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VARIATIONS IN THE ACTIVITY OF THE THYROID GLAND OF THE COD, *GADUS CALLARIAS* L., IN RELATION TO ITS MIGRATIONS IN THE BARENTS SEA

I. SEASONAL CHANGES

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(Text-figs 1 and 2)

Relatively little is known of the exact role of the thyroid gland in teleosts. Although the results of a few studies have suggested that the thyroid influences respiratory metabolism, as in the higher vertebrates, a greater number of experiments have failed to show that either treatment of fish with thyroid hormones or inactivation of the gland produces any significant effect upon the oxygen consumption of the fish. Thyroid activity has been linked with reproduction in some fish, although there is little evidence to show that the relationship is more than coincidental. The thyroid has also been connected with osmoregulation, but reviewing this work Pickford (1957) concludes that the relation with osmoregulation is only a secondary or collateral one. Recently Hoar (1953, 1955) has suggested that the thyroid may control the migratory response of fish. However, in the migratory species which have been studied in detail, the salmon, *Salmo salar* L. and *Onchorhynchus* spp. and the eel, *Anguilla vulgaris*, changes in the salinity of the environment during their migrations were complicating factors since salinity changes alone have been shown to stimulate thyroid activity in non-migratory fish (Olivereau, 1954).

The present paper describes the seasonal cycle of activity in the thyroid gland of the cod, *Gadus callarias* L., in the Barents Sea, and is one of a series on the physiology and behaviour of the fish. This species is of particular interest because of the great length of its monadromous spawning migration, the adults often travelling more than 800 miles before reaching the spawning grounds. The distribution and movements during the course of the life cycle have been described in detail (Trout, 1957).

The cod mature for the first time at an average age of 8 or 9 years old. Throughout the summer months, they are found on the shallow-water feeding grounds of the Bear Island–Spitsbergen Banks. In late September, at the onset of maturation, the ripening fish begin to move south and west to leave the shelf, and migrate to the spawning grounds inside the Lofoten Islands on the north Norwegian coast. Spawning occurs each year from mid-February until mid-April. After first maturity, the cod spawns annually, the spent fish dispersing to the feeding grounds where they remain until the following autumn. The young larvae are distributed from the spawning grounds over large areas of the Barents Sea by surface currents. Lundbeck (1932) suggested that they become migratory at 3 years old. From length measurements of immature cod caught by the commercial trawlers, Maslov (1944) demonstrated a pattern of migration which has since been confirmed and extended (Trout, 1957). During the summer months, June to September, the immature fish are found in large numbers in the shallow-water feeding grounds of the Bear Island–Spitsbergen Bank. In autumn the fish begin to leave these grounds and migrate into deeper waters around the shelf where they remain throughout the winter, until the late spring, when they return to the Banks. This migration is repeated annually until the fish mature.

MATERIAL AND METHODS

The thyroid glands were collected from the cod, *Gadus callarias* L., in the Barents Sea. Mature and immature fish, from 50 to 120 cm. were selected from the catch of the M.A.F.F. Research Vessel 'Ernest Holt'. All the fish used in this investigation were caught at temperatures of between 1° and 6° C and at salinities of 34·5 to 35·2‰. The cod were killed by a sharp blow on the head; a sample of blood was taken for chemical analysis, and the thyroid was then removed. In the cod, as in the majority of teleosts, the thyroid is not encapsulated, but consists of a number of discrete follicles, closely apposed to the ventral aorta, and lying in the surrounding connective tissue. The aorta was therefore dissected out, from the heart to the level of the first gill arch;

TABLE 1. FISHING DATES, 1956–7

8–26 August	10–26 March (Spawning sample)
8–20 September	26–31 March (Norway coast)
7–23 October	23–30 April
20 November–5 December	1–10 June
20–31 January	16–31 July

this ensured that most of the gland was removed. The thyroids were fixed in Bouin's fluid for 24 h, routinely dehydrated and embedded in paraffin wax. Serial sections were cut at 4μ, and alternate slides stained with haemotoxylin and eosin, and Heidenhain's azan.

A quantitative value for the activity of the gland was obtained from measurements of the follicular cell height. Pickford & Atz (1957) have reaffirmed the reliability of this method of estimating the activity of the thyroid. In order to ensure that the same follicle was not measured twice, every twentieth section was selected for study. Four diametrically opposite cells were measured in each follicle and not less than two hundred readings were made on each fish.

Samples were obtained throughout the year, at times corresponding to the major phases of the migratory and reproductive cycles of the fish. The dates of capture are given in Table 1. Each sample consisted of ten fish, five males and five females. A statistical analysis of the results showed that there was no difference in the activity of the gland between the two sexes at any time of the year. The state of maturity was determined by examination of the gonads as the fish were dissected; in addition, the gonads were fixed, and sections studied under the microscope.

The results presented below, and in the following paper, are based on between 40,000 and 50,000 follicular cell height measurements.

RESULTS

Adult cod

The mean values for the cell height measurements of the thyroids of the mature cod are given in Fig. 1 and Table 2. The reaction of the colloid to azan staining confirmed the results obtained from cell height measurements. In resting glands the colloid stained a deep red, and had a dense laminated appearance. The surrounding follicular cells were low and stretched round the stored colloid: frequently the nucleus caused a distinct bulge in the centre of the cell. The cytoplasm of the follicular cells stained a uniform pink.

TABLE 2. SEASONAL VARIATIONS IN THE MEAN FOLLICULAR CELL HEIGHT IN THE THYROID OF THE ADULT COD

Sample	No. of fish	Mean follicular cell height (E.P.U.)	Standard deviation
August	10	47·8	5·1
September	10	61·5	6·5
October	10	69·0	6·1
November–December	10	76·9	4·3
January	10	81·5	7·5
March (Spawning)	10	70·0	3·6
March (Coast)	10	67·7	5·5
April	10	54·4	3·4
June	10	50·1	2·4
July	10	54·1	4·6

75 E.P.U. = 10 μ

In active glands the colloid stained blue and appeared granular. The follicular cells were high and columnar, with a large round nucleus situated at the distal end of the cell. Cytoplasmic granules, staining a deep pink, were often present, usually surrounding the nucleus, and extending half way down the cell. The inner edge of the cell near the follicle stained much more faintly. Deep red droplets were sometimes seen at the outer edge of the colloid. In some active thyroids the follicular membrane had ruptured, and the colloid was discharged out of the follicle. Other follicles had been invaded by leucocytes.

Throughout the spring and summer months, from April to late September, the follicular cells were low, and the thyroid appeared, histologically, to be in an inactive state. However, during this period, there was a small but significant ($p = 0{\cdot}03$) increase in follicular cell height. Marked secretory activity began in late September. The height of the follicular cells continued to increase throughout the winter, reaching a maximum in January, prior to spawning. The follicular cell height was less in fish caught in March at spawning time. The thyroid glands of cod caught some 50 miles north of the spawning grounds, and in which the gonads were ripe but not yet running freely with spawn, showed no significant difference in cell height from thyroids of 'running-ripe' cod caught on the spawning grounds, inside the Lofoten Islands. In spent fish the gland re-entered the resting condition.

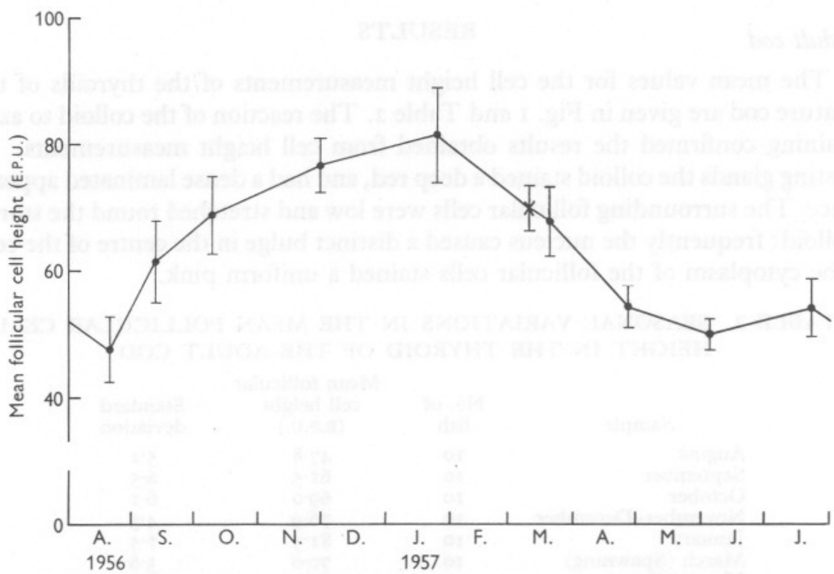

Fig. 1. The seasonal variation in the mean follicular cell height of the thyroid gland in adult cod. ×, ripe cod caught on the spawning grounds inside the Lofoten Islands. The follicular cell height is expressed in eyepiece units (E.P.U.).

A histological study of the gonads showed that throughout the summer these organs were quiescent. Maturation began in late September with the enlargement of the eggs, and the production of primary spermatocytes; at the same time the thyroid became active. Maturation continued throughout the winter migration, the gonads being fully ripe by March, as the fish reached the spawning grounds on the North Norwegian coast.

Immature cod

The cycle of activity in the thyroid of the immature cod is shown in Fig. 2 and Table 3.

The gland became active in September, as in the adult fish, but the maximum cell height was reached in December, after which the follicular cell height decreased, returning to the resting state by April. A second smaller peak of activity occurred in July, as in the adult fish. The magnitude of the thyroid cycle of the immature fish was of a lesser order than that of the adults.

The gonads of the immature fish showed no changes throughout the year. The ovaries and testes remained small, and were filled with primary germ cells.

TABLE 3. SEASONAL VARIATIONS IN THE MEAN FOLLICULAR CELL HEIGHT IN THE THYROID OF THE IMMATURE COD

Sample	No. of fish	Mean follicular cell height (E.P.U.)	Standard deviation
August	10	48·4	4·5
September	10	58·3	6·2
October	10	66·5	6·5
November–December	10	67·9	7·2
January	10	64·8	8·7
March	10	55·1	3·2
April	10	49·5	4·5
June	10	48·4	4·5
July	10	53·6	4·3

75 E.P.U. = 10 μ

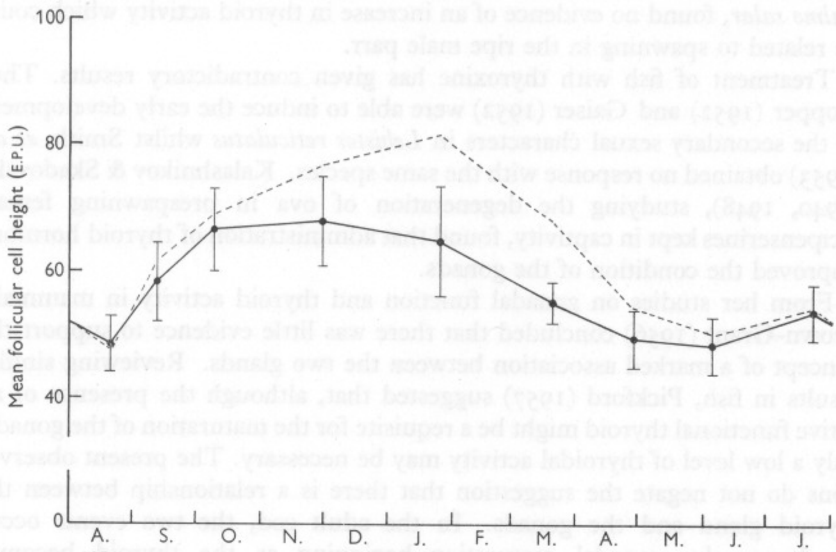

Fig. 2. The seasonal variation in the mean follicular cell height of the thyroid gland in immature cod. The broken line gives the seasonal variation in adult cod for comparison. The follicular cell height is expressed in eyepiece units (E.P.U.).

DISCUSSION

Barrington & Matty (1954) have suggested that there is a correlation between the activity of the thyroid gland and the phases of the reproductive cycle in fish. They found that in the minnow, *Phoxinus phoxinus* L., the thyroid was maximally active at spawning time, the activity decreasing as spawning ceased. Similarly, in the pike, *Esox lucius* (see Zaitzev, 1955), and in the herring, *Clupea harengus* (see Buchmann, 1940), there is increased thyroidal activity at spawning time. Lieber (1936) associated a period of thyroid activity prior to spawning, with the enlargement of the gonads in *Misgurnus fossilis*; a second period of thyroid activity occurred after spawning, but the gland was less active during the actual spawning period.

Laboratory experiments in which fish have been maintained in antithyroid drugs have suggested that these substances may have an inhibiting effect on maturation of the gonads. Chambers (1951) found that the testes of *Fundulus heteroclitus* kept in a solution of thiourea had regressed. Barrington & Matty (1952) working with the minnow, and Smith, Sladek & Kellner (1953) with *Lebistes reticulatus* achieved similar results. However, in a further series of studies on the minnow, Barrington (1954) reported that he could stimulate the development of the testes in winter, by artificial light, although the fish were immersed in thiourea, and Hoar (1939) in his studies on the Atlantic salmon, *Salmo salar*, found no evidence of an increase in thyroid activity which could be related to spawning in the ripe male parr.

Treatment of fish with thyroxine has given contradictory results. Thus Hopper (1952) and Gaiser (1952) were able to induce the early development of the secondary sexual characters in *Lebistes reticulatus* whilst Smith, *et al.* (1953) obtained no response with the same species. Kalashnikov & Skadovskii (1940, 1948), studying the degeneration of ova in prespawning female Acipenserines kept in captivity, found that administration of thyroid hormone improved the condition of the gonads.

From her studies on gonadal function and thyroid activity in mammals, Brown-Grant (1956) concluded that there was little evidence to support the concept of a marked association between the two glands. Reviewing similar results in fish, Pickford (1957) suggested that, although the presence of an active functional thyroid might be a requisite for the maturation of the gonads, only a low level of thyroidal activity may be necessary. The present observations do not negate the suggestion that there is a relationship between the thyroid gland and the gonads. In the adult cod, the two events occur simultaneously, gonadal maturation beginning as the thyroid becomes active, and the thyroid returning to a resting condition in the spent fish. But these results do not indicate whether the activity of the thyroid is necessary for gonad maturation, or whether the occurrence of the two events is coincidental. However, a similar cycle of activity occurred in the thyroid of the immature cod, although the gonads remained quite inactive throughout the cycle.

The results of the present work suggest that the thyroid cycle in the cod may be related to the migratory activity (see Woodhead, 1959, p. 421 of this *Journal*). In both adult and immature fish, the cycle of activity in the thyroid began at the start of their southward migration over the Bear Island–Spitsbergen Bank, and declined as the migration was completed. The thyroid remained active in the adults until March, when the cod reached the Lofoten Island spawning grounds, but in the immature cod, the activity had already begun to fall by January, when most of the fish were completing their migration to the overwintering grounds.

The spawning migration of the adult cod and the overwintering migration of the immature fish are active contranatant migrations against the West Spitsbergen current. In contrast, it has been suggested that the northward return of the spent cod to the feeding grounds might be accounted for by the passive carriage of the fish within the water mass (Trout, 1957). Perhaps the simplest explanation of the active contranatant migration would be that there was a change in the reaction of the fish to water currents, probably accompanied by an increase in the general level of locomotory activity. Since fish readily orientate against a strong water current, if provided with adequate sensory clues, it seems likely that the change in the reaction of the cod to current would be in the nature of a lowered threshold for initiation of the response, rather than a completely new response. The passive denatant return of the spent fish to the feeding grounds could similarly be explained by a rise in the threshold for the reaction to current, and probably a fall in the general level of activity, the fish swimming randomly within the northward moving waters of the Norwegian current. Trout (1957) states that the cod shoals are largely pelagic at this time, which would facilitate this passive displacement.

Fontaine (1954) has emphasized the role of internal factors in the causation of migration in fish and Hoar (1955) has suggested that the secretory activity of the thyroid gland and gonads may be responsible for increased locomotory activity, sometimes involving long migrations, associated with reproduction. Hoar *et al.* (Hoar, Mackinnon & Redlich, 1952; Hoar, Keenleyside & Goodall, 1955) have shown an increased level of locomotor activity in fish maintained in thyroxine solutions, and decreased activity in thiourea; immersion in solutions of sex steroid hormones also increased the general level of activity. In the minnow, *Phoxinus phoxinus*, Woodhead (1956) has shown that during mid-April, prior to spawning, the mean swimming speed was 159% higher than in December; in April the thyroid would be maximally active (Barrington & Matty, 1954), the gonads would also be secreting hormones since the minnows had begun to assume nuptial coloration, and both gonadal and thyroid hormones may have contributed to the increased swimming speed observed in the minnow.

In the adult cod, the gonads were ripening throughout the spawning migration, when the thyroid gland was active, and the action of the thyroid and gonadal hormones may have been additive, both causing an increase in migratory activity. However, the results obtained with the immature cod, in which the gonads remained inactive, suggest that an increase in the activity of the thyroid gland alone may initiate and sustain a lengthy migration.

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SUMMARY

A seasonal cycle of activity has been demonstrated in the thyroid gland of both adult and immature cod. The gland became active in late September and activity continued in the adults until spawning time in March; in spent cod the gland had re-entered the resting condition. In the immature fish activity had declined by March.

In the adult cod the thyroid gland was active throughout the period of maturation of the gonads, but the present results did not indicate whether these events were causally related or coincidental; a thyroid cycle occurred in the immature cod, although the gonads remained quiescent.

It has been suggested that thyroid activity may initiate and sustain the active migration of the cod.

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