area were used in the comparison.

It was found that the thyroid glands of immature cod caught on the Norway coast in March were in a more active condition than those of immature fish taken around Bear Island. In the latter, follicular cell height had declined from a January level of 8.6µ to a level of 7.2µ by March. However, the fish caught on the Norway coast had a follicular cell height of 8.6µ, and the glands were still as active as the January thyroids (Table 1). In immature cod the thyroid cycle did not rise

TABLE 1. MEAN FOLLICULAR CELL HEIGHT OF IMMATURE COD CAUGHT IN MARCH

Sample area		Number of fish	Mean follicular cell height $\mu \pm$ S.D.
Around Bear Island	1956	10	7.3 ± 0.4
	1957	10	7.2 ± 0.6
"Dummy run" immatures:			
Norwegian coast *c.* 270 miles south of Bear Island	1956	3	9.2 ± 0.9
	1957	10	8.6 ± 0.7
Norwegian coast *c.* 410 miles south of Bear Island	1957	10	8.8 ± 0.5

to a peak as in adult cod, but once the gland had become active, activity continued at a steady level. Thyroid activity continued for a longer time in the "dummy run" cod caught off the Norwegian coast than in fish caught around Bear Island, and this coincided with the increased length and duration of their overwintering migration (Woodhead, 1959*b*). It seemed that in these "dummy run" cod the migration continued as long as the thyroid remained active. This evidence lends further support to the suggestion that the activity of the thyroid gland may initiate and sustain active and lengthy migrations.

4. Thyroid and migration in the spurdog

In view of these findings in the cod, it is of considerable interest that a correlation between thyroid activity and migration has also been found in the spurdog, *Squalus acanthias* (Woodhead, 1963, 1964). Spurdogs are ovoviviparous elasmobranchs and their reproductive cycle lasts for two years, but they migrate annually between Scotland and the southern Norwegian coast (Aasen, 1963; Holden, in press); reproduction and migration could therefore conveniently be studied in relation to thyroid activity. A marked annual cycle of thyroid activity was found in female spurdogs, the gland becoming active at the beginning of migration, and activity increasing throughout the migration. Although some thyroid activity was also related to reproduction, the primary association appeared to be with the annual migration.

5. Thyroid hormones and the migratory mechanism

Although thyroid activity has been related to migration in the Barents Sea cod, the problem of its mode of action remains. Thyroid hormones have numerous diverse metabolic and morphogenic functions in vertebrates. However, their effects upon motor activity and upon the nervous system are strikingly consistent in all animals; these hormones increase locomotory activity and heighten excitability and the sensitivity of the animal to external stimuli (Gorbman and Bern, 1962).

There is some experimental evidence to show that thyroid hormones produce similar effects in fish. Young salmon and goldfish, kept in solutions of thyroxine, were considerably more active than the controls (Hoar *et al.*, 1955). Thyroxine treatment increased the excitability of the fish, so that they responded to electrical stimulation at lower voltages than the untreated fish; also the experimental fish swam more vigorously against water currents than the control fish. Conversely, Vilter (1944) and Fontaine (1948) working with the elvers of the eel, *Anguilla anguilla*, found a decrease in rheotactic behaviour when the elvers were treated with drugs inhibiting thyroid activity.

Trout (1957) suggested that the spawning migration of adult cod, and the overwintering migration of the immatures, were active contranatant movements; in contrast the return of the spent cod to the feeding areas took place by passive carriage of the fish within the water mass. Although such a hypothesis is not without difficulties, it appears to fit many of the known facts, and it is therefore of interest to consider theoretically what might be the effects of thyroid hormones in inducing an active contranatant migration of this type. A simple theory, and one which would be in keeping with the experimental results, would be that thyroid hormones could cause a general increase in swimming activity and an increased tendency to swim against water currents. Many fish readily orientate against a strong water current, if provided with adequate sensory clues, and it seems likely that a change in reaction to current would be in the nature of a lowered threshold for initiation of the swimming response, rather than a completely new response. The passive denatant return of spent fish to the feeding grounds might similarly be achieved by an increase in the threshold for the reaction to current, probably accompanied by a fall in the general level of activity, the fish swimming randomly within the northward-moving waters of the Norwegian current. In this manner, thyroid hormones could act upon the fish to potentiate certain characteristic activities which lead to migration, rather than to produce specific new orientations or complately new behaviour patterns - modes of activity which would fit well with the known functions of these hormones.

THYROID ACTIVITY AND GONADAL MATURATION

There is a considerable body of evidence to suggest that thyroid activity may be associated with reproductive cycles (reviewed in Pickford, 1957; Barrington, 1963). Hyperactivity of the thyroid coincident with spawning has been reported in several species of fish (Buchmann, 1940; Olivereau, 1954; Fortune, 1955), while treatment of fish with thyroxine or with antithyroid drugs may accelerate or retard the onset of maturation (Hopper, 1952; Gaiser, 1952; Barrington and Matty, 1952; Smith, Sladek and Kellner, 1953).

Although the thyroid gland of the large "dummy run" immature cod migrating to the vicinity of the adult spawning grounds remained active over a similar length of time to that of the adult cod, the degree of activity attained was significantly lower than in the ripe adults. The thyroid of the immature cod was equally as active as that of adult fish in September and October, but by November the adult thyroid had become significantly more active, while thyroid activity in the immature cod remained at a fairly steady level throughout most of the winter (Table 2). This difference between the adults and immatures had become even more pronounced by January, when the adult thyroid was maximally active.

Pickford (1957) has suggested that some thyroid activity is necessary for gonadal maturation in fishes, and in many non-migratory species increased thyroid function has been found during the reproductive cycle (Koch and Heuts, 1942; Heuts, 1943, Ivanova, 1954*a*, *b*; Zaitsev, 1955*a*, *b*). It seems likely that in the Barents Sea cod this may be represented by the differences in the degree of activity between the immature and mature thyroid cycles, which became noticeable in November, coinciding with the period of rapid gonad growth.

TABLE 2. COMPARISON OF THYROID ACTIVITY IN ADULT AND IMMATURE COD

	Adult	Immature	
	Mean value of follicular cell height μ	Mean value of follicular cell height μ	Significance of difference p
August	6.4	6.5	0.75
September	8.2	7.8	0.30
October	9.2	8.9	0.40
November-December	10.3	9.1	< 0.01
January	10.9	8.6	< 0.001
March (pre-spawning)	9.0	8.6*	< 0.001
April	7.3	6.6	0.01
June	6.7	6.5	0.30
July	7.2	7.1	0.80

*Value for "dummy run" immature cod which had migrated to the Norwegian coast with the adult fish

l. Thyroid activity and reproduction in the spurdog

There was evidence that some thyroid activity in the spurdog might be associated with reproductive events. Maximum thyroid activity occurred during the winter, both in spawning females and in non-spawning females which had reached the middle of the gestation period, but the magnitude of the observed changes was invariably greater in the spawning females.

THYROID CYCLES AND TEMPERATURE

Seasonal changes in the activity of the thyroid gland of yearling trout have been inversely related to environmental temperatures by Swift (1959, 1960), who considered that temperature was a major controlling factor in influencing the cycle of activity. He suggested that thyroid activity acts as a temperature-compensating mechanism (Swift, 1959). Swift's results were re-investigated by Hoffert and Fromm (1959) who questioned the value of his data and doubted that the trout thyroid was involved in temperature compensation. Our investigations showed no obvious relationship between thyroid activity in cod and temperature; highest water temperatures of about 6°C. were encountered by adult cod on the Norwegian coast in winter when the gland was fully active, and the gland was inactive at lowest summer temperatures of 0°C. The comparison of thyroids taken from fish caught at different temperatures on the same cruise failed to show any significant differences either in the summer or during winter, suggesting that, in the cod, the thyroid cycle was not associated with temperature compensation (Woodhead, 1959*b*).

GONAD CYCLES IN THE BARENTS SEA COD

The Barents Sea cod matures for the first time between 5 and 15 years of age, the average age at first maturity being about 8 or 9 years. The distribution of spawning zones on otoliths suggests that once maturity has been attained reproduction occurs annually (Rollefsen, 1933).

1. The ovary

1.1 Ovarian maturation

During the summer months of May to early September there was little ovarian activity, although some slow growth of the gonad took place. Histological sections of ovaries collected during the summer showed that they contained oocytes in three phases of development: oogonia, small cells which had recently differentiated from the germinal epithelium; primary oocytes, which had undergone a period of minor growth; and larger oocytes in the "circumnuclear ring" phase. Circumnuclear ring oocytes are large, round cells, with a central, well defined reticular nucleus. Characteristically these cells have a ring of coarse, deep-staining granulations within the lightly-staining and finely granular cytoplasm, which initially appears within the cytoplasm close to the nucleus, but, as the oocyte increases in size, the ring moves outwards until eventually it lies close to the periphery of the egg. Only cells which achieve the circumnuclear ring phase by the late autumn complete their growth and maturation within the subsequent reproductive cycle. Rapid ovarian growth was resumed in late September, when the growth of the circumnuclear ring phase oocytes began. Initially, the eggs increased in volume, and the follicle membranes surrounding them became distinct. In November, some time after this phase, vacuoles appeared in the periphery of the oocyte, in the region of the circumnuclear ring. (These vacuoles may represent areas of oil deposition which are removed during routine fixation (Sorokin, 1957).) Following the formation of the vacuoles, the first yolk droplets appeared amongst them; initially the yolk granules are small and separate, but as growth continues and increasing amounts of yolk are incorporated into the oocytes, the droplets coalesce and yolk extends towards the nucleus. In the circumnuclear ring oocytes, the nucleus contains numerous small nucleoli which closely adhere to the nuclear membrane; in the ripening egg, the nucleus undergoes transformation, its outer membrane becomes indistinct and irregular, while the nucleoli become detached from the nuclear membrane and scattered throughout the nucleus. In sections the average diameter of the oocytes at the beginning of ripening in September was 140µ; by December the oocytes had reached a diameter of 300µ (Fig. 3).

Vitellogenesis continued throughout the winter months, until the cod reached the spawning areas in February and March. In January the oocytes measured about 400µ; by late February-March the eggs were completely filled with large spherical yolk granules, and were about 580µ in diameter. The outer membrane of the egg had thickened considerably and showed radial striations, while the egg nucleus had frequently become eccentrically displaced and its membrane was very indistinct. The final stages of ripening occur rapidly and may be completed within a comparatively short time (possibly only a few days (Sorokin, 1957)). Fluid is taken up by the ovaries, the eggs increase in size and their yolk becomes homogenous throughout. The follicular membranes surrounding the eggs are ruptured as the eggs swell, the lobule walls are broken and the eggs pass into the centre of the ovary for spawning.

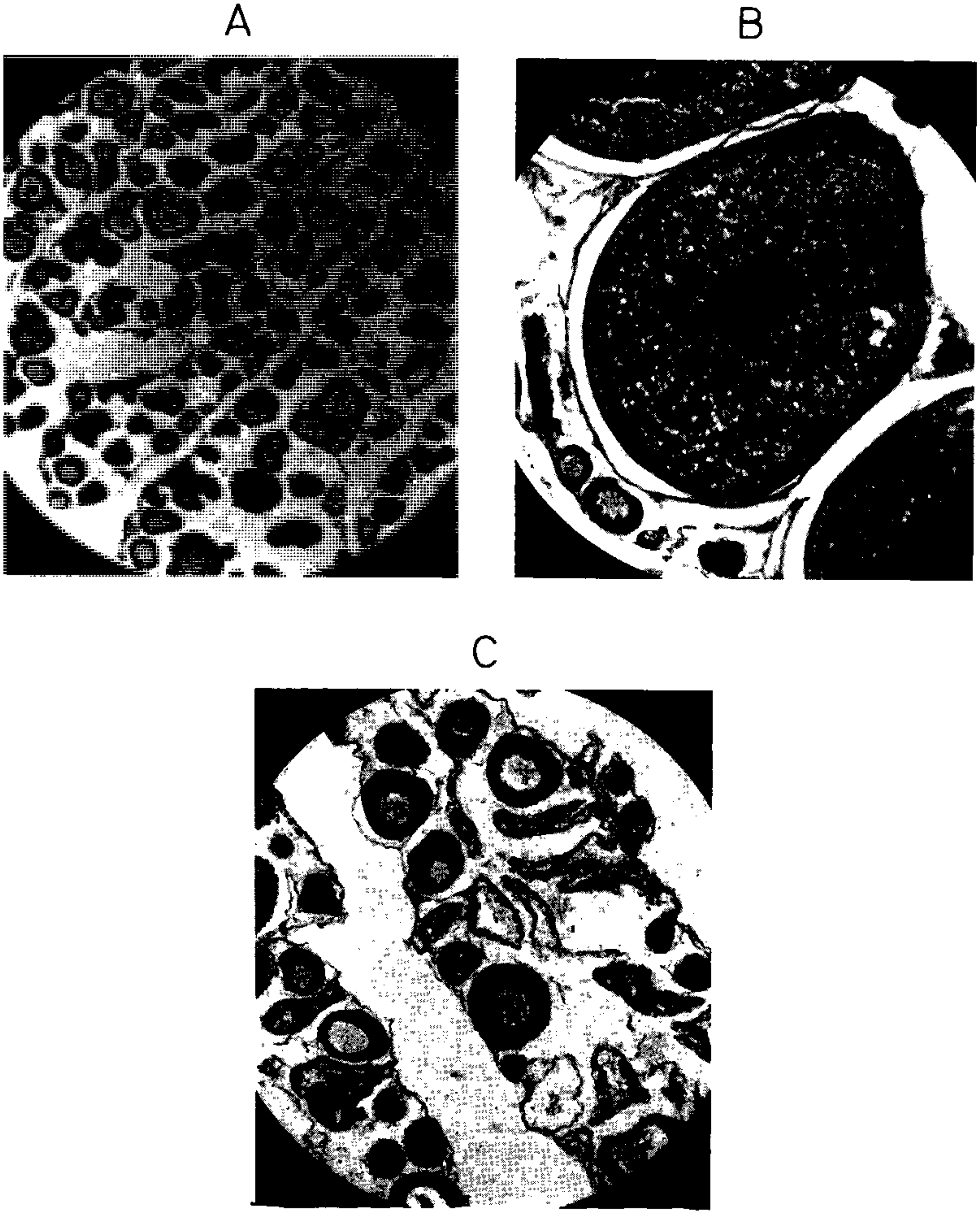

Fig. 3. A. Resting ovary showing small oogonia, oocytes which have undergone a phase of minor growth, and "circumnuclear ring" phase oocytes.
B. Ovary collected in January-February showing ripe eggs filled with yolk.
C. Ovary from spent female, showing large number of empty follicle membranes. Oocytes which had been present throughout the previous maturation cycle can be seen.

Ovarian regeneration and reorganisation starts soon after spawning. The ruptured follicular membranes shrink, any remaining unshed eggs are broken down and resorbed, and the lobule walls reform. Oocytes which had been present throughout the previous spawning grew rapidly to reach the circumnuclear ring phase. Simultaneously, a new generation of oogonia were produced from undifferentiated germ cells. The regeneration of the ovary appeared to be accomplished by May, but the remains of follicle membranes were found in the ovary for some four or even five months after spawning.

Quantitative changes in biochemical components accompanying the maturation cycle in the ovary of the cod have been described in recent years (Braekkan, 1958; Plack, Woodhead and Woodhead, 1961; Braekkan and Boge, 1962).

1.2 The effect of feeding conditions upon fecundity

It has been established that feeding conditions can have considerable effects upon the fecundity of fish, affecting the rate of maturation, the numbers and size of eggs, and the frequency of reproduction; various effects of nutrition on reproductive capacities of fish have been reviewed by Woodhead (1960*a*). Studies of the seasonal changes in the cod ovary revealed a mechanism whereby fecundity could be related to the conditions which had prevailed during the previous feeding season.

The numbers of oocytes in each phase of development in the ovaries of spent fish were compared with those collected at the end of the summer and during maturation; eggs were classified as minor growth phase oocytes, circumnuclear ring phase oocytes, and ripening eggs (those containing oil or yolk). The spent ovaries contained small oocytes which had not developed during the previous maturation cycle. By May, regeneration had taken place, and the numbers of eggs in the minor growth phase had increased by the development of further oocytes; growth of the oocytes had occurred and eggs in the circumnuclear ring phase were abundant. Comparison of the May ovaries with those collected in August showed no significant differences in the number of eggs in each of these phases, suggesting that there had been little ovarian activity during the summer months.

Ovarian growth was resumed in late September when oocytes in the circumnuclear ring phase began to increase in size. Simultaneously, some oocytes in the minor growth phase began to increase in size, and a circumnuclear ring appeared in the cytoplasm close to the nucleus. In October and November there were further increases in the numbers of small oocytes reaching this phase; these newly formed circumnuclear ring oocytes could be distinguished by their size, and by the position of the cytoplasmic ring close to the nucleus. Thus, before the start of the maturation cycle in autumn, the number of eggs which would start to ripen was already partly determined. The numbers of these eggs were then further increased by growth of some of the minor growth phase oocytes, and this growth process continued until November when vitellogenesis became well established. The November ovaries could be divided into two groups; those in which yolk deposition was just beginning, and those in which vitellogenesis was established; a comparison of ovaries at the initiation of vitellogenesis with those at the stage where vitellogenesis had become well established showed that there was no further increase in numbers of eggs which would ripen, and very few small circumnuclear ring phase oocytes could be found in ovaries at the latter stage (Table 3).

These results suggest that the fecundity of the cod is partly determined after spawning, when the new generation of circumnuclear ring phase oocytes is produced, and is probably related directly to the size of the fish. However, the number of oocytes which will ripen during the maturation season is increased during the period of ovarian growth in the autumn, before vitellogenesis is well established. The growth achieved by the fish during the summer feeding period could therefore be reflected in the numbers of extra eggs which develop to the circumnuclear ring phase in autumn.

In some species of fish, fecundity appears to be adjusted by atresia of the developing oocytes. Thus, in the rainbow trout, *Salmo gairdneri*, during the summer months atresia reduces the numbers of developing eggs and this has been associated with a decrease in feeding; experimentally restricting the intake of food in this species increased the numbers of atretic eggs (Scott, 1962). In the carp, *Cyprinus carpio*, a considerable number of eggs do not ripen fully but are resorbed after spawning, and Vasnetzov (quoted by Nikolsky, 1950) has suggested that when there is a marked improvement in feeding conditions these eggs may develop completely, increasing fecundity.

Atretic eggs were found in the majority of the cod ovaries examined, but their numbers were few, and they rarely formed more than one per cent of the ripening eggs in the ovary. In the present study there was no evidence of wholesale atresia of eggs, nor did it appear likely, from

TABLE 3. THE NUMBERS OF OOCYTES IN DIFFERENT PHASES OF DEVELOPMENT THROUGHOUT THE YEAR

Month	Percentage of eggs in minor growth phase	Percentage of circumnuclear ring eggs	Percentage of eggs with yolk
May	68	32	0
August	64	36	0
September	62	38	0
October	46	44	10
November- December	(Vitellogenesis (beginning (43	40	17
	(Vitellogenesis (established (44	23	33
January	45	4	51
March (spawning)	45	2	53

their infrequent occurrence, that oocyte atresia was an important factor in regulating fecundity in the cod under normal conditions. This dual mechanism of fecundity determination in spring and autumn has obvious advantages, since it involves minimum oocyte atresia, while probably closely relating the fecundity of the female to size and growth.

1.3 Oestrogen secretion

1.3.1 Control of vitellogenesis

There is considerable evidence that during gonadal maturation in lower vertebrates, including fish, the transport in the blood of yolk phospholipid-glycolipoprotein to the developing eggs is associated with an increase in the level of plasma calcium, the calcium being bound to the yolk protein complex (Bailey, 1957; Simkiss, 1961; Urist and Schjeide, 1961). These conditions have been produced in laboratory animals in a non-reproductive condition with a single dose of exogenous oestrogen and it would seem that they are under estrogenic-control. It was thought likely that similar changes in the calcium-protein complex would occur in the blood of adult cod during maturation, and that they might be used as an index of oestrogenic activity. Plasma samples were collected from Barents Sea cod throughout the year to see whether such variations occurred.

The analyses showed a marked seasonal cycle in plasma calcium in adult cod, the magnitude of the changes being greater in females than in males. During the spring and summer, plasma calcium remained at a resting level in both sexes, but in October the level had begun to rise slowly, reaching maximum values in the period January to March; these increases coincided with the period of gonadal maturation and were highest when the gonads were ripe. Immediately after spawning, plasma calcium levels fell to their minima in both sexes, later returning to the summer resting values. No significant changes in calcium were observed in the plasma of immature fish of either sex throughout the year (Woodhead, P.M.J., in preparation).

The increased levels of calcium observed in adult cod during the autumn and winter were associated with gonad maturation; plasma calciums had increased significantly by the onset of vitellogenesis and achieved their greatest height when vitellogenesis was well established; it seemed that in the female cod, at least, hyper-calcaemia was associated with vitellogenesis. That these changes were oestrogen-controlled in cod, as had been shown for other fish (Bailey, 1957; Urist and Schjeide, 1961; Fleming and Meier, 1961), was given some support by laboratory experiments in which cod were injected with oestradiol and with oestrone. The hormone injections caused an increase in plasma calcium, which was directly proportional to the dose of hormone given; oestradiol was more effective than oestrone in producing this response (P.M.J. Woodhead, unpublished experiments). It therefore seemed probable that the calcium changes in the cod were in response to changes in oestrogen secretion by the ovary. Increased oestrogen secretion during the period of vitellogenesis suggested that the two were related, the oestrogens perhaps controlling, or being involved in, the elaboration of yolk proteins in the liver for transport to the ripening ovaries. Recent studies on vitamin A aldehyde in the cod lend support to this conclusion; vitamin A aldehyde only appeared in the ovary after the onset of vitellogenesis (Plack, *et al.*, 1961) and analyses showed that it was also present in the blood of female cod during vitellogenesis; it was absent from the blood or present only at a low level when the gonad was resting, but, as for plasma calcium, a high level can be produced experimentally by injecting non-reproducing cod with exogenous oestrogens (P.M.J. Woodhead and P.A. Plack, unpublished).

From the seasonal changes in blood calcium it is inferred that in the cod, oestrogen secretion occurs during the latter part of the maturation cycle, from November onwards, achieving its highest level during January to March.

The seasonal changes observed in the plasma calcium of adult male cod are less easy to explain, since androgens have not been shown to cause such changes in any lower vertebrates. Although oestrogens have been demonstrated in the blood of some maturing male teleosts (at a lower level than in females; Cedard and Nomura, 1961) and it seemed possible that oestrogens might also produce the hypercalcaemia observed in male cod, Gottfried *et al.* (1962) have failed to find any substantial quantities of oestrogens in mature cod testes.

1.3.2 The secretion of hormones from the fish ovary

Oestrogens have been isolated from fish ovaries (Donahue, 1941) and recently oestradiol-17 β and oestrone have been found in the mature ova of the cod, at concentrations of 4.8 μg/kg and 1 μg/kg respectively (Gottfried *et al.*, 1962); some oestradiol, but no oestrone, was also contained in the ovarian sac. However, there is considerable uncertainty about the site of oestrogen production. The ripening ovary of fish usually contains a number of degenerating eggs or corpora atretica, and a hormonal function has been ascribed to these by several workers, notably Bretschneider and De Wit (1947), D'Ancona (1950), Hoar (1955) and Ball (1960), although as yet there is no critical evidence to show that these atretic eggs have a secretory function, or, indeed, any function at all.

Corpora atretica are present in cod ovaries, and they appear similar in many respects to those described previously in other teleosts (Bretschneider and De Wit, 1947). In September, at the beginning of gonadal maturation, very few atretic eggs were found; in October about a quarter of the ovaries examined contained atretic eggs, but by November-December more than 90% of the ovaries examined contained a few atretic eggs. Their appearance coincided with the start of vitellogenesis in the ovary, and they were rarely formed outside this period.

Histological results from the study of the Barents Sea cod ovaries did not provide further evidence to show whether corpora atretica had a secretory function, or if they were simply degenerating eggs in the process of resorption. A finding apposite to this problem was obtained from the analyses of plasma calcium levels (described above).

The hypercalcaemia found in adult female cod during the winter months was associated with oestrogen production and vitellogenesis in the maturing ovary. Corpora atretica were formed at the onset of vitellogenesis and persisted throughout ripening. If the size and complexity of the resorbing corpora atretica corresponded to secretory activity, they would appear to have been most active at the onset of vitellogenesis, their activity declining in the later phases of yolk deposition. Their occurrence in the ovary corresponded with the period of increased plasma calcium levels, and if hypercalcaemia reflected increased levels of oestrogen in the blood, these results could suggest that the corpora atretica had a secretory function.

Surprisingly, a few "apparently immature" females had ovaries in which all the eggs which had begun to mature had become atretic. Plasma calcium analyses showed that these fish had values above the usual immature range, suggesting that oestrogens were being secreted by the ovaries, possibly associated with the presence of atretic eggs. However, the relationship was by no means so simple and direct. These "immature" cod had much greater numbers of atretic eggs than normally ripening females, and accordingly it might have been expected that they would have proportionately higher levels of calcium in the plasma; in fact, the levels of their plasma calcium fell within the normal range for maturing females.

2. The testis

2.1. The maturation of the testis

The summer "resting" testis consisted almost entirely of cysts containing large, faintly staining spermatogonia, with large, round, central, lightly staining nuclei. There was little gametogenic activity during this period; occasionally the cells within a cyst divided and produced groups of secondary spermatogonia, distinguishable by their dense nuclei and indistinct cell boundaries. Secondary spermatogonia appeared in large numbers in late September, as maturation of the testis began; probably the existing spermatogonia divide to produce more spermatogonia, while groups of these give rise to secondary spermatogonia, the two processes occurring simultaneously. Primary spermatocytes, secondary spermatocytes and spermatids, representing the following three stages of spermatogenesis, predominated in the testis from mid-November to early January. The primary spermatocyte is largest, and usually has a nucleus in which the chromatin threads appear as a tangled mass, or are aggregated at one side. Secondary spermatocytes are smaller, with evenly dispersed chromatin; spermatids are smaller still, and have an elliptically shaped nucleus, and a very small cytoplasmic rim, so that the cells appear kidney-shaped.

Spermatozoa began to appear in the ripening testis from December. Initially the sperm were localized in bundles amongst the other cells, but, as more were produced, the cyst walls ruptured, the orientation of the bundles was lost and the testis became filled with ripe sperm. Almost immediately after spawning regeneration of the testis began; unshed sperm was resorbed, and the testis filled with primary spermatogonia (Fig. 4).

2.2. Seasonal changes in the interstitital cells of the testis

Lipid positive cells, analogous to the mammalian Leydig cells, which secrete male sex hormones, have been demonstrated in the testes of fish (Marshall and Lofts, 1956). Similar interstitial cells occur in the cod testes; they were readily distinguished in sections stained with Masson's trichrome stain, and their activity has been assessed on the basis of cytological characteristics. Four stages of activity were adopted. Inactive cells were small, with a central, heavily staining, dense nucleus and a thin rim of faintly staining cytoplasm. Cells classified as slightly active were larger, with increased cytoplasmic area; occasional faint granules were seen in the cytoplasm, and the nucleus showed chromatin threads aggregated at one side. Active cells were larger, and the cytoplasmic granules were coarse, conspicuous and more closely packed, whilst in maximally active cells there had been a further increase in cytoplasmic area, so that the cells were now approximately three times as large in diameter as the inactive cells, and the cytoplasm contained numerous coarse granules. There was little change in nuclear volume as the cells became active.

Testes collected throughout the spring and summer contained inactive cells, and in September the tissue still showed few signs of activity. Secretory activity appeared to begin about November-December when about one third of the interstitial cells were ascribed to the "slightly active" category (although less than 10% were characterised as "active" or "maximally active"). By January, activity had increased and was well established; cells in all four stages of activity were present, but "active" and "maximally active" cells predominated (about 60% of all cells). The testes of fish caught in early March, probably some three weeks before spawning, contained large numbers of maximally active cells. Samples from "running ripe" males, very kindly collected inside the Lofoten Island spawning grounds by Dr F.R. Harden Jones, showed that interstitial cell activity had begun to decline, and, after spawning, the activity of the gland had returned to its summer level (Fig. 5).

The interstitial cells of the cod testis show well marked seasonal variations in activity. Secretory activity became apparent in November-December, reaching a maximum just prior to spawning (as appeared to occur for oestrogens in the female). Testes collected from spawning fish showed that activity had begun to decline, and in spent cod the gland had become inactive.

It is assumed that the interstitial cell changes in the maturing testis are associated with sex hormone secretion in cod. Androgens have been shown to be present in the testes of mature sockeye salmon, *Oncorhynchus nerka*, and chum salmon, *O. keta* (Potter and Hoar, 1954; Idler and Tsuyuki, 1959), but no analysis has been described for the cod testis.

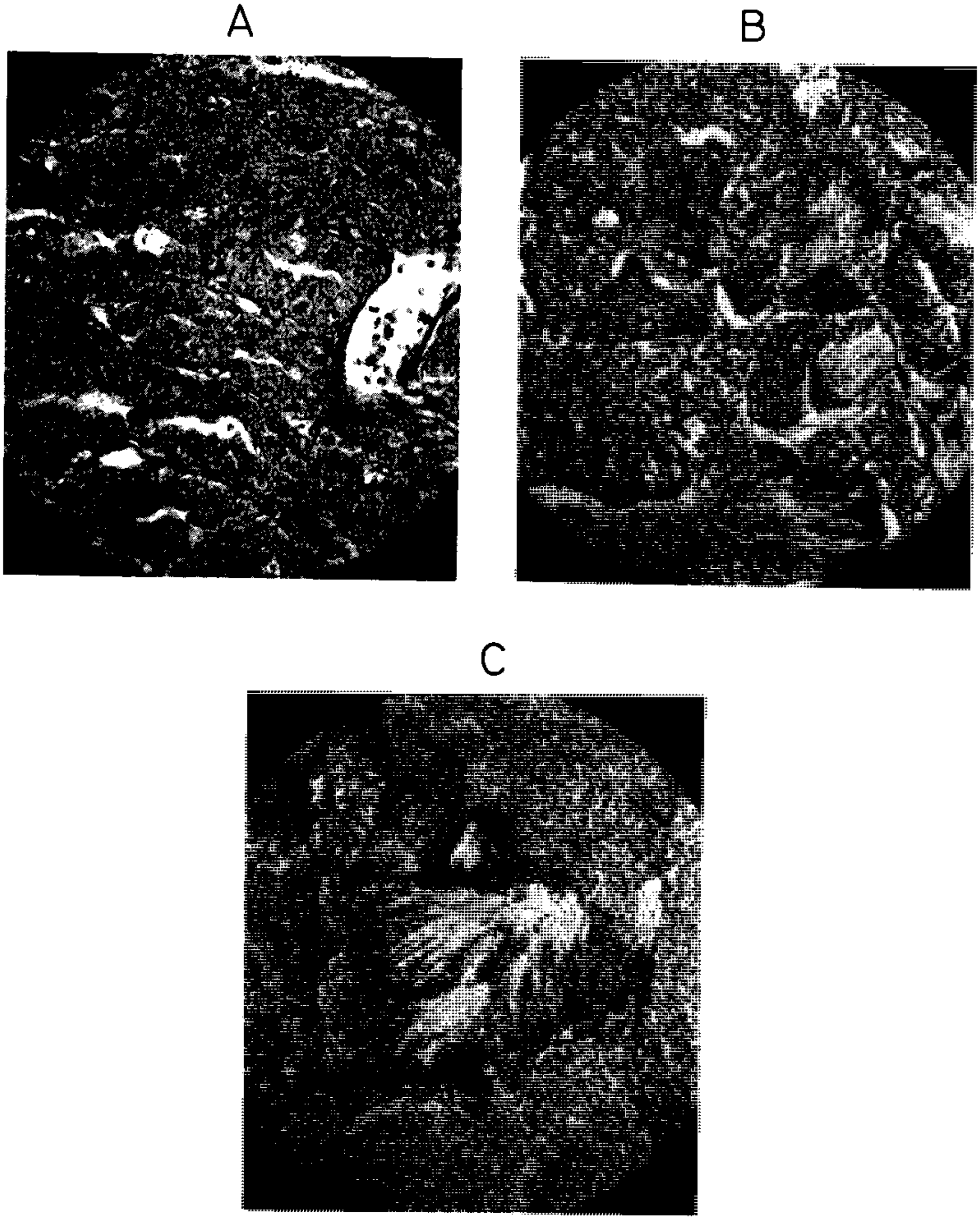

Fig. 4. Photomicrographs of the cod testis during maturation.

A. Resting testis, completely filled with large primary spermatogonia.

B. Ripening testis collected in December showing all later stages of spermatogenesis. Bundles of sperm can be seen.

C. Testis collected in February, almost completely filled with spermatozoa.

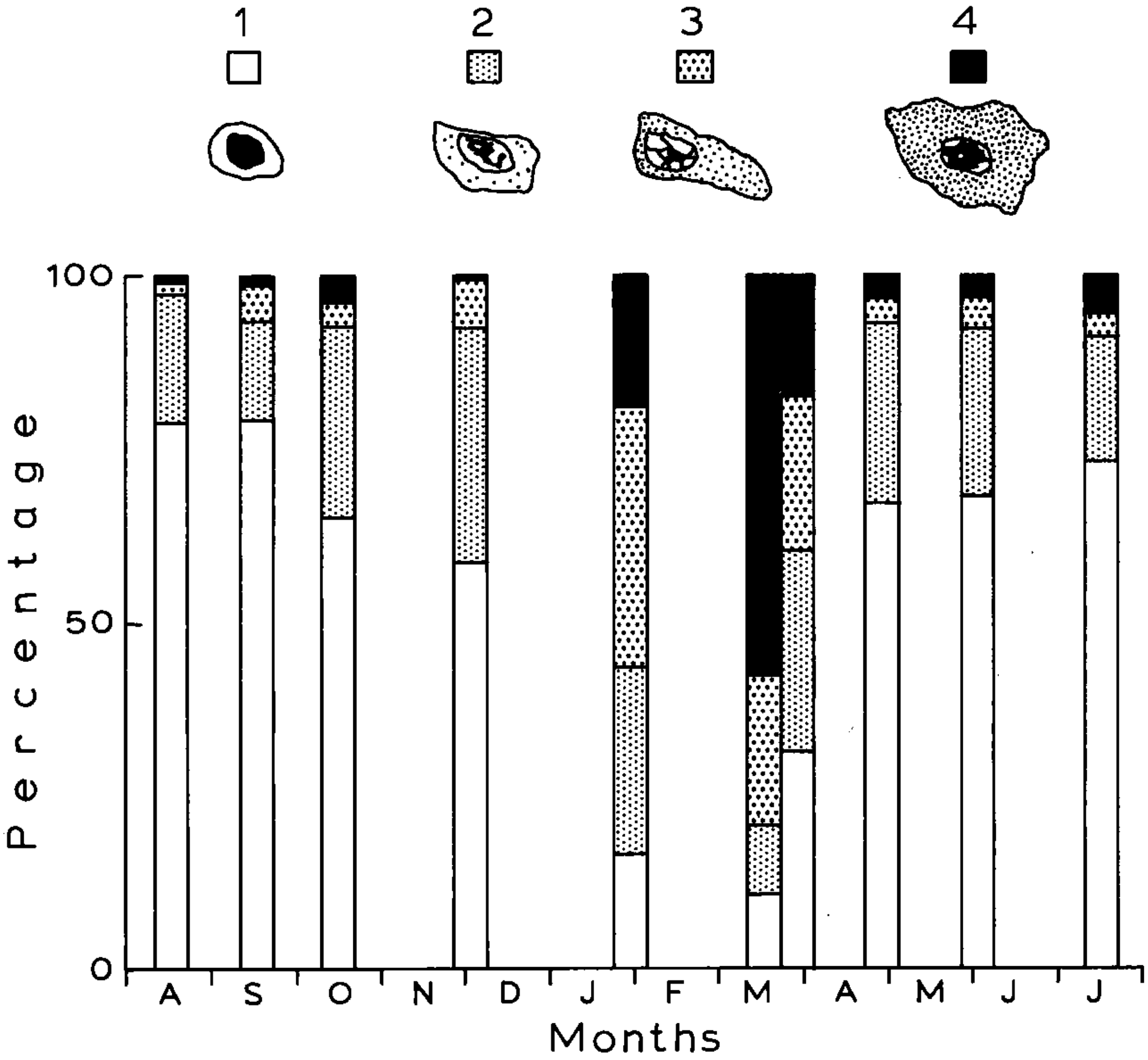

Fig. 5. Interstitial cell cycle in the testis, shown as percentage occurrence of cells of different activity, estimated histologically.

2.3. Gonadal hormones and the spawning migration

While the migration of the Barents Sea cod has been primarily associated with thyroid activity, the functions of gonadal hormones in this behaviour may also be of considerable importance. Hoar and his co-workers (1955) showed that sex steroids had similar effects to thyroxine upon the activity of fish, and on their sensitivity to stimulation. Goldfish and juvenile salmon kept in solutions of testosterone or stilboestrol were more active than untreated fish; they had a lower threshold for the response to electrical stimulation, and showed increased rheotaxis. Sex steroids had greater effects on this behaviour than thyroxine, and their maximum influence was generally seen sooner after treatment (after ten days, in contrast to fifteen days for thyroxine). Goldfish fed with beef testes have been found to show a 400% increase in locomotory activity (Stanley and Tescher, 1931) and Woodhead (1956) observed that the mean swimming speed of minnows, *Phoxinus phoxinus*, was 159% higher in April, prior to spawning, than during the winter months; these experiments have since been confirmed by Aminul Haque (in Barrington, 1960). In prespawning minnows, the thyroid has been found to be active (Barrington and Matty, 1954), but the gonads were apparently also secreting hormones, since the fish were in breeding dress. Both thyroid and gonadal hormones may therefore have contributed to the increased swimming activity.

In the adult cod, the effect of thyroid and gonadal hormones on migratory behaviour is probably additive. However, the cycle of secretory activity in the gonads of both males and females did not begin until November-December, about two months after migration had begun; as discussed above, thyroid hormones would appear to play a dominant rule in controlling migration, but their effects may be augmented by sex steroids secreted during the later stages of the migration.

THE INTERRENAL GLAND OF THE COD (ADRENAL CORTICAL TISSUE)

The interrenal tissue in fish does not form a discrete gland, but lies scattered amongst the head kidney, in close proximity to the cardinal veins and their branches. The anatomical position of the gland makes surgical removal impracticable, and hence data on its functions, and on the roles of the adrenal cortical hormones in fish, are often inconclusive.

In the present context it is particularly interesting to find that there is evidence of variations in interrenal activity during the spawning migrations of some fish. Changes in the histological appearance of the gland have been found during the spawning migration of Pacific salmon, accompanied by a progressive rise in the level of blood corticosteroids (Idler, Ronald and Schmidt, 1959; Robertson, *et al.*, 1961). In Atlantic salmon, blood corticosteroids also rose during the spawning migration but later fell at spawning (Fontaine and Hatey, 1954).

1. Seasonal changes in the interrenal gland of cod

A study was made of the histological changes in the interrenal gland of adult Barents Sea cod during their spawning migration. Changes in the cytological characteristics of the interrenal cells were studied, in particular the size and shape of individual cells and their staining properties with Masson's trichrome stain, the arrangement of the tissue into chords, or groups of cells, and the degree of vascularisation of the gland.

From July to October, the interrenal gland was composed of chords of cells, uniform in appearance, extending from the branches of the cardinal veins into the kidney tissue. Individual cells were large and columnar, with a round reticular nucleus, and faintly granular cytoplasm. Within each chord, the cells tended to be orientated in the same direction, with the nuclei of adjacent cells in alignment. Small blood vessels were present between the chords (Fig. 6A). The histological appearance of the gland suggested a resting condition, with little secretory activity.

Changes indicating the onset of secretory activity, were apparent in the late November sample. Whilst considerable areas of the interrenal tissue were still disposed in regular chords, some cells had formed into clumps; within these clumps two new types of interrenal cells had appeared. The most conspicuous and numerous of these were small, shrunken, intensely staining cells, in some of which degenerative changes were apparent; the cytoplasmic area had become very reduced, consisting in some cases simply of a thin rim of cytoplasm, slightly elongated at one side, surrounding the dense nucleus (Fig. 6B,C). The second type of cell was large, round, lightly staining, and approximately twice the diameter of the columnar interrenal cells. Both the cytoplasmic and nuclear areas had increased, and the cytoplasm showed a few faint granulations; sometimes vacuoles were present in the cytoplasm. Interrenal cells of this second type are characteristic of a hyperplastic gland (Robertson and Wexler, 1959; Mahon *et al.*, 1962). Histologically, the interrenal gland showed signs of increasing activity.

The interrenal glands collected from cod in January showed greater degenerative changes. The majority of chords had broken down and the cells had become grouped together, while the numbers of small degenerating cells had increased considerably (Fig. 6D). Large interrenal cells were present in the groups of cells. Interrenal glands collected in March had a very similar appearance, but the vascularisation of the gland was more pronounced than in the January sample, and the gland appeared to be extremely active.

Interrenals collected from spent cod in May-June showed some evidence of recovery. Many of the cells were grouped together, but chords had begun to reform. A striking feature of these chords was the occurrence of numerous thin elongated closely packed cells, which stained lightly. Mitoses were seen occasionally in these cells, and it appeared that regeneration of the interrenal tissue

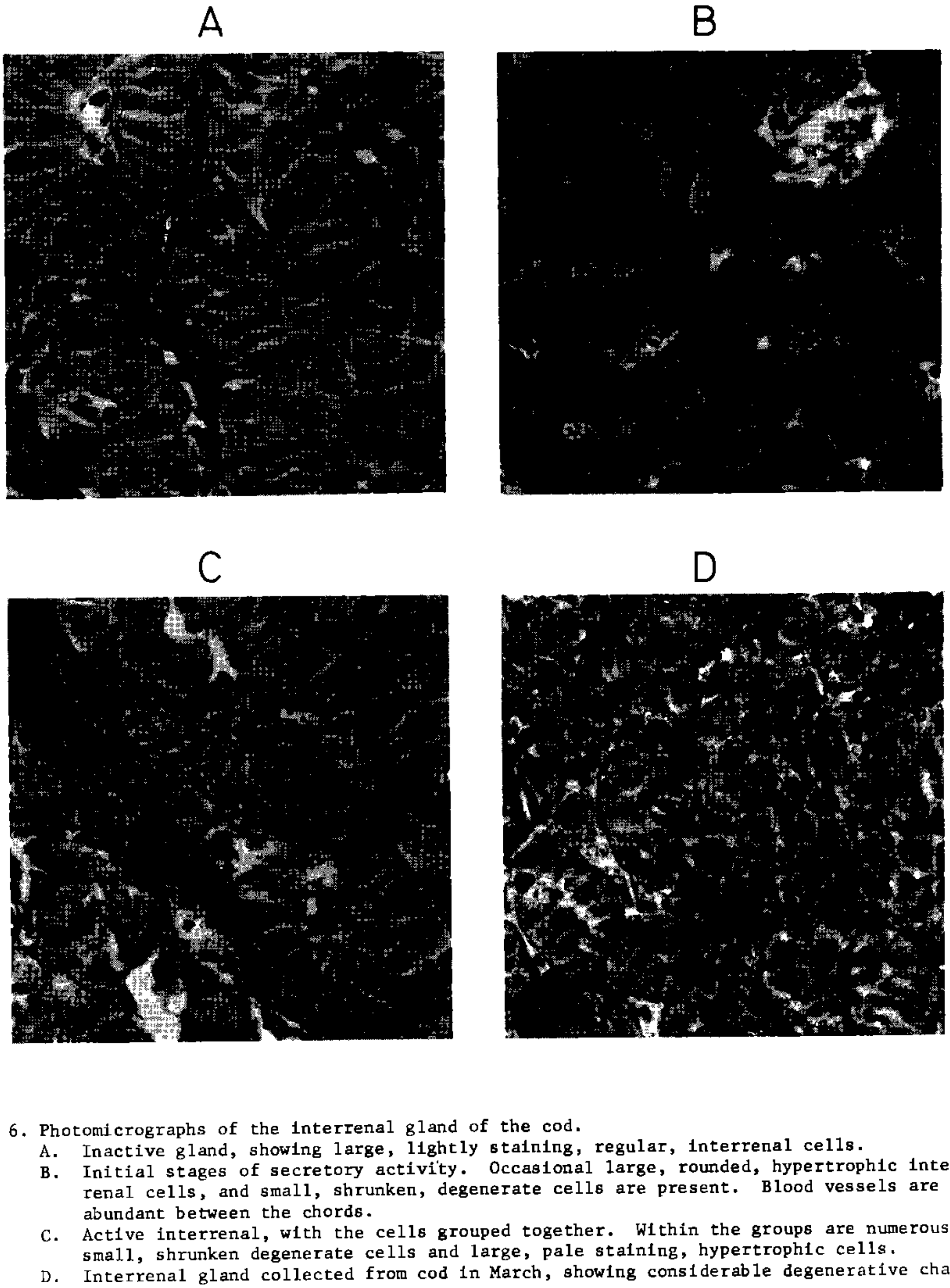

Fig. 6. Photomicrographs of the interrenal gland of the cod.

A. Inactive gland, showing large, lightly staining, regular, interrenal cells.

B. Initial stages of secretory activity. Occasional large, rounded, hypertrophic interrenal cells, and small, shrunken, degenerate cells are present. Blood vessels are abundant between the chords.

C. Active interrenal, with the cells grouped together. Within the groups are numerous small, shrunken degenerate cells and large, pale staining, hypertrophic cells.

D. Interrenal gland collected from cod in March, showing considerable degenerative changes.

was taking place. Degenerate interrenal cells were also present, although numbers had diminished considerably, and there were few large rounded interrenal cells. Histologically the interrenal gland appeared to be regenerating, but whilst secretory activity had declined considerably, the gland had not re-entered the resting condition, and it seemed likely that some secretory activity was still taking place. The changes described appeared to be the same in male and female cod.

2. The role of adrenal cortical hormones

It seems likely that the interrenal tissue in fish secretes corticosteroids which are similar or identical to some of those found in higher vertebrates. The presence of steroids concerned with carbohydrate metabolism and with salt and water balance has been demonstrated in fish blood (Phillips, *et al.*, 1959; Idler, *et al.*, 1959). However, the functions of these hormones in regulating mineral metabolism in fish are not fully understood. Experimental evidence has shown that corticosteroids can influence osmoregulation in freshwater fish (Secton, 1955; Holmes, 1959), but there is as yet little evidence to show whether they have a similar function in marine teleosts, and Chester Jones, Phillips and Holmes (1959) concluded that the adrenal cortical hormones are relatively inactive in osmoregulation in marine teleosts.

However, experiments in which freshwater fish were transferred to sea water resulted in an augmentation of plasma corticosteroids (Leloup-Hatey, 1959; Faure, 1960), while there is histological evidence of increased interrenal activity in salmon smolt transferred from fresh water to sea water, which has been interpreted as a feature of osmoregulation incident to the migration of the fish from fresh water to the sea (Olivereau, 1962); such experiments suggest that corticosteroids may indeed have a role in mineral metabolism in the marine environment. In this respect the changes in the interrenal of the cod are of particular interest, since the preliminary examination of their annual cycle of activity showed some evidence of coincidence between the duration of the low temperature limit to the cod in the winter and spring (which appears to influence the osmoregulatory mechanism - discussed in Part II of this paper) and activity of the interrenal gland.

Corticosteroids in fishes may be involved in the stimulation of metabolic processes, and it has been suggested that the increased activity of the gland during spawning migrations may be correlated with heightened carbohydrate metabolism and muscular activity (Fontaine and Hatey, 1954; Chester Jones, *et al.*, 1959). Robertson *et al.* (1961) found a marked hyperglycaemia during the spawning migration of Pacific salmon, which they associated with gluconeogenesis, when the interrenal glands were hyperactive. However, the causes of adrenal hyperplasia in salmon are difficult to determine, and the situation is complex, since migration and gonadal maturation occur whilst the fish are starving. Further, the fish encounter marked salinity changes during their migration. All these factors have been shown to affect adrenal cortical activity in either fish or mammals. Robertson and Wexler (1959) examined this problem in detail, and they suggested that neither osmoregulation nor the stress of migration is the dominant factor causing interrenal hyperplasia, but that the interrenal activity might be related to the stress of the development of gonads whilst the fish were starving.

The hypertrophy of the interrenal gland during the spawning migration of the Barents Sea cod might reflect an intrinsic cycle of activity, mobilizing carbohydrate reserves in relation to migration. However, if this was the case, activity would have been expected to start earlier, but there was no evidence of any secretory activity coincident with the onset of migration. Hypertrophy and degenerative changes became apparent in late November, when the fish are often feeding poorly (due to lesser availability of food in winter); this was the period of most rapid gonad growth and vitellogenesis in the female, so that the degenerative changes might equally have been the result of the increased demands of gonad maturation during a period when the fish were in poor nutritional condition.

A preliminary consideration of interrenal changes in immature cod indicated a similar, although lesser, cycle of activity. Hypertrophy of the gland was seen from late November, but extensive degenerative changes, such as occurred in the adult maturing cod, were infrequent. The interrenal gland in the immature cod remained active after their migration had ceased; this is in contrast to the cycle of activity in the thyroid gland, which declined as migration was completed. On the basis of these results it would appear that interrenal activity in immature and mature cod may be related to the winter period of poor feeding, and that the greater activity in adult fish is associated with the pronounced physiological demands of gonadal maturation.

Nevertheless, the possibility that the activity of the interrenal gland does play a part in migration cannot be precluded, even though it had not become active at the initiation of migration; it is hoped that these factors will be separated in a more detailed study now in progress.

EXTERNAL FACTORS REGULATING MATURATION AND MIGRATION

Marshall (1936) emphasised that breeding seasons were dependent upon external environmental factors, and suggested that their influence was exerted by nervous stimulation of gonadotrophic hormone released from the pituitary gland; this concept has been supported by later work, and the pathway linking external variables to internal physiological rhythms has been well established in higher vertebrates. The mode of regulation appears to be similar in fish (Olivereau, 1954; Zaitsev, 1955*a*, *b*). Changes in the physical, chemical or biological environment of the animal affect nervous receptors communicating with the hypothalamus, which, in turn, stimulates the pituitary gland to release hormones initiating activity in the endocrine target organs.

There seems little doubt that internal rhythmical changes may occur in the absence of external stimuli, and evidence of endogenous rhythms of breeding activity have been found in fish kept under constant experimental conditions (Bullough, 1939; Scrimshaw, 1944). However, the regular coordination of sexual cycles tends to break down under such constant conditions; thus Bullough (1939) found that in the minnow certain phases of gametogenesis were unduly lengthened, and Robinson and Rugh (1943) observed that the regularity of the 24-hourly spawning cycle in *Oryzias latipes* disappeared under constant illumination. The results from experiments with fish and other vertebrates suggest that seasonal rhythms in physiological activity are innate, but the role of external environmental factors is to precisely time these rhythms.

Two of the most important physical factors which have been shown experimentally to affect the timing of breeding cycles in fish are light and temperature. The relative importance of each varies with the ecological environment of the particular species, but in many marine fish photoperiod appears to be critical, provided that temperature does not deviate too far from the normal seasonal range.

Discussing the importance of external factors Bullough (1939) concluded that temperature would probably be important in the marine environment, since temperature variations over wide areas of the ocean were slow and changed in a regular manner throughout the year. But in many offshore regions this is not the case and if the temperatures are considered in detail over the range of a species, or from year to year, the changes do not seem to be sufficiently precise to form a basis for control, or even for temperature to be a dominant regulating factor. On the Svalbard Shelf of the Barents Sea the cod encounter only a small temperature range, from about -1°C to 5 or 6°C, and during most of the summer feeding period abundant catches may be made over most of this range (see Part II of this paper, Fig. 2). There is no sudden fluctuation in the autumn; indeed in September when migration and maturation commence the temperatures are about the same as in August and it seems unlikely that these physiological changes are initiated by temperature.

It seems probable that changes in the light regime, varying steadily from season to season, might initiate the spawning migration, and gonad maturation, in the Barents Sea cod. The initiation of these reactions occurs at the time of the autumnal equinox, when diurnal periods of light and darkness are equal throughout the northern hemisphere; we suggest that at this time, when diurnal periods of light and darkness are equal, the internal physiological rhythms resulting in migration and maturation are "triggered off". This change would be a common environmental factor throughout the range of the Barents Sea cod, so that characteristic changes would occur on all grounds; although theoretically photoperiod would vary with depth according to the penetration of light, these variations would not be great since at this time the cod in the Barents Sea are mainly found in shallow water (Trout, 1957) where light would be easily detected throughout most of the daytime period (Woodhead, 1964, this symposium). It appears less likely that other light factors such as intensity, rate of change of intensity, daily absorption of radiation, or rate of change of photoperiod would be the principal controlling factors, since they all vary with the latitude and water transparency and more critically with the depth at which the fish occur, and it is more difficult to see how such factors might synchronize the widespread behaviour change. To be able to detect daily changes in photoperiod the fish must be able to measure the relative length of day and night with reasonable accuracy; the fish would therefore need a 24-hour "clock" on which to make the comparison. There is abundant evidence to show that many animals do have such "clocks"; fish are no exception, and show well defined diurnal rhythms in behaviour and physiology (Woodhead, 1964, this symposium). Recent data have suggested that in some species "internal clocks" of individual animals may not be synchronous, but that there is a basic precision within a population. Webb and Brown (1959) have suggested that this would ensure that the population as a whole was maintained, rather than individuals. Single fish might show some variation in the time at which they began their spawning migration, but the movement of the population as a whole would be co-ordinated and synchronized.

At the time of the equinox marked changes may also occur in the biological environment, both in the plankton and to a lesser extent in the benthos. Such changes could act secondarily as "triggers" for the physiological rhythms of the fish. However this would seem a less likely mechanism than the direct influence of photoperiod, since due to the discontinuous nature of the biological environment much precision of timing would probably be lost.

Using trawler catch per unit effort data Trout (1962, 1963) has demonstrated a regular seasonal cycle of changes in catch, not only for the Barents Sea stock, but also for cod of several other stocks in the North Atlantic; these catch changes were interpreted as indicating a specific pattern of seasonal behaviour for the cod. It is of interest to speculate whether the coincidence of the equinox throughout the range of the cod might account for the similar timing of the patterns in widely separated stocks.

CONCLUSIONS

It is now generally accepted that many of the seasonal changes in the distribution, density and availability of fish stem from fundamental behavioural changes which are internally induced. This is especially the case in such species as the Barents Sea cod, which remain within a rather narrow range of temperature and salinity throughout the year. In these fish there are regular and well defined seasonal changes in distribution, direction and speed of movements, concentration and availability, depth change and reactions to low temperatures; evidence is accumulating which suggests that environmental changes are superimposed upon, and modify, many of these basic patterns, rather than the reverse. The basic behavioural patterns appear to be characteristic of the species and are probably controlled largely by internal physiological changes releasing different levels, or patterns, of metabolic activity, locomotion, sensory perception, or shifts in the control of homeostasis. In order to interpret the reactions of the fish to their external environment, it is therefore necessary to understand the internal changes which are also occurring; thus although seasonal migration is essentially a problem of fish behaviour in relation to environmental stimuli, it can only be understood in relation to the endocrine changes which initiate, maintain and possibly also terminate this complex of behaviour patterns.

In this paper we have attempted to describe in semi-quantitative terms the annual changes in three of the most important endocrine organs of the cod of the Barents Sea— the thyroid, gonads and interrenal glands. These are the glands whose activities are most likely to bring about annual changes in the reactions of the cod to the external environment; the pituitary would also be involved in such changes, but has not been discussed here, although one of us has previously described the presence of gonadotrophic, thyrotrophic and adreno-corticotrophic hormones in the cod pituitary (Woodhead, A.D. and Fontaine, 1959; Woodhead, A.D., 1960*b*, 1961), and Heller (1963) has suggested that the neurohypophysical lobe also contains arginine vasotocin and another active peptide ichthyotocin. Although the present descriptions refer to only three glands, and we are aware that they are incomplete, they are presented here as parts of the essential framework within which the detailed analysis of the seasonal changes in the physiological reactions of the cod must be made. The technique of studying changes in single endocrine organs in respect to the reactions of the fish is limited, since the endocrine glands tend to work in an integrated manner and their interrelationships may be complex; nevertheless it may be claimed that this study of the cod has already yielded several results of apparent importance to the investigation and understanding of the behaviour of commercial fish stocks.

At present very little work has been done in this field. Thus, despite the remarkable plasticity of the reproductive processes in fish, it has been said that our knowledge of reproduction in the classes of fishes is based mainly on about fifty species out of some 20,000 available, and very few of these have been marine fish of commercial importance. Considering other endocrine glands, much less information is available; indeed, the present descriptions of thyroid activity in the cod and spurdog are the only quantitative analyses of the seasonal changes in this gland made for any marine fishes; this would also seem to apply to the interrenal gland. Studies in the field of freshwater fisheries research are based upon far more detailed work.

We consider that similar physiological studies of the reactions and capacities of marine fish would provide data of fundamental importance to fisheries biology. To take one relevant example, although many investigations have been made concerning the relationships between cod and temperature, it has often been impossible to disentangle the critical features of the ecological complex, so that the results have been largely inferential. Approaching this problem from a physiological viewpoint (second part of this paper) has yielded apparent evidence of direct effects of low temperature on cod, even though the study has so far been of limited scope. The application of this physiological approach to some of the complex problems of fisheries biology should provide rewarding additions to the results of the better established fisheries disciplines related to the study of the environment and its influences upon the fish.

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F-6B

SEASONAL CHANGES IN THE PHYSIOLOGY OF THE BARENTS SEA COD *GADUS MORHUA* L., IN RELATION TO ITS ENVIRONMENT

II. PHYSIOLOGICAL REACTIONS TO LOW TEMPERATURES

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and

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ABSTRACT

Studies on cod distribution in relation to temperature in the Barents Sea are discussed and data on 1,451 trawl hauls at various temperatures and times of year are presented. Abundant cod catches were not made below about 1.7°C from October to June, although during the summer feeding period large catches were made to at least 0°C.

Cod caught below 2°C between October and June were shown to have elevated blood salt contents, although this did not occur during the summer. Very similar changes were found in North Sea cod in the severe winter of 1963; cod from below 2°C had increasingly high blood sodium contents.

There are many records of cod being killed by low temperatures; to investigate their thermal tolerance cod were tagged and released at different low temperatures in the Barents Sea; recaptures clearly showed that many cod survived but also suggested that low temperatures may have reduced the survival rate.

Histological examination of gill epithelium in cod caught below 2°C (with elevated blood salts) showed signs of increased secretory activity in the so-called chloride secretory cells, suggesting a compensatory response to establish homeostasis. Mucous secretion appeared to have broken down in the gills of these fish. These changes did not occur in cod from low temperatures in the summer.

From the close correspondence of the details of seasonal temperature distribution, and of the physiological changes in Barents Sea cod, it was concluded tbat these fish encounter a limit to normal physiology at about 2°C between October and June, but that this limit changes in summer, perhaps to 0°C. Considering the causes of seasonal changes it seems likely that both feeding and encocrine changes are involved, but the relationships are not yet clear.

Laboratory experiments have shown that cod may survive supercooling for some weeks; such thermal tolerance, even temporarily, would have obvious survival value for Arctic cod, but need not conflict with our view that cod undergo an essential change in normal physiology at low temperatures.

Preliminary investigations of the effects of low temperatures on 0-group and I-group cod suggested that young stages may not be so critically effected as the adult fish.

INTRODUCTION

In an earlier paper (Woodhead and Woodhead, 1959) we considered the effects of low temperatures (below 2°C) upon the physiology of the Barents Sea cod, and found a close association between these effects and seasonal changes in the distribution of the cod with respect to temperature, which have been described by other authors. These studies on the Barents Sea cod have now been taken further, and related investigations were also made on the cod of the North Sea during the severe winter of 1963 when temperatures fell to abnormally low levels. This paper presents these new results and goes on to reconsider our previous conclusions in relation to them. Eliassen *et al.* (1960) repeated

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our observations in the Barents Sea, obtaining similar results but applying an interpretation different from our own, and Leivestad (1964) has further shown experimentally that cod can tolerate very low temperatures; their views are discussed.

DISTRIBUTION AND TEMPERATURE IN THE BARENTS SEA

When considering the details of the distribution of the cod with reference to changes in the marine environment, there have been frequent investigations into the relationships between the catches of cod and sea temperatures, an obvious choice since many of the cod stocks in northern seas live in regions where Arctic waters form cold fronts with warmer waters of Atlantic origin and temperature gradients may be steep. But since the cycle of temperature in the seas tends to follow a regular pattern, in many cod fisheries — just as for other fish which make well defined and regular migrations — there are sure to be apparent relationships between the distribution of the fish and temperature, which may be no more than coincidence. Thus, although cod have been caught over a wide range of temperature from about 17°C to -1°C there would be little significance in the statement that on the Svalbard Shelf (Spitsbergen, Bear Island, Hope Island) of the Barents Sea the best catches of cod are made at between 0° and 5°C, since the temperature range available on the Shelf covers only about seven degrees, from -1°C to 6°C.

There have been several detailed reports of low temperature limiting the distribution of the cod in the Barents Sea. Maslov (1944, 1960) and Mironova (1958) showed that the cod catches of the Russian trawler fleets were related to the position of the 2°C isotherm, few cod being caught below that temperature, and they showed that the fishable area could vary from year to year with changes in hydrographic conditions. Over ten years, from 1949 to 1958, the R/V *Ernest Holt* made many trawling surveys in the north-western Barents Sea on the cod of the Svalbard Shelf, and the fish were frequently found to be limited at a temperature of about 2°C (Graham *et al.*, 1954), and for perhaps the most detailed of these surveys it was suggested that the critical limit lay at 1.75°C (Lee, 1952). Extensive echo-sounder surveys both in the north-western and south-eastern Barents Sea have also shown the fish to be limited by low temperatures (Saetersdal, 1956; Cushing, 1959; Midttun, 1959; Beverton and Lee, 1964), although from the surveys of both Cushing and Saetersdal it appeared that 1.5°C was probably nearer the limiting temperature. There has therefore been considerable agreement between the results of these independent surveys, that the low temperature limit to the distribution of the cod lay between 1.5 and 2.0°C. An exception to this general picture was found during the summer months of July to September, when some cod may enter colder waters, down to about 0°C, to feed heavily upon planktonic krill and on the capelin (*Mallotus villosus*) or herring (*Clupea harengus*) (Lee, 1952, 1956).

Although these surveys reported apparently critical situations in a given area at a particular season, it was difficult to assess the temperature relationships throughout the year. For this purpose results have been provided from the cruises of the R/V *Ernest Holt* fishing on the Svalbard Shelf over the ten years from 1949 to 1958; temperatures at the sea-bed were observed at the beginning and end of the trawl hauls, and the cod catches could therefore be compared directly with temperatures throughout the seasons of the year. The catch of cod, in baskets per hour (a basket of cod weighs about 38 kgm), was compared with the mean of the temperatures recorded at each end of the trawl haul. (Catches made when the temperature differences between the beginning and end of the trawl hauls exceeded one degree have been excluded as too inaccurate.) It was found that the same relationship generally held for the whole of the period October to June, and that, as previously reported by Lee (1956), large catches of cod were not taken in water below 2°C in this period. These results for 1109 trawl hauls are shown in Fig. 1. From this figure it appears that temperatures between 1.7°C and 2.0°C were critical in limiting the distribution of abundant cod (although it is also apparent that small catches of cod were frequently made at lower temperatures). There were a few exceptions where high catches had occasionally been made at 1°C, or even lower; these were usually made at the edge of the bank south of Bear Island in February-March; it is not uncommon for water cooled on the banks to cascade off the shelf in this region (Lee, 1963), and these fish may well have been surrounded or trapped by such cold cascading waters, as happened in March 1955 (Beverton and Lee, 1964). During October in both 1957 and 1958, however, some fairly high catches were made on cod which were feeding heavily in cold waters (see also the discussion of conditions in October 1960 later in this paper), and it appears that the temperature distribution of cod, when feeding heavily on fish, is not so precisely defined at this time.

The observations of Lee (1956) that the limiting effects of low temperatures were not apparent during the summer months of July, August and September are in accord with the results of the present

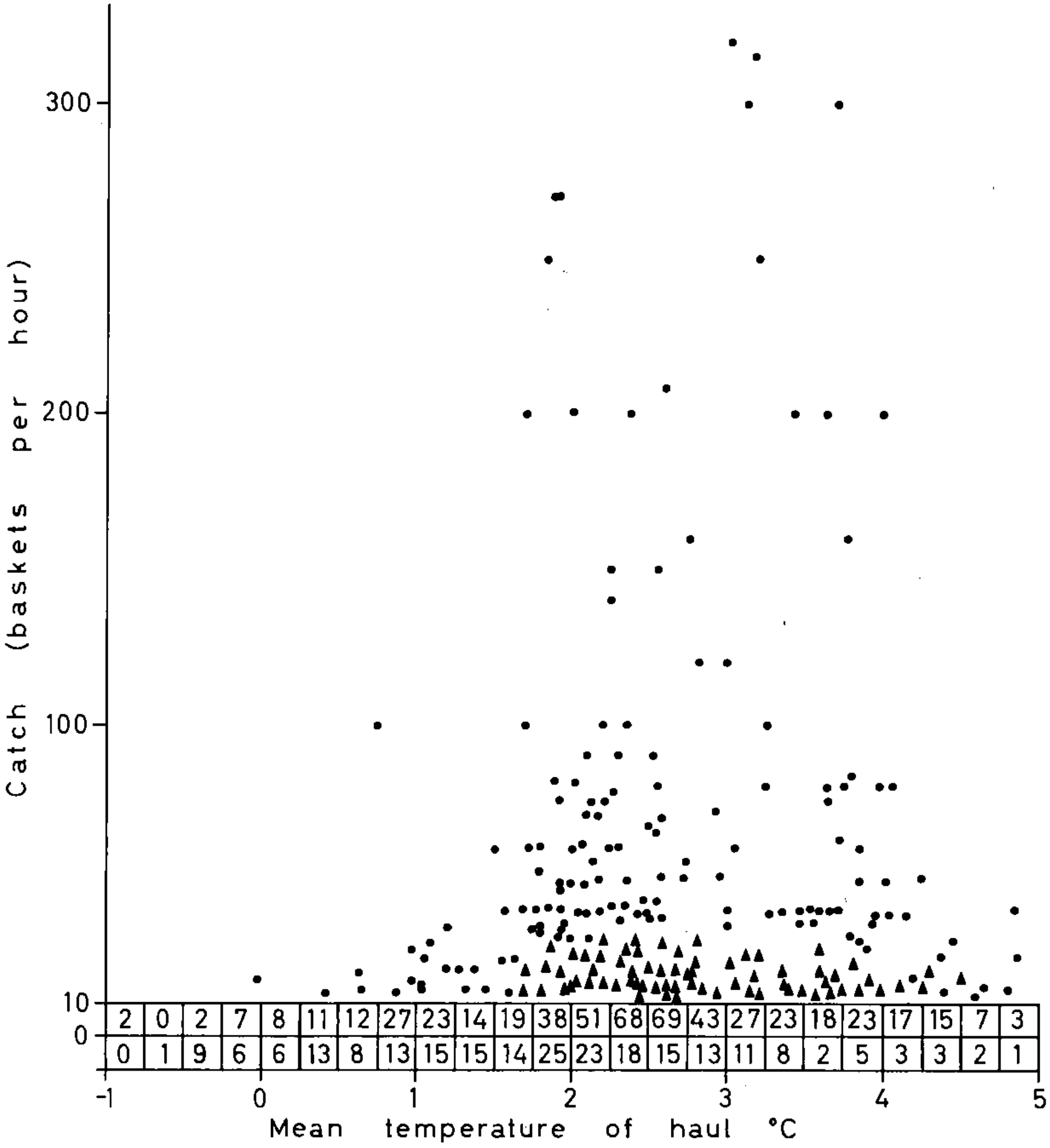

Fig. 1. Catches of cod in relation to temperature in the Barents Sea, October to June; for 1,109 trawl hauls between 1949 and 1958. The number of empty hauls for each quarter degree of temperature is shown below the zero-catch line; similarly the number of catches of cod of between 1 and 10 baskets per hour are shown above the zero-catch line. Higher catches are generally given as single points except at some of the lower levels, where it was necessary to combine similar trawl hauls in groups of three for illustration purposes; these groups are shown as small triangles.

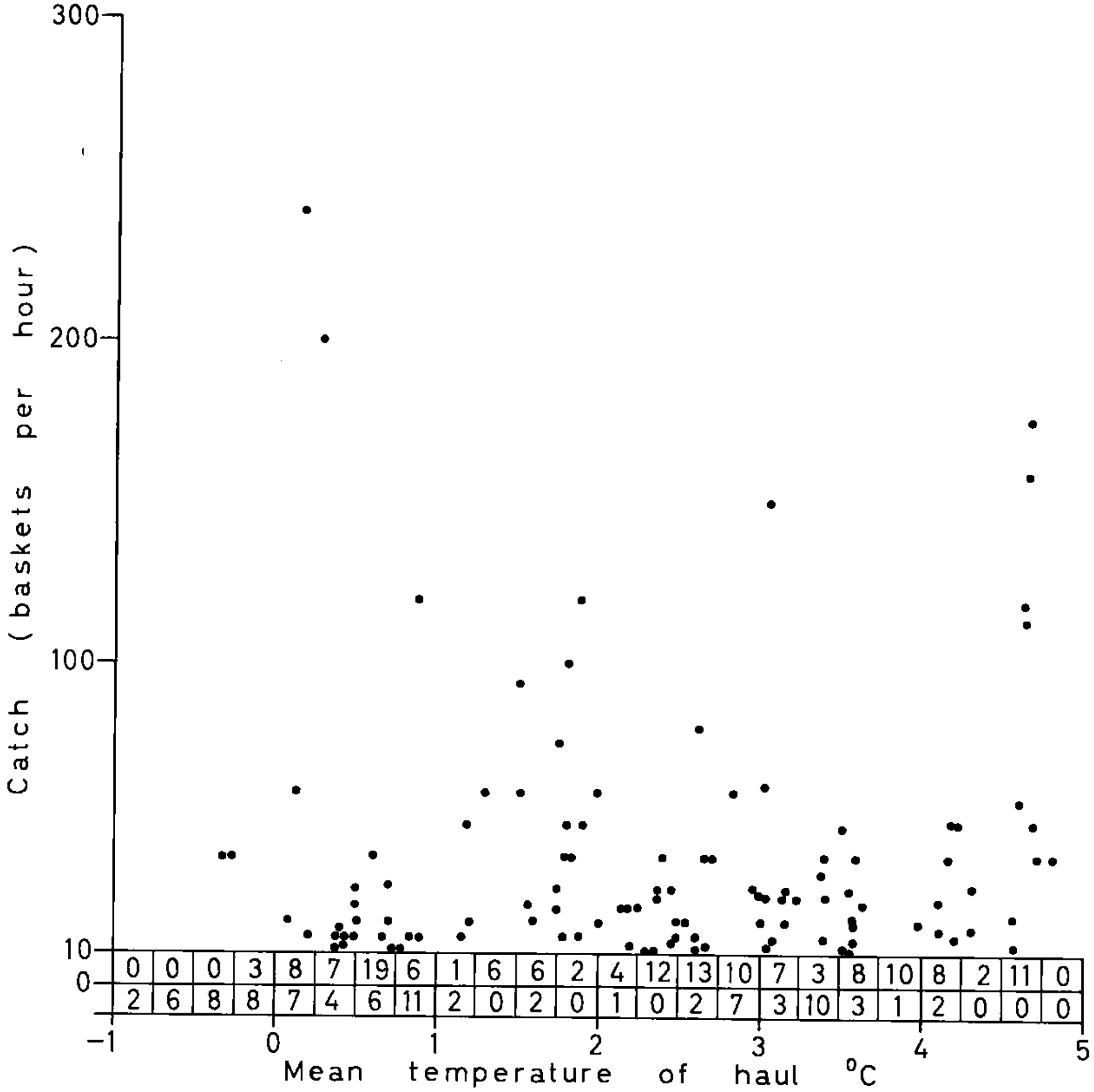

Fig. 2. Catches of cod in relation to temperature in the Barents Sea, July to September; for 342 trawl hauls between 1949 and 1958. Empty catches, and catches of 1 to 10 baskets per hour are given as numbers below and above the zero-catch line, as in Fig. 1.

analysis, shown for 342 trawl hauls in Fig. 2, in which there was no evidence of a temperature limit to catches of cod during those months, at least down to 0°C.

Although these observations on the distribution of the cod suggested a close relationship to temperature and emphasized the apparently limiting effect of temperatures below 2°C for much of the year, they did not necessarily imply active avoidance by the fish, because if the cod were associated with currents rather than with temperatures, those cod living in the waters of Atlantic origin would be found in warm waters (*i.e.* temperatures greater than 2°C), and would therefore appear to avoid the cold Arctic waters. However, in this case it might be more difficult to account for the concentration of cod at hydrographic boundaries, and for the occasional finding of very large numbers of cod in pockets of warm water almost surrounded by colder water which contained few cod (Lee, 1952; Beverton and Lee, 1964). The problem was therefore whether low temperatures exerted a direct effect upon the behaviour or physiology of the cod.

PHYSIOLOGICAL EFFECTS OF LOW TEMPERATURES IN THE BARENTS SEA

We have previously considered the problem from a physiological point of view (Woodhead and Woodhead, 1959). It seemed unlikely that the cod were aggregating about a preferred temperature of 2°C since they were frequently also caught in large numbers at higher temperatures, but not at lower ones. It appeared that the cod had reached a limit at about 2°C and it was postulated that this might be the temperature limit for some physiological process. Relatively little is known of the effects of prolonged exposure to low temperatures upon the physiological reactions of teleosts, but at an incipient lower lethal temperature death of both marine and freshwater fish appears to be associated with osmotic imbalance in the blood (Doudoroff, 1942, 1945; Brett, 1952; Wikgren, 1953), and in some species the time to death may be significantly prolonged by immersing them in a solution approximately isotonic with the blood.

If the temperature limit to the distribution of the cod in the Barents Sea acted through a similar physiological mechamism, blood taken from cod caught below the limiting temperature of 2°C would be expected to show an increased salt content. Analyses for sodium, potassium and chloride, and total salt content (estimated by freezing-point depression) were all higher, on the average, in cod caught in cold water - sometimes as much as 25% higher than in fish caught at above 2°C. Typical results for plasma analyses are shown in Fig. 3. It was considered that the values for cod caught at temperatures above 2°C represented the range for fish in a normal condition of salt balance, since no differences were found between the salt content of the blood of fish caught at 2°C and at 4° or 5°C; similar levels of sodium and potassium have also been obtained for North Sea cod at 5°C and at 12°C. But for fish caught below 2°C the high values obtained suggested that many were in a state of salt imbalance, even though many of these cod were caught at only about half a degree below 2°C and only 10% of the "cold water" fish were caught below 1°C.

Similar results were obtained on a number of cruises made between October and June. However, this did not apply during the summer months, when analyses showed that there was no difference in the salt content of the plasma taken from cod caught at above and below 2°C in July and in September, even though some of these summer fish were caught at 0°C. Typical results are shown in Fig. 4 (see note for Fig. 3).

We interpreted these results as showing that during the winter and spring temperatures below 2°C exert direct effects upon the physiology of the cod, which are reflected in the disturbance of the normal levels of salts in the blood; during the summer months of July to September low temperatures do not have these effects and the cod are able to regulate their blood salt contents normally. It is suggested that these observations on the physiology of the cod afford evidence that the apparent relationship between the distribution of the cod and low temperatures is not coincidental, and it seems likely that cod avoid water below 2°C (except during the summer months), although nothing is known of the behavioural mechanisms involved.

Our view that cod caught at below 2°C, and having a high blood salt content, were in a state of salt imbalance, has been opposed by Eliassen *et al.* (1960) who repeated the observations on the Barents Sea cod, with similar results to our own, showing a higher salt content in blood from fish caught below 2°C than from above 2°C. But they considered that the hypotonicity of the blood was largely maintained, and that the higher salt content in the blood of cod caught at temperatures below 2°C simply indicated a "small shift in osmolarity" in adapting to a lower temperature. In support of their hypothesis, Eliassen *et al.* (1960) presented data from experiments slowly acclimatising *Cottus scorpius* L., to a temperature of -1.5°C, showing that after two or three weeks at this temperature most of the fish had survived, although the plasma freezing point depression had increased by about 25% (compared with plasma from *Cottus* at 4.5°C). They considered that "some new kind of balance must have been acquired". *Cottus* is a Norwegian shore fish and it might be expected to have a greater resistance to low temperatures, but Leivestad (1964, this symposium) has now shown experimentally that cod can also tolerate prolonged exposure to a temperature of -1.4°C, and that they have an elevated blood salt content under these conditions. It is therefore quite possible that the cod in the Barents Sea may adapt to a higher level of blood salts at temperatures below 2°C, although we had previously supposed that prolonged exposure to such low temperature conditions might be lethal.

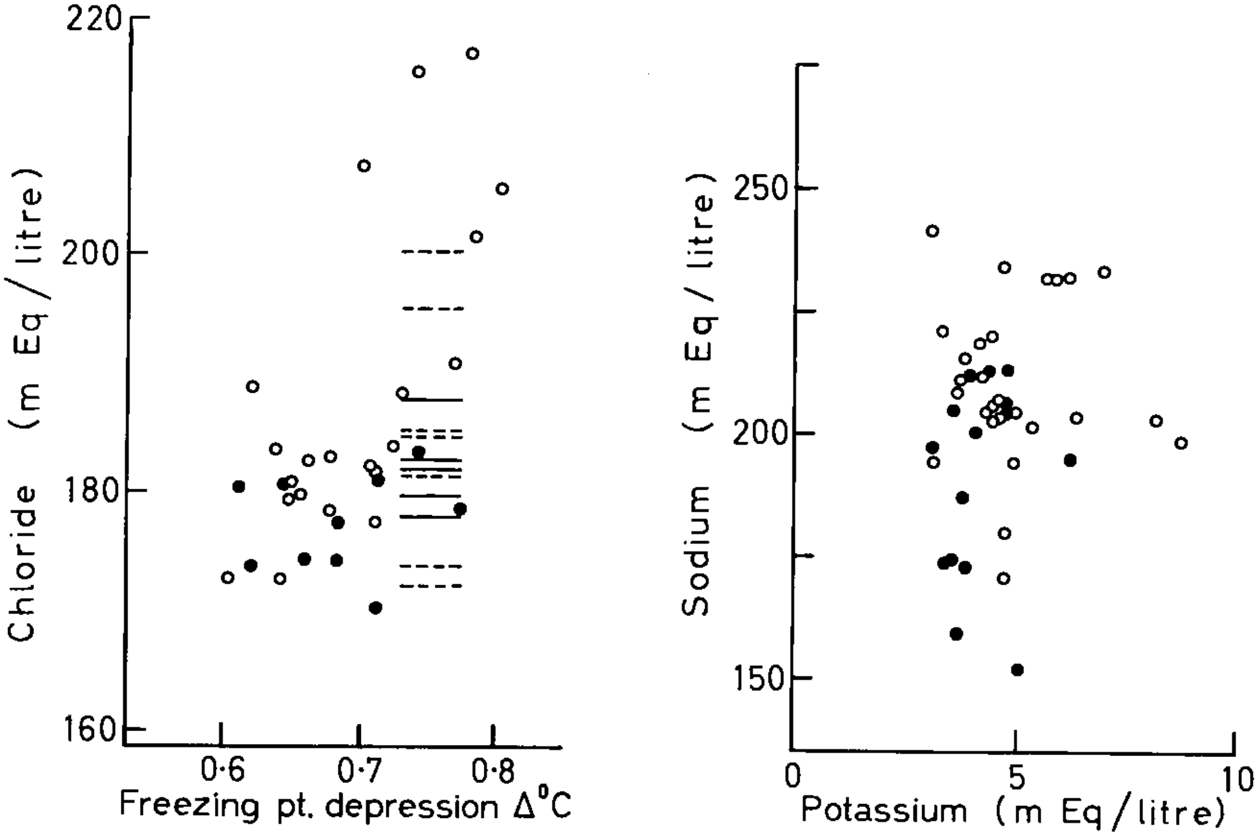

Fig. 3. Plasma salt contents of cod caught above and below 2°C in the Barents Sea, June, with cod distribution limited at 2°C.

● = Cod caught above 2°C
○ = Cod caught below 2°C
——— = Cod caught above 2°C, chloride analysis only
- - - = Cod caught below 2°C, chloride analysis only.

N.B. The values given for plasma chloride and freezing-point depression in Figs. 3 and 4 are different from those previously reported by us (Woodhead and Woodhead, 1959). It was found that the earlier results covered rather different ranges to those reported by other workers. The results were therefore re-checked against new standards and it was discovered both that the freezing point thermometer was inaccurate and that the chloride standardisation has been incorrect; the corrected values are presented here. It must be emphasised that these corrections in no way affect the arguments or conclusions previously drawn, since the discussions were based upon the direct comparison of results from cod caught at different temperatures, and the same methods and equipment were used throughout the investigation. The present corrections will allow the results to be compared with those for other fish.

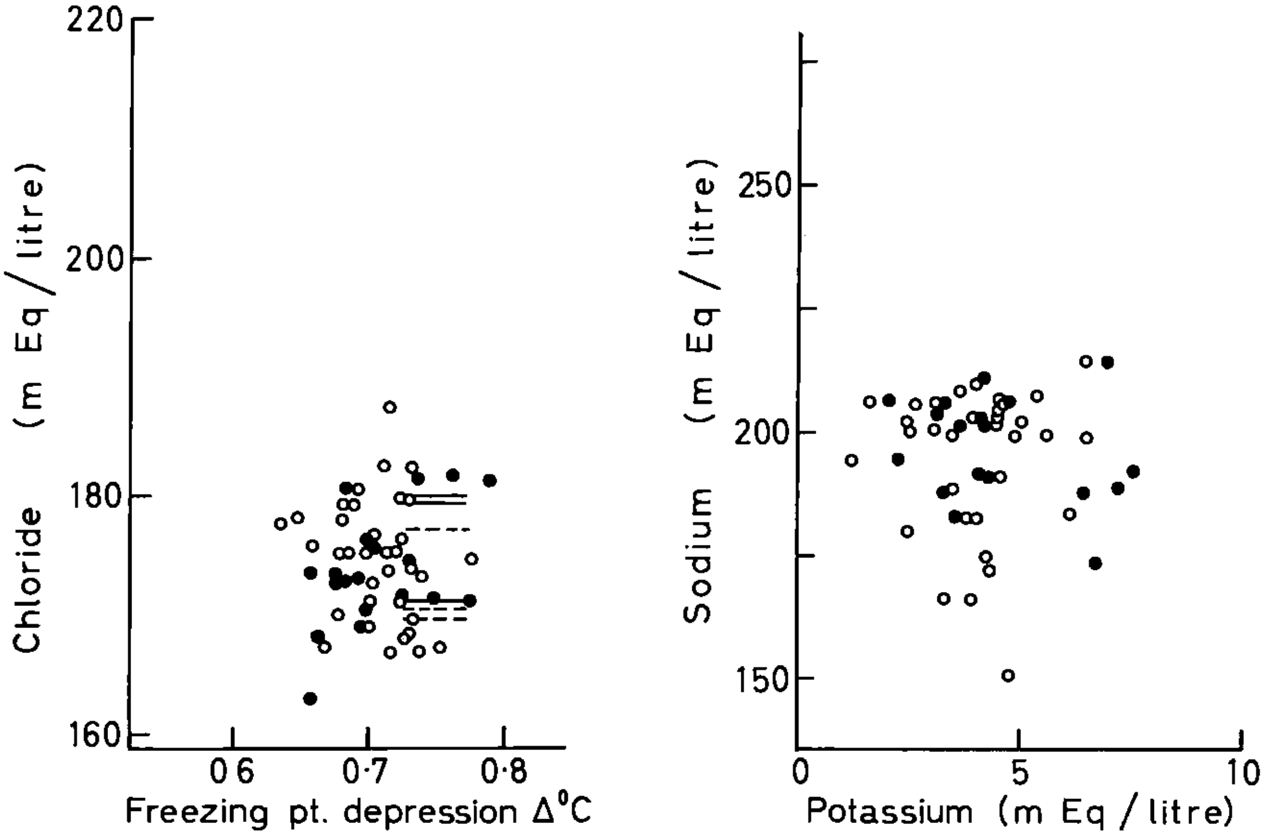

Fig. 4. Plasma salt contents of cod caught above and below 2°C in the Barents Sea, July, with cod distribution <u>not limited</u> at 2°C.

Symbols and note as for Fig. 3.

COD AT LOW TEMPERATURES IN THE NORTH SEA

During the severe winter of 1947 very cold waters extended out from the shallow continental coasts of the North Sea, and cod were concentrated along the edge of the cold water mass and provided large catches for trawlers (Simpson, 1953), thus reproducing conditions regularly encountered at Svalbard. In the cold winter of 1963 temperatures again fell exceptionally low, and a heavy cod fishery developed in the German Bight as the cod were concentrated by the advance of cold waters formed in the coastal areas; Danish fishermen caught about 1,000 tons of cod in this area compared with a normal catch of 200 tons (personal communication, Jørgen Møller-Christensen, Charlottenlund).

In view of our earlier studies it was considered of interest to examine the blood-salt content of cod caught at low temperatures under these exceptional conditions in the North Sea. A series of 89 serum samples was collected in March 1963 from cod caught at temperatures between 4° and -0.3°C, and in Fig. 5 the serum sodium values for these fish have been plotted against the mean temperatures of the trawl hauls.[3] For comparison with these winter serum samples the range, mean, and standard deviation for a further seventeen samples, collected in a similar manner, from North Sea cod caught in the summer at between 12° and 14.5°C have also been included in Fig. 5. It can be seen from this figure that increasing numbers of North Sea cod caught below a temperature of about

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[3] The blood was taken from the caudal artery into a chemically clean plastic tube and allowed to clot. It was intended to decant the serum for frozen storage, but due to some misunderstanding the whole clotted samples were frozen; this treatment later caused considerably haemolysis of fragmented red corpuscles on thawing, and denatured proteins were precipitated (Woodhead, 1964*b*). This regrettable error must have contributed to the wide scatter of results; nevertheless the serum samples from fish caught at different temperatures were directly comparable, since they were all treated in the same manner.

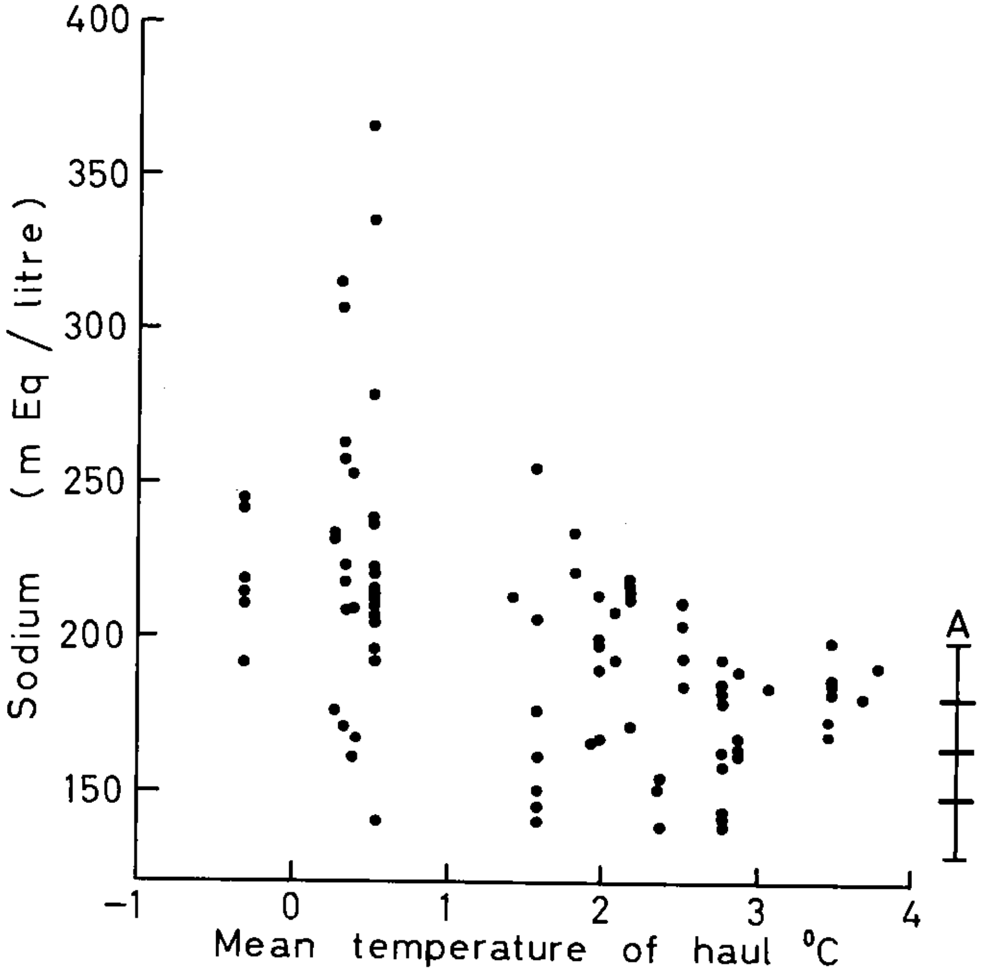

Fig. 5. Serum sodium values of cod in relation to mean temperatures of the trawl haul; North Sea in February-March 1963. The mean standard deviation, and range for 17 cod caught between 12° and 14.5°C are also shown (A).

2°C had a high serum sodium content, although the serum sodium contents of fish caught at above 2°C fell over about the same range as those of summer cod at 12° to 14.5°C. In some samples taken from cod caught at near 0°C, the sodium content of the serum was nearly double the values observed at temperatures above 2°C. These high levels appeared to be much greater than the slight shift in osmolarity suggested by Eliassen *et al.* (1960). It seemed that hypotonicity was not being maintained and that the sodium content of the blood of some of these cod was probably approaching lethal levels.

It was remarkable that during the cold winter of 1963, changes similar to those found in cod occurred in a more accentuated form in the North Sea populations of the sole, *Solea vulgaris*. Soles were heavily concentrated by the very cold waters which moved out from the shallows, and exceptionally high catches were made by trawlers (Woodhead, 1964 *c*); also, large numbers of soles were killed by cold in these areas. Analysis of serum collected from soles caught by trawl at different temperatures had increased levels of serum sodium (Woodhead, 1964 *b*). The temperature limit for normal serum sodium levels in the sole appeared to be between 3° and 4°C.

DEATH OF COD IN COLD WATERS

In our earlier paper we had assumed that if cod remained at low temperatures, below 2°C, they would finally die (except in the summer months), although this might take some time to occur. There is considerable evidence that cod are killed by low temperatures; thus Thompson (1943) reported dead cod over 20 miles in the Gulf of St. Lawrence in 1934 and concluded that the fish had been killed by encountering very cold Arctic water, and Templeman (1964, this symposium) has described similar reports for the Newfoundland area; Dannevig (1930) and Johansen (1929) have also reported the common occurrence of dead cod (and also *Pollachius pollachius* and *P. virens*) on the Scandinavian coasts during severe winters. Similarly during the winters of 1929, 1947 and 1963 large numbers of dead fish, including cod, were reported to have been killed by low temperatures in the North Sea (Lumby and Atkinson, 1929; Simpson, 1953; Woodhead, 1964*a* and *b*); in both 1947 and 1963 some dead cod were reported by trawlers in areas where temperatures did not fall below 1°C. Dannevig (1930) also reported a brief experiment in which five cod from water at 3.5°C were placed in a tank at 0.6°C which was being cooled fairly rapidly; within 20 min of being placed in the tank, when the temperature was -0.4°C, the cod appeared "agitated", and they were dead after 50 min, by which time the temperature had reached -1.0°C; however, this fall in temperature was rapid and would not allow time for acclimation, so that the results cannot be compared directly with most observations at sea.

Live cod have been frequently caught in smaller numbers many miles inside the cold water masses of the Barents Sea; often they have been in very poor condition when caught (and unfit for tagging experiments), but on other occasions they have been lively, and it is obvious that they must be able to withstand the physiological effects of low temperatures for a period of some days at least. This was investigated by an experiment in October 1957 when cod were caught and tagged in low temperatures between Hope Island and Bear Island; these fish were feeding heavily on capelin. Recaptures of the cod were all made more than one month after release and analysis of the total returns over the following six years, for fish released at different temperatures, suggested that low temperatures significantly reduced the survival rate of the cod, particularly for those fish released at 0.5°C, or less (Table 1). From this result it was thought that the tolerance of low temperatures by cod might be rather limited. In order to verify this, an experiment was made at Bear Island in October 1960 when 382 tagged cod were released at temperatures above 2°C and another 450 cod were released in areas where the bottom temperatures were about 0°C (189 of these cod were transplanted from warmer water areas before being released). The returns of tagged cod from these experiments have not been high, and the marked differences in recaptures observed in the 1957 experiment were not repeated, the recaptures of fish released above 2°C being only 26% better than for those released at 0°C (Table 2). The cod were all recaptured more than one month after release and clearly many had survived their sojourn in cold waters. However, all cod in the area were feeding heavily on small herring at that time and there was no evidence that low temperatures were limiting their distribution; many fish were feeding within the cold water masses and chemical analyses made on their blood showed only small increases in their blood salt contents. (This is discussed in more detail below). Since the cod did not appear to be critically limited by low temperatures on these occasions, the tagging experiments were perhaps not as definitive as would at first appear, and the question of prolonged survival of the cod in cold water remains open.

TABLE 1. TOTAL RECAPTURES OVER SIX YEARS FOR TAGGED COD RELEASED IN WATERS OF DIFFERENT TEMPERATURES, BEAR ISLAND AND HOPE ISLAND, OCTOBER 1957.

Temperature °C	Number released	Number recaptured	Percentage recaptured
< 0.5	138	5	3.6
0.5 to 1.0	216	19	8.8
1.0 to 2.0	131	16	12.8
> 2.0	158	21	13.3

HISTOLOGICAL CHANGES IN COD GILLS

It has been established that extrarenal excretion plays a considerable role in osmoregulation in fish (Keys, 1931, 1933; Schlieper, 1935) and that excess ions are excreted by the gills (Smith,

TABLE 2. TOTAL RECAPTURES OVER THREE YEARS FOR TAGGED COD RELEASED IN WATERS ABOVE AND BELOW 2°C, BEAR ISLAND, OCTOBER 1960.

Number released	Number recaptured	Bottom temperature (capture and release)	Distance from 2° isotherm
15	3	+ 2.45	All caught
104	11	+ 2.30	and released
97	6	+ 2.42	at temperatures
76	4	c. + 2.45	above 2°C
Total released above 2°C, 382; total recaptures, 24; = 6.3%			
189[a]	8	+ 0.05[a]	16 miles
131	8	0.00[b]	17 miles
24	2	-0.25 to -0.66[b]	> 14 miles
106	4	-0.40[b]	> 16 miles
Total released below 2°C, 450; total recaptures, 22; = 5.0%			

[a] Fish caught at 2.4°C and transplanted to cold water before release.

[b] Fish caught and released in water about 0°C.

1930; Keys, 1931). Specialized large acidophilic cells, the "chloride-secretory cells", located in the gills close to the afferent branchial blood vessels, were first described by Keys and Willmer (1932), who believed that these cells were responsible for salt excretion. This classical hypothesis was first challenged by Bevelander (1935, 1936) who considered these cells as mucous cells, and more recently other authors have questioned whether they have a salt-excretory function (Parry, *et al.*, 1959; Holliday and Parry, 1962; Dayle and Gorecki, 1961). Despite these objections to the "chloride-secretory cell" being a site of ionic regulation in fish, there is considerable evidence showing adaptive changes in these cells when fish are subjected to salt loading (Liu, 1942; Copeland, 1948, 1950; Getman, 1950; Morris, 1957, 1960; Colombo, 1961; Vickers, 1961), suggesting that if these cells are not the actual site of salt extraction in the gills, it is probable that they have at least associated functions.

The high salt content found in the blood of cod caught below 2°C from October to July could have been due to the primary effect of low temperatures on the mechanism of osmotic regulation, or to the secondary effect of a primary lesion elsewhere. A study was therefore made of the gills of fish from warm and cold waters, in order to ascertain whether histological differences could be observed (Woodhead and Woodhead, 1959). Examination of the gills of such cod caught at temperatures below 2°C, which were known to have abnormally high blood salt contents, showed that the numbers of "chloride-secretory cells" had increased by about four to seven times above normal. Individual "chloride-secretory cells" were almost twice as large as in cod caught at above 2°C, the cells stained more deeply and showed increased cytoplasmic granulation. From their histological appearance the chloride cells appeared to be in a state of increased secretory activity, and together with their increased numbers, these changes were interpreted as being a compensatory response to the abnormally high salt content of the blood. Since there was no evidence of breakdown or exhaustion of these cells, the primary site for the effect of low temperatures would appear to be elsewhere.

Examination of the gills of cod caught in waters above and below 2°C in the summer months of July to September did not show any increased activity of the "chloride-secretory cells" in cold-water fish, except for some fish caught at between 0.26° and -0.14°C. In the latter sample, the "chloride cells" of a few fish showed some evidence of an increase in activity, although this was not marked, and was not found in all the fish; it seemed likely that these cod were beginning to approach their summer limiting temperature just below 0°C, although serum analyses showed that they were not yet in a state of salt imbalance.

The gills of cod caught below 2°C, in a state of salt imbalance, also exhibited a marked depletion of mucus, which was almost absent from the gill leaflets; the numbers of mucous cells were reduced, and those that remained were usually atrophied and discharging their contents. Muscus depletion would permit more rapid entry of salts from the environment into the circulation, and since the gills offer the greatest area of body surface of the fish to the external environment, this increase in the osmotic load on the fish could be considerable. In this way the dislocation of mucus production, either as a primary or a secondary effect of low temperature, might well be the cause of the increased salt content found in the blood.

Marked mucus depletion was not observed in the gills of fish caught in cold water during the summer months, and analyses of the blood of these fish showed no evidence of osmotic imbalance.

DISCUSSION OF THE EFFECTS OF LOW TEMPERATURES

In considering the present data concerning effects of low temperature on the cod we conclude that, on balance, the results suggest that Barents Sea cod approach or encounter a limit to normal physiology at a temperature of about 2°C (between October and June), and that this is reflected in the increased salt content of the blood of fish caught at lower temperatures. Apparently marked increases in salt content were observed in the blood of some cod caught at only 0.5° or 1°C below this limit, whereas no such changes were found in the blood of cod caught at higher temperatures of 4° or 5°C. These effects were perhaps even more clearly shown in the large collection of sera made from North Sea cod during the winter of 1963, in which increasingly high levels of serum sodium were recorded for fish caught below approximately 2°C, but above that temperature serum sodium values fell within the same range as those for summer cod caught at between 12° and 14.5°C. The magnitude of these changes in the blood, in response to only small changes in environmental temperature, suggested to us that there was an essential change in the physiology of the cod below 2°C, rather than the hypothesis of Eliassen *et al.*(1960) that the cod had simply acquired some new level of ionic balance, dependent upon temperature. This view was also supported by the marked histological changes seen in the gills of cod caught below 2°C, suggesting that the increase in blood salts had stimulated compensatory activity in the salt excretory mechanism, presumably in an attempt to regain salt balance; such changes might not have been expected if the cod were already in a new state of ionic balance. Furthermore, the cod were apparently unaffected by the same low temperatures during the summer; there were no signs of increased secretory activity in the gill epithelium, yet the fish were able to maintain a steady level of blood salts at least down to 0°C, although on the hypothesis of Eliassen *et al.* (1960) it might have been expected that some differential in level of blood salts would still have been observed at low temperatures.

The close correspondence between the details of the seasonal distribution of the cod at low temperatures in the Barents Sea and the physiological changes observed in the fish are persuasive; from comparisons of Figs. 1 and 5 it can be seen that at temperatures at which the catches of Barents Sea cod fall rapidly, the sodium content of the blood (of North Sea cod) increases. In some cases very high levels of blood salt have been observed in cod, and we have previously assumed that prolonged exposure to low temperatures might be lethal to them as was observed for North Sea soles in 1963 (Woodhead, 1964*b*). However from the fishing data for the Barents Sea, and the results of the experiments releasing tagged cod in cold water, there can be no doubt that many cod are able to tolerate the effects of low temperatures for some time, though possibly with reduced survival. Indeed, Leivestad's experiments (1964) have demonstrated that cod may even survive supercooling for some weeks in the laboratory.

The ability to tolerate low temperatures, at least temporarily, would have obvious survival advantages for cod living in close proximity to the arctic water masses. Nevertheless the results of the various fish surveys have consistently shown that relatively few cod were normally found at low temperatures, except during the summer feeding period. We consider that the fact that cod have been shown to tolerate very low temperatures after acclimation in the laboratory need not conflict with our view that in the Barents Sea cod undergo a change in their normal physiology at low temperatures, - at about 2°C from October to June and 0°C or lower during the summer. The important questions of how long cod are able to tolerate low temperatures in the sea, and whether some form of acclimation can finally be acquired under these conditions (as occurred in Leivestad's experiments), remain at present unanswered.

SEASONAL CHANGES IN REACTIONS TO LOW TEMPERATURES

The results of the serum analyses showed that the effects of low temperature changed during the year; similar seasonal changes in physiological reactions have frequently been shown in cold-blooded vertebrates (Wells, 1935; Precht, 1955); in particular, changes have been reported in the thermal tolerance and osmoregulatory ability of fish (Koch and Heuts, 1942; Brett, 1946; Hart, 1952; Hoar, 1955; Hoar and Eales, 1963). Such variations can occur independently of seasonal changes in temperature and may be related to activity of the endocrine glands, or to the nutritional history and condition of the fish, or may be part of the growth processes. The experiments of Hoar (1955, 1956) are of some interest in this context; he showed marked seasonal variations in the ability of goldfish to withstand low temperatures although kept under constant nutritional and thermal conditions. He was able to induce similar changes experimentally by keeping goldfish under different conditions of daily illumination, and concluded that the differences in thermal tolerance were due to photoperiodically controlled changes in endocrine physiology. Possible causes of the seasonal variations observed in the Barents Sea cod are considered below.

Nutritional condition

A number of experiments have shown that thermal tolerance in fish may be increased by different diets or decreased by starvation (Ellis, 1947; Hoar and Dorchester, 1949; Hoar and Cottle, 1952; Irvine, *et al.*, 1957) and there is evidence that starvation may also affect the ability of the cod to tolerate low temperatures. On the Svalbard grounds cod frequently have little food available during the winter and spring (Trout, 1957), and are usually in very poor condition by the end of May; they are then thin and weak, the skin is flaccid, the liver small and highly discoloured with bile pigments. With the heavy summer feeding the fish regain condition rapidly; they become firm and smooth to the touch, brightly coloured and very lively when caught, and at the same time high catches of cod may begin to be made also below 2°C. It seems that the cod must begin to feed heavily before they regain the ability to withstand temperatures below 2°C. In the autumn, on the other hand, when the fish lose this ability they are in good condition after the summer feeding and may still be feeding well, so that there does not appear to be a direct link with starvation at that time; it seems likely that changes in endocrine physiology are involved.

However, on a cruise made in October 1960, large numbers of cod were found to the south of Bear Island feeding heavily, their stomachs being packed full of young herring, at temperatures both above and below 2°C. Analyses made on the blood taken from these fish showed that of 32 plasma samples taken from fish caught at 0°C, 21 had plasma sodium values which fell within the range for 12 control cod caught between 4° and 5°C. Although the complete sample of cod caught at 0°C had a significantly higher mean serum sodium content than the 12 control fish (Table 2), the mean difference between these fish and the cod from higher temperatures was less than 4%, a much smaller difference than would have been expected from our previous analyses for Barents Sea cod and for North Sea cod, at 0°C. These results were surprising when compared with similar analyses made on the blood of cod caught in October 1954 and 1955, when the cod were more obviously affected by temperatures just below 2°C, and it would seem that the cod were better able to tolerate low temperatures when feeding heavily on other fish (which would form an iso-osmotic food). If this were generally the case, the possibility would arise that cod might occur in large numbers at temperatures below 2°C at any time of the year when abundant food was available, although this laboratory has not observed this to actually occur during our own work in the Barents Sea; indeed in early spring of 1954 cod were feeding south-east of Bear Island, yet did not enter cold water although this was only a few miles away (Beverton and Lee, 1964, this symposium).

Endocrine changes

The maintenance of a constant internal ionic milieu involves the coordinated activity of many endocrine glands; several of these have been examined in the cod and are described elsewhere at this symposium (Woodhead and Woodhead, 1964). Some changes which may be related to the seasonal changes in temperature tolerance are discussed briefly here.

Gonads:

It seems unlikely that gonadal secretions, or the onset of maturation, were responsible for the seasonal changes, since the effects occurred in both immature, juveniles and maturing adult cod.

Thyroid:

Activity of the thyroid gland, and treatment with thyroid hormones and inhibitors, have been shown to significantly change the tolerance of low temperatures in goldfish (Hoar, 1955; Hoar and Eales, 1962) and it was thought likely that thyroid activity might similarly affect the physiology of the cod. The thyroid became active at the end of September, agreeing well with the development of the 2°C limit in October, but thyroid activity had declined in most immature cod in February, and in adults by the end of March (Woodhead, A.D. 1959), although the cod did not regain their ability to enter cold water until some two or three months later. (However, in the spring starvation may be a complicating factor, as discussed above.) Thyroids from fish caught at above and below 2°C showed no significant differences in histological appearance and we previously concluded that the results "neither prove nor disprove that the thyroid gland itself is directly involved in the changes in the resistance of cod to low temperatures" (Woodhead and Woodhead, 1959).

Interrenals:

Histological evidence of secretory activity became apparent in November, some weeks after the development of the 2°C limit. This would appear to rule out interrenal activity as controlling the seasonal changes. However, the onset of the 2°C limit may be less precisely timed than previously assumed (as shown by the cod feeding at 0°C in October, 1960, discussed above). Interrenal activity continued into the spring and appeared to be associated with poor feeding or starvation, which was certainly a complicating factor in the seasonal changes. Both cortisol and deoxycorticosterone may strongly affect the rate of sodium excretion through the gills of freshwater fish under a sodium load (Holmes, 1959), and the interrenal might therefore be involved in the changes observed in the cod; more critical evidence may be obtained when the interrenal analysis is completed.

From these results it can be seen that we have not found a close correspondence between the period of secretory activity of a particular endocrine gland and the seasonal changes in thermal tolerance in the cod. Perhaps this is not surprising since endocrine regulation of physiological changes is frequently complex and the integrated activity of several glands may be involved. That endocrine changes occur in cod during the autumn, at about the same time as the changes in the effects of low temperatures, is demonstrated by the activity of the thyroid gland (and of the gonads in adult fish), but it seems likely that the final understanding of which gland, or glands, are responsible for such changes can finally only come from experimental studies in the laboratory.

EFFECTS OF LOW TEMPERATURES UPON O-GROUP AND I-GROUP COD

Since low temperatures may have a limiting effect upon immature and adult cod, it seemed quite probable that they may have similar effects upon the cod larvae and O-group fish. Several authors have suggested that the recent climatic warming in northern latitudes has been accompanied by an increase in size of cod stocks, both in the Barents Sea and at Greenland (Tåning, 1953; Lee, 1956; Hill and Lee, 1957), and this might be accounted for in part by there being a greater area of the shelf feeding grounds over which temperatures were above the limiting threshold of the young cod, allowing successful settlement from the pelagic phase to the bottom, and increased survival. Tåning (1953) and Jensen (1939) have reviewed evidence for higher sea temperatures at West Greenland, and Blacker (1957) and Nesis (1960) have produced biological evidence which strongly suggests that warm Atlantic water now covers much greater areas of the banks in the Barents Sea.

The observations of Hermann at Greenland (Hachey, *et al.*, 1954; Hermann, *et al.*, 1964, this symposium) have shown that in years when temperatures fell below 1.8°C on the Fyllas Bank (where cod larvae were found) only poor year-classes survived, but in years of higher temperatures much stronger year-classes resulted. However catches of large numbers of very small cod have been made at sub-zero temperatures off Newfoundland (Templeman and Fleming, 1964, this symposium).

To investigate the temperature tolerance of young cod, blood analyses were made on O-group and I-group cod caught in a shrimp-mesh covered trawl fished south of Bear Island at depths of about 200 m in October 1960. (This heavy gear obviously is poor for capturing small fish for physiological work, since they are easily damaged.) Analyses for sodium content in haemolysed whole-blood samples showed no significant differences in the levels of sodium in the blood of either O-group or I-group fish taken at 0°C, when compared with control fish taken at about 2.5°C (Table 3), suggesting that

TABLE 3. PLASMA SODIUM CONTENT FOR FEEDING COD[a] CAUGHT AT ABOVE AND BELOW 2°C, BEAR ISLAND, OCTOBER 1960.

Temperature	Plasma Sodium (m Eq./litre)	Significance p
12 fish; 4 to 5°C	210.8 ± 5.8	Significant difference p =< 0.01
32 fish; 0°C	217.5 ± 7.2	

[a] All cod (above and below 2°C) were immature fish, 50 to 80 cm long.

TABLE 4. BLOOD SODIUM CONTENT IN O-GROUP AND I-GROUP COD FROM LOW TEMPERATURES BEAR ISLAND, OCTOBER 1961

Group	Number of fish	Blood Sodium m Equivs	Significance p
0-group, 2.5°C	26	211.2± 28.7	Not significant
0-group, 0°C	23	216.3± 24.5	p= approx. 0.5
I-group, 2.5°C	14	195.6± 27.3	Not significant
I-group, 0°C	18	192.4± 25.1	p= approx. 0.5

the small cod were able to tolerate the low temperatures. However, we would emphasize that our analyses were made on only the one cruise, and on the same cruise only small differences were observed in blood salts of adult cod caught above and below 2°C; the evidence for low temperature tolerance would have been more convincing had it been shown that the older cod were affected by temperatures when the young fish were unaffected. We present these results as being of considerable interest, but would hesitate to draw far-reaching conclusions. concerning post-larval survival and distribution until more work has been done.

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F-7

FACTORS DETERMINING OR LIMITING THE PHYSIOLOGICAL REACTION OF HERRING TO ENVIRONMENTAL CHANGES

By

T.D. Iles[1]

ABSTRACT

The variation in the seasonal timing of zooplankton production over the range of herring stocks is much smaller than that of the spawning times and there can be no simple relationship between food availability, representing a variable environmental factor and the seasonal cycles of growth maturation and spawning.

Data from North Shields herring indicate that rapid seasonal somatic growth precedes rapid gonad growth and from other stocks and for sprat, that these processes do not go on at the same time of year. The Shields data confirms Holliday's work by demonstrating the acceleration of the gonad growth resulting from pituitary gonadotrophic activity, and the prolongation of stage V in some herring stocks indicates that the timing of the production of luteinising hormone controlling ovulation may differ considerably in its relation to the timing of the gonadotrophic activity of the pituitary. It follows that the reaction to changes in environmental factors, which might affect growth, maturation and spawning, may depend on the way in which they are mediated by the hormonal cycles.

The use of partial condition factors in defining seasonal fat, water and protein cycles, reveals new information and the significance of the fat cycles in these terms is discussed. It is suggested that in Shields herring an earlier physiological stage during which protein provides energy for all purposes, coincides with that of rapid food intake and somatic growth. Later the fat reserves are mobilised to provide energy and the protein is conserved to allow overwintering. This physiological arrangement is part of the adaptation to feeding on zooplankton, which is available in abundance for only a short period each year.

THE ORGANISATION OF GONAD AND SOMATIC GROWTH IN HERRING

The changes in the environments of the herring that occur during the course of a single year are greater than the changes for the same season from year to year, for almost all of the environmental factors. During the first 50 years of this century, for instance, the seasonal temperature range in the North Sea, about 9°C, was more than twice the range of either the winter minimum or the summer maximum (ICES tables 1962), and similar conclusions could be drawn for such changes in food abundance and many other factors both physical and biotic. A particular herring stock reflects its adaptation to the seasonal changes by undergoing parallel or related physiological changes, indicated by variation in feeding and growth rates and in maturation, migration and spawning cycles; hence, the study of the physiological processes underlying these cycles is, essentially, a study in the adaptation of the population to its environment.

In the last decade marked changes have been recorded in important European herring stocks, involving, for example, increases of growth rate of the East Anglian herring, and in the Norwegian winter herring changes in the mean spawning time and the location of spawning grounds, in both cases accompanied by decreases in stock abundance.

It is unlikely that the biological changes associated with these events can be unequivocally correlated with environmental factors until more is known of the organisation and control of the relevant seasonal cycles, and as herring fisheries are typically restricted to short periods during the year the amount of detailed knowledge of the timing of quite basic processes, such as somatic growth or gonad maturation, even in important stocks, is not great.

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One of the most important seasonal variables is that of available food; the zooplankton on which herring feed is available reliably and in quantity for only a relatively short time of the year and its abundance is determined by the primary production cycles. The timing of these cycles varies over the whole range of the Atlantic herring (Colebrook and Robinson, 1960), but although this variation is, between extremes, quite large, it is small compared to the range of spawning times shown by the different spawning communities. Spawning herring can be found at any time of the year and moreover at any time relative to the zooplankton production cycle, either before it (for example the Channel spawners or the Norwegian spring spawners), during it (Icelandic summer spawners, Jakobsson, 1962) and Onega herring,(Mikhailovskaya, 1957) or after it (Dogger autumn spawners of central North Sea). It follows that no simple relationship exists in the herring between feeding and the time of spawning. If we consider somatic growth we find for Norwegian immature herring that seasonal somatic growth begins at a time when the temperature, although beginning to rise, is near the seasonal minimum, and that the rate of growth declines sharply before the highest seasonal temperature is reached (Lea, 1911). This is indicated also for maturing herring of the North Sea in Fig. 1 below, so that we can assume also that somatic growth and environmental temperature are not simply related.

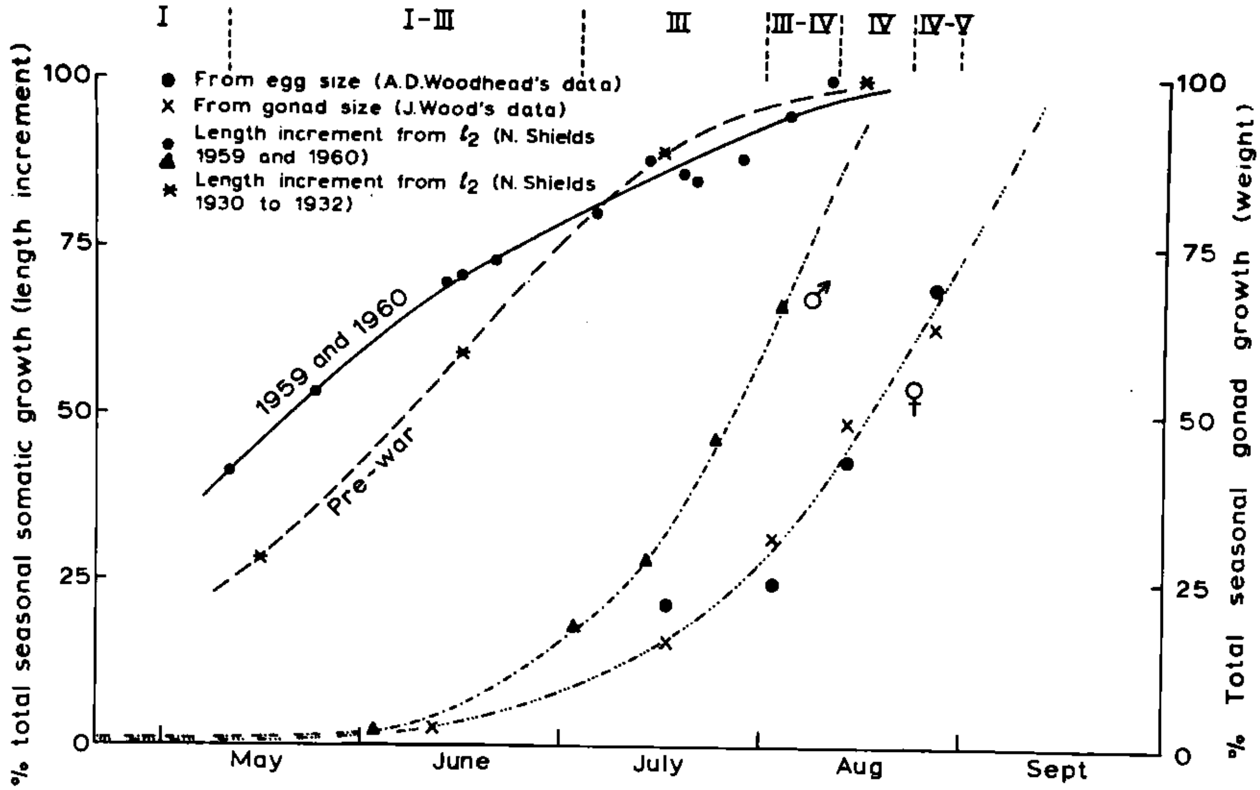

Fig. 1. Seasonal gonad and somatic growth, North Shields herring.

Recent work at the Lowestoft laboratory has concentrated on the time relationships between somatic growth and gonad maturation in relation to feeding and to spawning times, and Fig. 1 illustrates the somatic and gonad growth cycles for herring caught in the North Shields area from May to September in the 1950's.

The somatic growth was determined by back calculation on scale readings (Lea, 1911) and gonad growth from data on the distribution of maturation stages (Iles, 1964) converted to durations for individual stages. The gonad data for males and females have been dealt with separately to illustrate the growth differences between the sexes first suggested by Holliday (1962).

The point to be emphasized is that the period of rapid somatic growth does not coincide with that of rapid gonad growth, and Fig. 2 (compiled from data available for the 1920's and 1930's when the growth of the North Sea herring differed significantly from that found in the 1950's) gives substantially the same picture. (The data in Fig. 2 are based on Hodgson (1924) and on maturation data for the period 1924-28 collected at the Dove Marine Laboratory at Cullercoats and kindly made available by the Director).

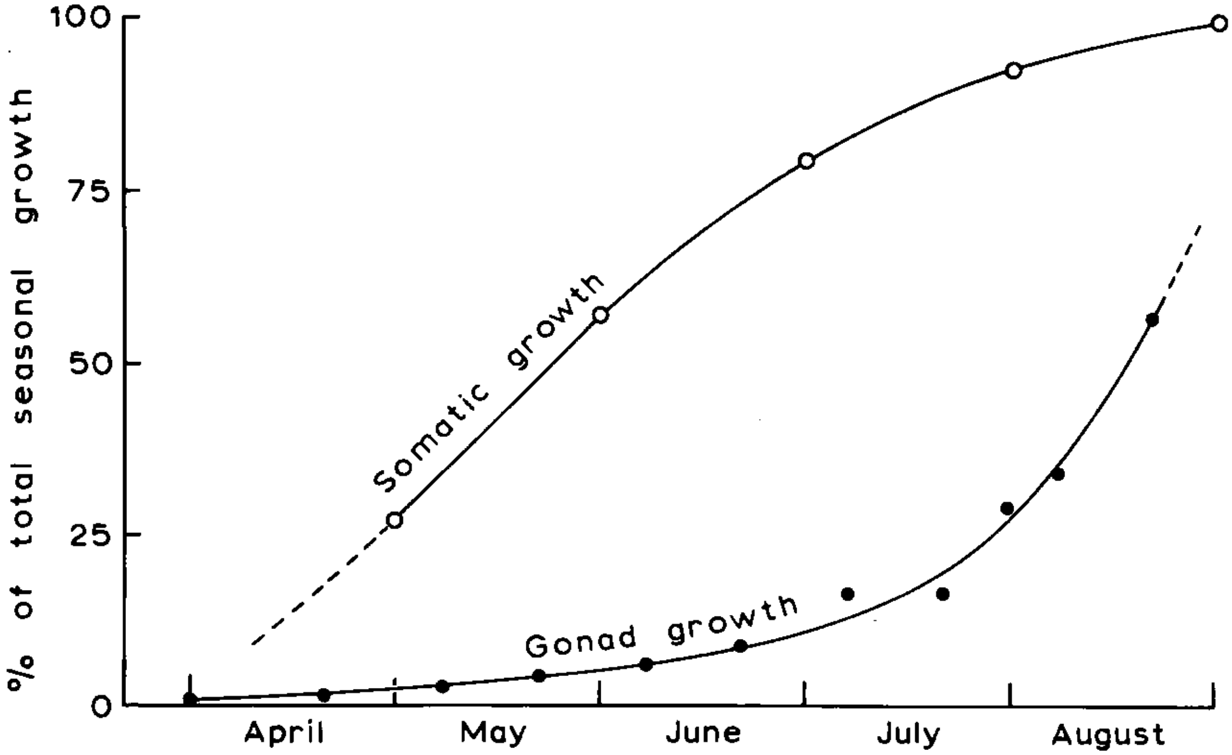

Fig. 2. Seasonal gonad and somatic growth, pre-war period.

Comparative data for other herring stocks are difficult to find, but we do have the observations of Mikhailovskaya (1957) on the herring of the Gulf of Onega, which spawn from late May to July. Mikhailovskaya states that the herring begin to feed at about the end of April, which coincides with a time of "intensive development of the gonads", and do not feed during the spawning period. It is not until July and August, after spawning has taken place, that the zone of growth is observed on the scale, this coinciding with a period of intensive feeding. Elwertowski and Maciejczyk (1960), in their study of the adult sprat of the Gdansk Bay, state that feeding in the spring (May and June) is "rather intensive" but is not "accompanied by an increase in length" due to the fact that "the sprat organism is developing the reproductive organs exclusively". The end of the spawning period in July is marked by the beginning of an intensive feeding period, as a result of which the body length increases and fat is accumulated.

Now, Holliday (1960*a*) distinguished two phases in the maturation of the herring gonad, the first being dependent on adequate feeding conditions and occurring in the absence of pituitary gonadotrophic activity, and a later stage (during which most of the increase in gonad size occurs) coinciding with increased pituitary gonadotrophic activity. These two phases are demonstrated in Fig. 1, which also confirms Holliday's suggestion that the effect of the pituitary gonadot ophin is to accelerate gonad growth. It would appear therefore, from Fig. 1 and 2 and the observations on the Onega herring and Gdansk sprat, that rapid somatic growth and pituitary-stimulated gonad growth do not usually go on simultaneously, and if it be accepted that somatic growth in fishes generally is controlled by a pituitary growth hormone (Holliday, this symposium) then it must be accepted also that differences between herring stocks in the seasonal timing of somatic and gonad growth can be related to and influenced by differences in the cycles of production of two distinct pituitary hormones. Any change in growth rate or in maturation rate resulting from environmental changes must therefore be effected via changes in two pituitary hormonal cycles which, although probably interconnected, do not necessarily react in the same way at any one time.

The position is complicated by the demonstration (Holliday, 1960 *b*) that the process of ovulation in the female herring, and the shedding of gametes for both sexes, is under the control of another pituitary hormone, the luteinising hormone, and it is well established for fishes in general that the release of this hormone may depend on the action of environmental factors other than those ultimately responsible for the production of gonadotrophic hormone. That this applies to herring is indicated by the fact that, in some herring stocks, stage V, at which the gonad has been provided with all the necessary proteinaceous materials and at which maturation in terms of gonad growth can be said to be completed, may be prolonged and therefore not followed immediately by spawning. This applies to the Manx stock of autumn spawners, for instance, and also to the winter spawners sampled in the East Anglian fishery (Iles, 1964). In one respect at least it probably applies to most herring stocks, for Jakobsson (1962) shows that in both Icelandic spring and summer spawners the males mature earlier than the females; this is also shown by the data presented by Bowers (1963) for the West Coast Manx herring. This phenomenon is demonstrated quantitatively in Fig. 1 and it must be accepted therefore that the time relationships between maturation and spawning differ between males and females for many and perhaps all herring, in that maturation takes place at different times but spawning, presumably, is synchronised.

These considerations strongly suggest that changes in growth rates, maturation rates and spawning times in herring, resulting from environmental changes, are mediated through complex hormonal cycles and that in any given stock the different physiological processes may, at any particular time of year, be "sensitised" to a greater or lesser degree and therefore be more or less able to react. It is possible, for instance, to postulate that in a particular year the spring outburst of zooplankton in May would be markedly greater than usual, both for the Onega herring and for the Shields herring. It is unlikely that the physiological reaction would be the same in both stocks as far as the growth and maturation cycles are concerned.

GROWTH AND FAT CYCLES IN HERRING

A particular seasonal cycle in herring which has been investigated in some detail is the fat cycle, and Wood (1958) lists the important work of the last 50 years or so.

The ability to store fat in large quantity to tide the herring over the long period when food is not available is a necessary part of the adaptation to feeding on zooplankton. Wood (1958) describes fat cycles for North Sea herring and shows the marked seasonal variation in percentage fat in whole herring, rising to a peak by the end of June and falling thereafter to low values during the winter; the overall relationship between the fat cycle and the feeding cycle is close (Savage, 1931 and 1937 for the timing of the feeding cycle in North Shields herring).

Many workers have drawn attention to the inter-relationships in herring between fat and water percentages, Brandes and Dietrich (1953), for instance, recording an inverse relationship with a high degree of correlation for herring muscle; and Wood (unpublished data), for whole herring, finds correlation coefficients as high as 0.997. Blaxter and Holliday (1963) suggest that this linear relationship is in fact artificial, resulting from the expression of fat and water content as percentages. Wood's extensive original data are available and they have been re-calculated to yield not percentages, but what may be called *partial condition factors* for fat and water, by expressing the weight of each of the two constituents as a proportion of the cube of the length. These partial condition factors are in fact concentrations and their use as indicators of fat and water content (and by implication, of gross protein content) has revealed interesting information concerning the physiological changes occurring seasonally in herring. Thus although during May and June the *water percentage* of individual herring falls from about 78 to below 60%, the *water condition factor* if anything rises. The "water" content of herring therefore changes seasonally much less than is indicated by percentages. Again, and comparing the cycles for different years, there is relatively little difference between the maximum fat percentages recorded. For herring caught in the North Shields area, for example, 1956 gives a near maximum *fat percentage* in July of 22.3% and 1957 one of 23.58%, a relative increase of rather less than 6%. The difference in *fat condition factor* for these years is much greater, the value for 1956 being 187 units and for 1957, 232 units, an increase of 22%. The importance of these observations lies in the fact that 1956 was, for the herring investigated, a relatively poor year for growth, whereas 1957 was a relatively good one (Burd and Cushing, 1962), a fact not reflected obviously in the fat percentage cycle but shown clearly in the condition factor cycle. Dementjeva (1956) dealing with growth of the salaka (the Baltic herring), which varies widely from year to year, comments on the poor growth of 1952, although her figure 6 indicates that the maximum fat percentage was as high as that of 1953. It is important, therefore, in describing seasonal changes in the composition of herring, to use units which reflect quantitative and not proportional changes.

It was consideration of facts such as these that led to the suggestion (Iles, in preparation[2]) that there is a limit to the percentage of fat that can be accumulated by the herring and that this may, in certain circumstances, limit growth by preventing further food intake; such little information as is available suggests that the fall in feeding intensity for North Shields herring recorded by Savage (1931, 1937) from May to July is not related to total food abundance. Thus figure 20, p. 45 (Savage, 1931) relating both numbers and volume of food in the stomachs of herring, on the one hand, and in the sea in the feeding area, on the other, indicates that during June, when fat is increasing in both percentage and condition factor, the intake of available food falls rapidly. More recently Bowers (personal communication), referring to Manx herring in 1962, stated that herring stomachs were virtually empty in July although zooplankton was still available. None of this evidence can be considered as proof that fat is a limiting factor for somatic growth, but it does indicate the possibility that appetitive factors may regulate food intake at certain times independently of available food, and if it is true that spawning Onega herring and Gdansk sprat stop feeding during the spawning period these would be other similar examples.

There is a final point to be made concerning seasonal growth. The period of rapid somatic growth rate in May and June is one of intensive protein metabolism. Now, Gerking (1954) and Menzel (1959), and others, have shown that in adult fish the conversion rate of food protein to growth protein is low, of the order of 20%, and perhaps for older fish even lower. It follows that the energy value of that portion not incorporated in new tissue is high. A herring recruiting for the first time as a 3 year old to the North Sea stocks will for instance increase its weight by about 20%, representing a protein uptake of something like 100% of its initial weight.

It is contended that the energy available from the 80% not incorporated as permanent growth will be sufficient for all energy requirements. This being so, the fat which is being assimilated at this time, for the rate of increase in fat content is most marked in May and June, is neither needed nor in fact used as an energy source. Now, Lovern's (1951) work on fat assimilation and metabolism indicates that during the time of rapid food intake fat is not an important metabolite, being laid down in the herring almost unchanged, which would fit well with the hypothesis. Another point to be mentioned is that the loss of fat is not marked until after July in North Shields herring (Wood, 1958, figure 3). Other workers on fat cycles in herring have usually associated the fall in fat levels with the time when final maturation of the gonad is going on or spawning is imminent. This is often interpreted as indicating that fat is used for gonad maturation, but the facts do not support this contention, for the amount of fat measured in ripe gonads is usually small, of the order of 3%, and this in terms of the total body weight is less than 1%, which is too little to account for the fall in fat content recorded over the maturation and spawning period. What is more likely is that the end of the somatic growth period, which coincides with the increased maturation rate, marks the end of a stage when protein is available for energy requirements and throws the herring back on to its fat reserves. While the herring is actively feeding and growing the fat reserves are shielded by a reliance on protein for energy, and while the gonads are maturing, during the spawning period, and during the long winter starvation period, the protein is shielded by the fat reserves; it is suggested that here is a key factor in the adaptation of the herring to feeding on zooplankton, subject to marked seasonal fluctuations in abundance.

A link-up with the basic hormonal cycles referred to above is achieved if it is assumed that the pituitary growth hormone phase is associated with the reliance on protein for energy, while subsequent stages are characterised by the use of energy derived from the oxidation of fat.

The herring is remarkable for the fact that although it produces a relatively large amount of high protein content gonad each year (about 20% of the weight of the fish) which in many stocks is

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[2] Report of Challenger Society Meeting held at Lowestoft, October 1963.

deposited towards the end of the relatively short feeding season, and although it undergoes annual migrations which may be very extensive, it has a relatively low natural mortality; neither migration nor spawning appears normally to be accompanied by the heavy mortalities such as occur, say, in salmon. The reproductive drain in herring is large and yet it does not, apparently, run down the essential protein of the body to a non-viable level. This indicates a high degree of adaptation, which in turn implies a level of seasonal control and organisation of the physiological processes which may well restrict the extent to which the herring, or a particular stock of herrings, is able to react to environmental changes.

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F-8

ENERGY METABOLISM AND MIGRATION OF FISH

By

Gunnar Sundnes[1]

ABSTRACT

The present paper deals with the energy required by Clupeiformes for swimming. Hydrodynamic measurements from experiments made by towing or dragging a fish body are presented. Increased growth by preventing migration is discussed.

In fisheries research some of the approaches and problems are similar to those in agricultural research. The production chain is one topic of great interest as the end products in both fields are of vital importance to man. In fisheries research we are also thinking, in a sense, of how to make "bigger and better fish" when we attempt to increase the total catch or to increase the catch in relation to effort.

Speculations on how to act upon the production chain to increase the yield have been made. While these approaches may be useful in freshwater fish farming, they are not yet possible in the sea. If we look at the production chain from phytoplankton to fish and marine mammals, we find that there are many links where the rate of energy utilization is unknown.

Another approach is to begin with the fish and try to obtain information on the minimum quantities of energy which they require. In order to do so we need data on the size of the stock; the basal metabolism; the growth metabolism and the swimming of the fish. The first three points will not be discussed here, but it may be mentioned that there are methods for making these calculations.

The fourth point is of considerable interest to fisheries dependent upon migrating species. The Norwegian fisheries are extensively based upon migrating fish stocks. From a physiological point of view it is very interesting to look into the problem of swimming and the energy budget on these long journeys. Experiments of Gero (1952) using a piscatometer give information on the dragging effect. Most experiments have utilized live fish, but indirect methods (Sundnes, 1957, 1963) have also given information about the energy required for swimming.

The Clupeiformes have been chosen for these studies. The hydrodynamic resistance data for salmon and herring are those reported previously, together with a description of the dragging or towing experiments (Sundnes, 1963). Figure 1 is a schematic drawing of a salmon prepared for a dragging experiment.

The salmon and herring show relatively low hydrodynamic resistance compared, for example, with the cod (Fig. 2). The body size also plays an important role in the total swimming distance but this factor is not investigated at the present stage. The energy required for overcoming the resistance is shown in Fig. 3. The curves are based on an assumption of 80% efficiency of the propelling effect of the tail fin. From calculations based on the dragging experiments and energy metabolism (Sundnes, 1963) we find that a reasonable cruising speed of salmon and herring is 2 knots. This figure is in accordance with the data found in tagging experiments on salmon (Dahl and Sømme, 1935) and the echo-survey on herring (Devold, 1963) and may not be too high when extrapolating the results of Boyar (1961).

Calculations based on this swimming speed and the resistance data presented above offer the possibility of obtaining an idea of what the stocks have to "pay" for the long journeys. The energy used for these migrations could possibly be used for increased growth if the fish could stay "at home".

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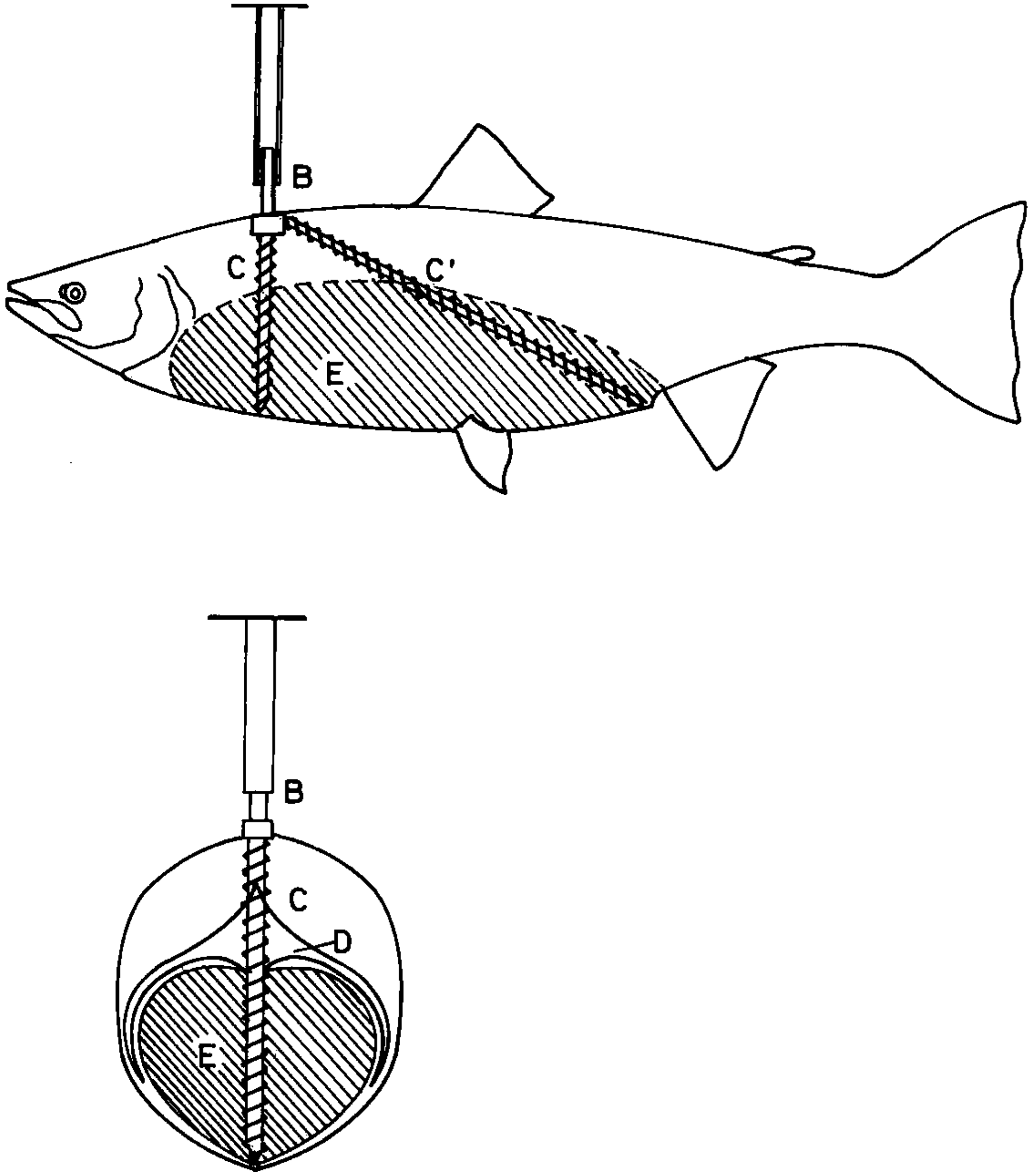

Fig. 1. B = attachment of vertical rod to towing machinery, C = vertical rod, C' = diagonal rod, D = backbones, E = cement filled body cavity.

This would give increased quantities of fish for human consumption if they took care of the fish stock and if the available food for the fish was unchanged. Similar results are seen with domestic animals which use the energy to increase body weight instead of expending it on locomotion as wild animals do. In freshwater fish farming the increased growth of the fish is possibly caused by the reduced locomotion.

In order to get a better idea of the quantities involved we can consider a salmon weighing 11.7 kg which travels 1,000 km at about 2 knots. To overcome the hydrodynamic resistance 840 kcal are required and this is equivalent to 93 gm of fat. However, the energy required for overcoming this resistance is only a part of the total increased energy metabolism during swimming.

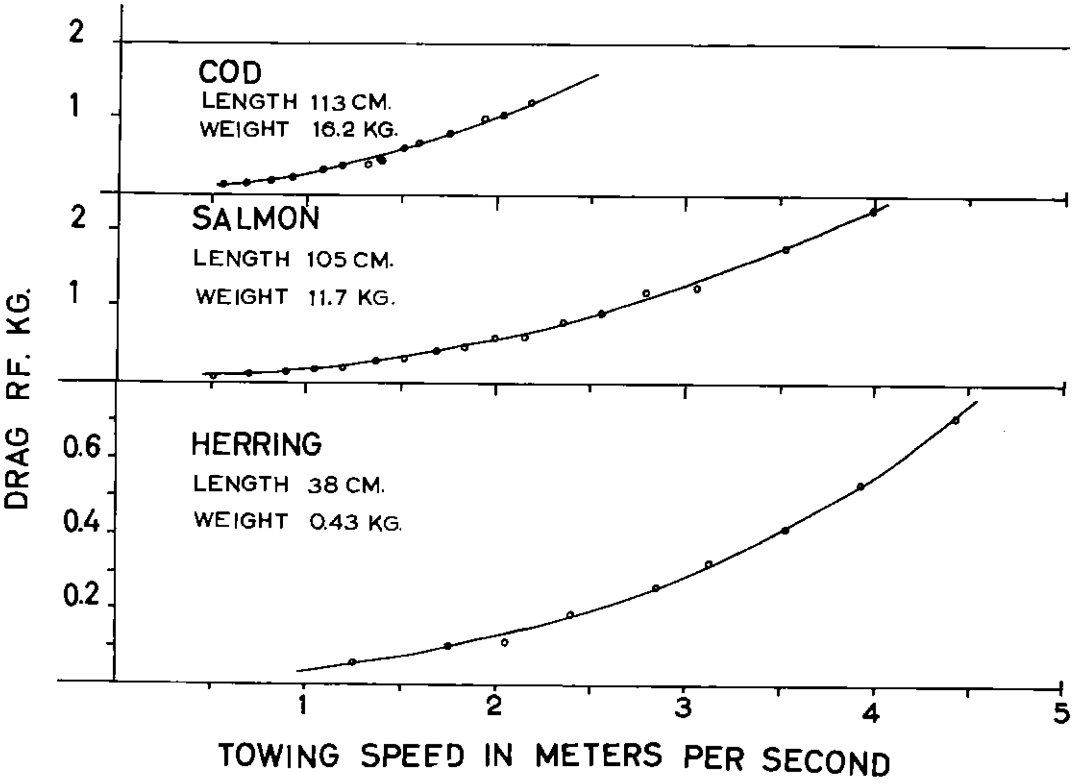

Fig. 2. The relation between drag and towing speed.

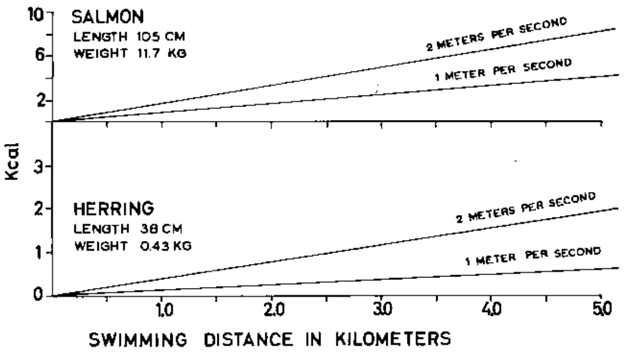

Fig. 3. The energy required for different speeds and swimming distances.

It is also interesting to make some calculations on a whole stock. Here we have to use a stock of fish of relatively uniform body size, such as the Norwegian spring spawning herring. Judanov (1963) estimates this stock in 1961 to consist of 6,515 million mature herring with an average weight of 366 gm. If we assume that half the individuals are bigger than 366 gm we can use the resistance data of herring, shown in Fig. 3, to calculate the energy required for that part of the stock. According to the data of Devold (1963) we will assume here that herring can swim with an optimal speed of 40 nautical miles per day for at least 110 nautical miles. This gives a total energy requirement for 3,257 million individuals of 74,911 million kcal or 8,323 tons of fat to overcome the hydrodynamic resistance. This estimate shows that tons of herring tissue could possibly be added to the body weight even if this migration of 110 miles could be prevented, which is only a small part of the annual migratory cycle. A reasonable figure is 10% increase of the total weight of the stock.

While these are interesting thoughts, is it possible that we can ever observe such a situation in nature? In the case of the Atlanto-Scandian herring this possibility would exist if the hypothesis of Devold (1959) is correct. Devold believes that for one year the herring will remain in Norwegian waters. If food could be available to the herring in the same amounts as it is in the Norwegian Sea we should have the possibility of measuring a growth difference in that part of the stock which is not migrating as usual.

When it comes to the question of what man can do in order to prevent the migration, we have a wide field with many difficult problems to face. While these approaches will not be discussed here, mention can be made of large-scale fish raising with controlled environment to condition the fish to a certain behaviour, or perhaps altering other factors within the fish to control migration. In a dense schooling population we may be able to affect the fish in nature to desired ends. These ways of thinking should be kept in mind when considering future fisheries research.

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F-9

SUPERCOOLING AND OSMOREGULATION IN TELEOSTS OF THE BOREAL AND SUB-ARCTIC

By

H. Leivestad[1]

ABSTRACT

Several species of teleosts found at subzero temperatures in the Barents Sea have their body fluids supercooled. Boreal cod tolerate supercooling if seeding with ice crystals is prevented. Low temperatures induce a rise in plasma osmolarity which is considered to be adaptive. The muscle cells lose potassium and gain sodium when exposed to low temperatures. The physiological consequences of these adaptations are discussed.

INTRODUCTION

Since the freezing point of sea water is 1°C lower than that of the teleost blood (-1.8°C against -0.5 to -0.8°C) the theoretical possibility exists that marine teleosts may meet temperature conditions in nature where an increased osmolarity of the body fluids, or a permanent supercooling, are the only alternatives for survival. It has been shown that both alternatives function in nature.

THE PLASMA

Scholander *et al.* (1957) showed that in Hebron Fjord, Labrador, the shallow water species increase the osmolarity of their blood during the winter, whereas the bottom species, living at a temperature of -1.7°C are permanently supercooled. In 1960, Eliassen *et al.* (1960) reported that cod (Fig. 1) and some other species (Fig. 2) are found in a supercooled state in the cold waters of the Barents Sea. We were able to acclimate the sculpin, *Cotteus scorpius*, to -1.5°C in the laboratory. As seen from the freezing point of their plasma, these animals were supercooled at this temperature (Fig. 3). Gordon *et al.* (1962) verified their earlier findings in Labrador and tried to supercool the sculpin and the tomcod in the laboratory in New Brunswick, but with a negative result.

At the aquarium of The Institute of Marine Research in Bergen I have made a series of experiments on cod, *Gadus morhua* (*callarias*), where the body temperature of the animals has been kept 0.2° to 0.9°C below the freezing point of the body fluids. In Figure 4 the animals at "60 days acclimation were kept supercooled by 0.65°C for 2 months.

We might question how stable is this supercooled state. Except for some of the shore fishes in Labrador (Scholander *et al.*,1957) and the acclimated sculpin (Eliassen *et al.*,1960) the supercooled animal will not tolerate the touch of ice crystals. It is fascinating to watch a supercooled cod after you have been touching it with a piece of ice. In a few seconds the body will start to shiver violently and after some minutes the fish will lie motionless at the bottom. Attempts at revival by immediate transfer to warmer water were without success. Few marine teleosts live in the absolute proximity of ice, however, and it seems as if the others will tolerate supercooled conditions for prolonged periods.

All the authors quoted have found that the osmolarity of the body fluids increases upon lowering the temperature. This increase is large in some of the shore fishes of Labrador (Scholander *et al.*, 1957) where the plasma was nearly isotonic with sea water. These animals were therefore able to tolerate ice crystals. The effect seems to vary with the species and with the thermal pre-history of the specimens (Fig. 1-4). That this "compensatory adaption" is not a question of a mere breakdown

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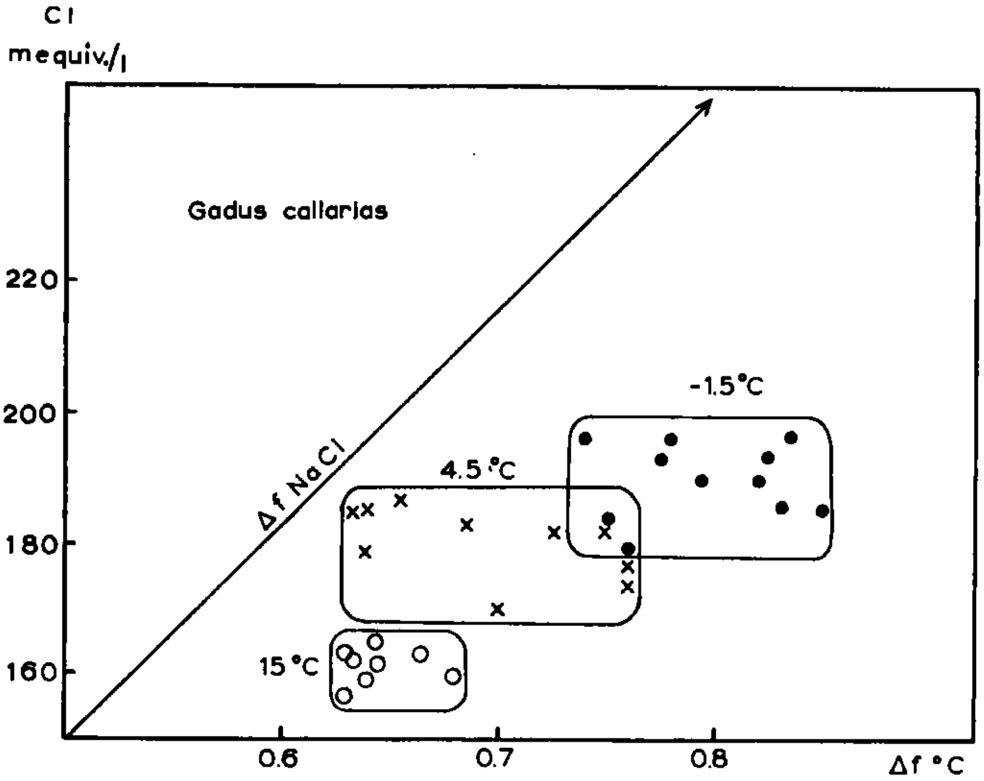

Fig. 1. Plasma freezing point depression versus corresponding chlorides in the cod. Data from the Barents Sea (+4.5°C and -1.5°C) and waters near Arendal (+15°C).

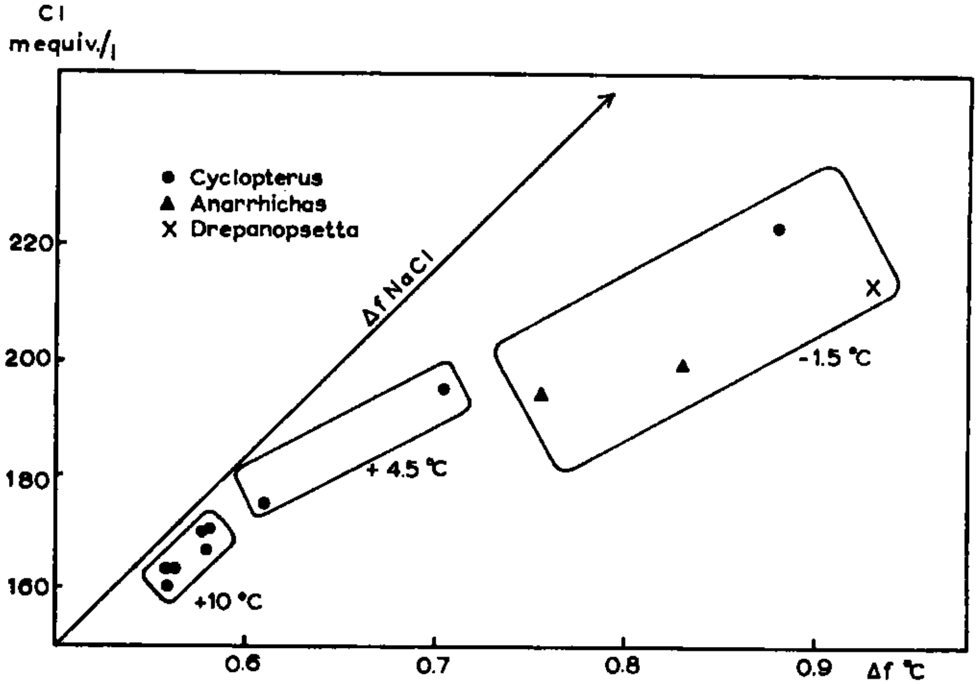

Fig. 2. Plasma freezing point depression versus corresponding chlorides in some teleosts from the Barents Sea (+4.5°C and -1.5°C) and from waters near Bergen (+10°C).

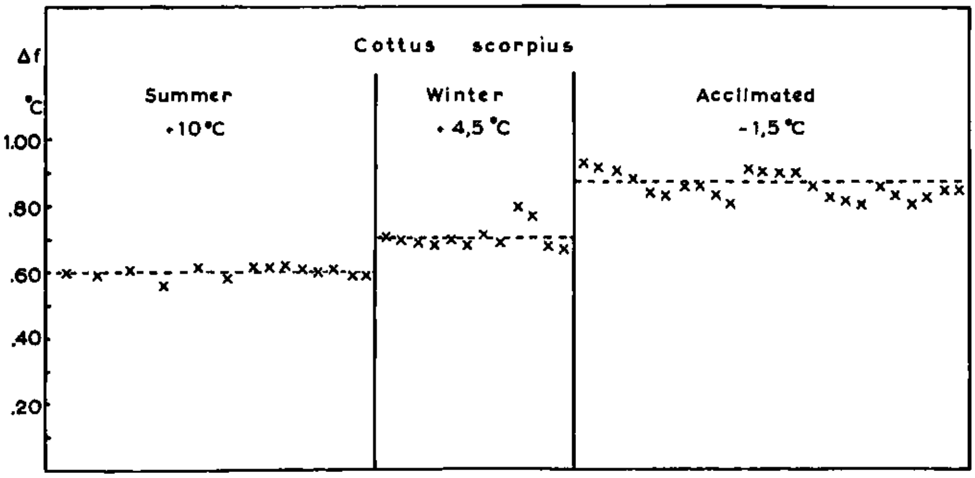

Fig. 3. Plasma freezing point depression in *Cottus scorpius* L. taken in June and September (Summer + 10°C), in February (Winter +4.5°C) and for animals acclimated to -1.5°C.

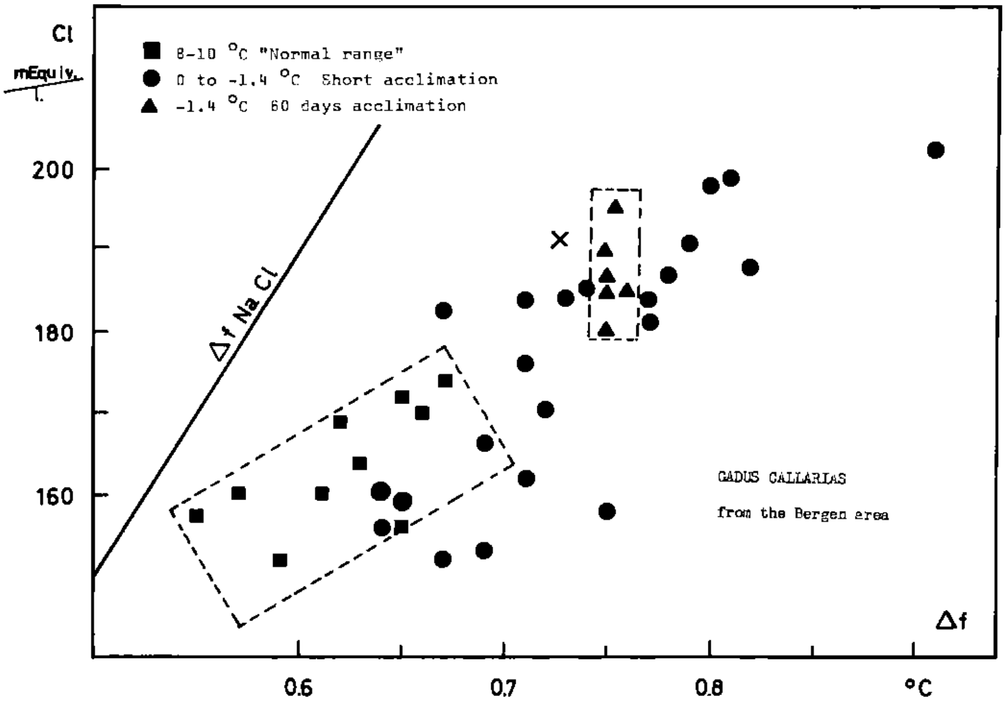

Fig. 4. Plasma freezing point depression versus corresponding chlorides in the cod. Data from animals kept at the research aquarium in Bergen. "Short acclimation" consists of experiments performed in the months from Dec. to Aug. mostly at subzero temp. and lasting from 2 to 14 days. The 60 days-acclimation was performed in Dec. and Jan.

of the osmoregulatory ability is seen from the fact that the chlorides are responsible for a smaller fraction of the osmotically active substances than in "normal" plasma (Fig. 1, 2 and 4; Scholander *et al.*, 1957; Gordon *et al.*, 1962). Gordon *et al.* (1962) have tried to identify this "non-salt" fraction or "anti-freeze substance". There are some indications that the non-protein-nitrogen fraction is responsible for at least some of the increased osmolarity in the fjord-cod (*Gadus ogac*) and in the tomcod (*Microgadus tomcod*). The present author has searched in vain to find an increase in the NPN-fraction in cold-acclimated cod.

Woodhead and Woodhead (1959) use the term "osmotic imbalance" to describe some measurements of increased osmolarity in the cod at low temperatures in the Barents Sea. Their values of both freezing point and chloride do not accord with the data in the literature for cod plasma. It is therefore difficult to assess whether their data verify the tendency for the salts to reduce their relative importance in the total osmolarity. Further they claim to have found a sharp "borderline" at +2°C, below which temperature the "imbalance" starts to function. Besides being physiologically improbable, I can hardly find this verified in their data. We have found that a decrease of 10° to 15°C in temperature represents a sufficient stimulus to induce an increase in osmolarity (Fig. 1, 2, 3) in three species.

It is always tempting to guess what a good reason an animal might have for changes in a physiological parameter. Gordon *et al.*(1962) put the label "antifreeze" and the Woodheads "osmotic imbalance" on the phenomenon described. We know that the osmoregulatory work needed is proportional to the osmotic gradient between the body and the exterior. This in-out gradient will be reduced in these fishes and the metabolic cost of osmoregulation will be reduced. I therefore tentatively propose that the "compensatory increase" is undertaken to reduce the metabolic load on the gills.

THE MUSCLE

Samples of muscle tissues were taken from all the species represented in trawl catches from cold waters in the Barents Sea. For comparison some samples were taken from the Bergen area (Eliassen *et al.*, 1960). The contents of sodium and potassium in the muscle tissue were determined.

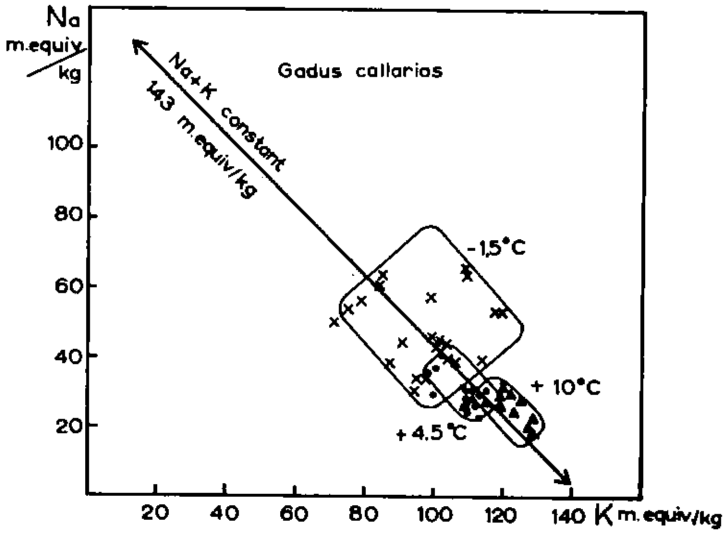

Fig. 5. The content of sodium and potassium in the muscles of the cod from Barents Sea (+4.5°C and -1.5°C) and near Bergen (+10°C).

For the cod (Fig. 5), it will be seen that there is a marked difference in the ratio between sodium and potassium in the samples from the three localities. The K/Na ratio decreases as the temperature is lowered. When presented on a molar basis as in the figure, it seems that sodium is added in similar amounts to the loss of potassium, thus keeping the sum of the two cations fairly constant. A line has been drawn representing the constancy of the K + Na concentrations

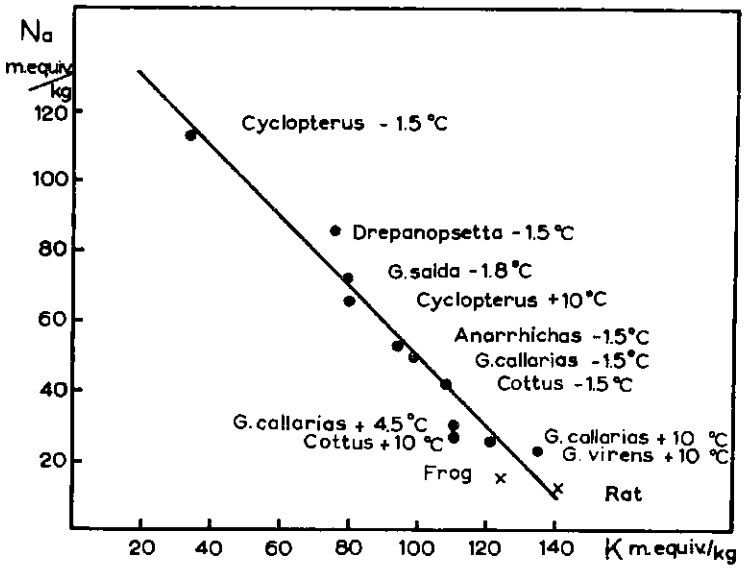

Fig. 6. The content of sodium and potassium in the muscles of teleosts taken in Barents Sea (at -1.5°C, -1.8°C and +4.5°C) and near Bergen (+10°C). *Cottus* at -1.5°C is after some weeks exposure at -1.5°C in the laboratory. The points represent arithmetic means. The data for frog and rat sarcoplasm are from Hodgin (1951).

(K + Na = 150 mEquiv.). In Fig. 6 the data on all the species are represented by the mean value for each species from the different localities. First it may be noticed that the sum of the two cations is reasonably constant, distributed around 145 mEquiv./kg. This is about the same as quoted for rat and frog sarcoplasm (Hodgin, 1951). For the cold locality it is surprising to find that the sodium concentration is increased at the expense of potassium and to such an extent that in some species the two are equal, or even sodium being present in higher concentration than potassium (*Drepanopsetta* and *Cyclopterus*). We conclude on the basis of these data that the intracellular content of potassium is greatly reduced in the subarctic species of the Barents Sea area, and that more boreal species like the cod will show the same tendency, but in a more moderate degree.

Potassium is known to be the typical intracellular cation. There is hardly a living cell that does not step up its potassium level in relation to its environment. For a multicellular organism this environment is the body fluid; for a protozoan it is the environment. This elevated potassium is responsible for the establishment of a membrane potential and thereby underlies such fundamental phenomena as excitability and nervous impulses. It is fascinating, therefore, to speculate how the nerves and muscles in *Cyclopterus* or in *Gadus saida* are able to function with a membrane potential a fraction of that in more southern species.

If I might suggest a possible ecological consequence along this line of thought, it would be the following: the ability to penetrate successfully into cold arctic waters is dependent on the ability of the body cells to function at low intracellular potassium levels. It is reasonable to place the basic reason for this special effect of cold exposure in the energy-demanding "sodium pump" mechanism of the cell. Future work along these lines should try to determine directly the decrease in membrane potential we suspect to be present on the basis of ionic equilibria.

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F-10

THE OPTOMOTOR RESPONSE AND THE SCHOOLING OF FISH

By
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ABSTRACT

Certain features of the response of fish in an optomotor apparatus resemble certain features of fish in a school. These similarities are discussed. It is proposed that the optomotor response may be the mechanism by which fish can change position and velocity within the school without disrupting the forward movement of the school.

INTRODUCTION

A school of fish is composed of like individuals which maintain parallel orientation and some set range of distances from one another when they are moving. It appears, at first glance, as if the members of a school are in the same positions during forward movement of the school, but closer study reveals that there are changes in the position and in the velocity of individual fish. These changes are necessarily within the limitations "imposed" by parallel orientation; nevertheless, fish move anteriorly, posteriorly, medially, laterally and horizontally, without disrupting the apparent cohesion of the school and without affecting the total forward movement of the school. Breder (1959) pointed out that "the movement of the school as a whole is a composition of the velocities of each individual in it, or is the geometric sum of their individual trajectories and speeds in which each fish represents a vector." Breder observed that there is little change of position in a tight school, but that there is constant shifting in a looser one. Thus, in schooling we have a situation where the intrinsic movement of the fish does not disrupt the forward movement of the entire school. In order to keep the forward movement continuous, during positional and velocity changes, the stimuli that maintain forward movement must be of such nature that they can function at a great range of speeds and also when the fish are in a variety of positions. In a previous study (Shaw and Tucker, 1964) we noted, in work with carangids, one experimental laboratory situation in which the behaviour of fish resembles the behaviour of fish in a school in the field. In the laboratory situation the fish are placed into an optomotor apparatus; within the apparatus the fish can change velocity, position and continue to move "forward". It duplicates some of the features of fish in a school.

This paper describes some studies on *Mugil* sp. in an optomotor apparatus.

THE OPTOMOTOR APPARATUS

It consisted of a stationary cylindrical lucite aquarium, 7 cm high, 6 cm diameter and a motor driven rotating horizontal turntable which was fitted with a vertical drum, 11.5 cm high, 10.5 cm diameter. The entire apparatus, except the motor, was submerged in sea water. The aquarium did not rotate, and an opening in the bottom allowed a continual inflow of fresh sea water. The drum rotated, clockwise and counterclockwise, at speeds of 1 to 22 rpm, and the interior of the drum was lined with one of the following various backgrounds:1) entirely white; 2) alternating black and white vertical stripes, each 3 mm wide, entirely lining the interior, 3) four panels, each 18 mm wide consisting of the above stripes, superimposed vertically on a white background at 90° intervals; 4) three panels, as above, at 120° intervals; 5) two panels, as above, at 180° intervals; 6) one panel, as above. In each test a *Mugil* sp., 25-35 mm in length, was allowed to adapt to the aquarium, and then observed for 1 min while the drum was stationary. Subsequently the fish was observed for 1 min at each one of five speeds, 3,6,10,14 and 20 rpm, clockwise and counterclockwise. Records of qualitative behaviour were made by motion picture and the number of times the fish rotated in response to drum rotation was counted (Table 1). Five fish were observed in each of the various backgrounds.

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[1] The American Museum of Natural History, New York, N.Y., USA.

TABLE 1.

Rotational speed of drum	Mean Rotational Speed of Fish: Field of vertical stripes	Field of 4 striped panels	Field of 3 striped panels
3	2.6	2.2	2.0
6	5.5	5.0	6.0
10	9.3	9.3	8.5
14	13.3	12.0	14.0
20	19.3	18.8	19.3

BEHAVIOUR OF THE FISH

In the white drum the fish were mainly motionless and they frequently rested in the same position, near the bottom, throughout the tests.

In the background containing uniform black and white stripes, the fish displayed a number of different behavioural activities. The first three were more frequently seen than the latter three. These activities were:

1) A continuous and regular movement in the same direction as the movement of the background stimulus lining the drum with increase in angular speed as drum speed increased. The fish were oriented parallel to the aquarium wall and close to the bottom.
2) During some revolutions the angular speed of the fish was faster than the speed of the drum, during others, it was slower, although at the end of a minute, each may have moved the same number of rpm. In some trials, fish consistently swam at greater angular speeds than that of the apparatus, and in others, consistently slower.
3) At 3 and 6 rpm a number of fish showed pronounced body vibrations.
4) Fish swam to the top of the aquarium, down to the bottom, up again, continuing to follow the direction of movement of the drum. The fish described a sine curve.
5) In two instances, suddenly interrupting a smooth course, the fish oriented perpendicular to the stripes and nipped at the wall of the aquarium, as if feeding for a few seconds.
6) At slower speeds fish sometimes remained stationary for a few seconds during which time they showed eye nystagmus.

Behaviour was similar in the backgrounds consisting of four or three panels. The following activities, some of which were unvaried during the entire series, were seen.

1) The fish oriented to one of the panels and remained next to that panel throughout. The eye was opposite the leading edge of the panel. Fish and drum showed the same number of rpm..
2) The fish oriented at a point midway between two panels, parallel to the aquarium wall, with the eye opposite a white section. The fish frequently maintained the same orientation throughout the entire series of increasing numbers of revolutions.
3) They swam in short bursts, sometimes more quickly than the angular speed of the drum, other times, more slowly. After the change in angular velocity they again oriented to a panel.

In the field of two panels, the fish kep altering their orientation, clockwise or counterclockwise, regardless of the direction of the drum. Their behaviour was consistently erratic.

In the field containing one panel only two fish responded by moving in the direction of movement of the background with consistent increase in angular speed as drum speed increased. The other fish followed for 1/4 or 1/2 of a revolution, stopped and then followed briefly again as the panel approached them, tail to head.

DISCUSSION

Many features of *Mugil* orientation to the moving stimuli of an optomotor apparatus were similar to *Mugil* orientation in a school. Fish altered positions and changed velocities relative to some of the moving backgrounds, but the fish continued to move in the same direction as the background movement. If we consider the entire school as a moving background, individuals within the school can be stimulated by the movements of surrounding fish. Since one fish is essentially equivalent to another each would be influenced by the neighbouring sphere of moving fish and the group would intrinsically impel itself forward. Fish in a school probably take an optical fix on other fish and fish in a drum probably take an optical fix on some stripes. But since there is constant movement in both conditions of the individual and the background, there is, in all likelihood, a temporal change of optical fixation points. Atz (1953) has suggested that one reason fishes of the same species and size generally school together is that they alone provide points of optical fixation which travel at comfortable speeds.

In order to keep the fish moving forward the movement of the background evidently must approach the visual field of the fish from tail to head (Horstmann, 1959; Harden Jones, 1963). Protasov and Altaknov (1961) reported that, in order to guide the movement of fish, the moving visual field of the fish must be horizontally greater than the visual field of the fish and the vertical stripes must be no less than one half the vertical visual field of the fish. If we combine these two features we may understand what occurred in the moving background consisting of two panels. There, when one panel passed the fish, tail to head, the other panel passed it, head to tail. Although fish do not follow the direction of movement of the far panel, without the additional stimulation of approaching panels on its near side, the fish was confounded by simultaneous movements in opposite directions. In the background containing only one panel, the panel was not a sufficiently strong stimulus to maintain a following response in three of five fish; movement was obtained in two. In this situation a fish had to contend with a stimulus moving in one direction, but the stimulus may have been of marginal intensity.

An objection that might be raised regarding the suggestion that the optomotor response is the mechanism by which fish change position, velocity and continue to move forward is that optomotor responses are found in non-schooling fish. However, as discussed here, this response operates in a school after it has formed. A combination of many other factors, such as, for example, the development of visual attraction (Shaw, 1960) and the general maturation of the nervous system, serve to give rise to schooling behaviour. It is only after the school has formed that the optomotor response may facilitate forward movement while fish reorient, accelerate and decelerate.

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