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Temperature and reproduction in tench : Effect of a rise in the annual temperature regime on gonadotropin level, gametogenesis and spawning. I. The male

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Summary. During a 9-month period (corresponding to a sexual cycle), the adult male tench, *Tinca tinca*, was kept in fish farm ponds receiving heated water from a power plant. In 1974, the males were submitted to three different temperature regimes : group I : ambiant temperature ; group II : ambiant temperature + 3 °C ; group III : ambiant temperature + 6 °C. The experiment was repeated in 1975, but only using groups I and III. The reproductive cycle and thermal treatment were studied from a quantitative analysis of spermatogenesis, the duration of the spawning cycle and radioimmunoassay (RIA) measurement of gonadotropin (GTH) in plasma and pituitary, using a carp RIA system turned out to be sensitive enough to assay tench GTH, which was expressed in a c-GTH equivalent. Spermatogenesis in the tench was a discontinuous process, starting in the spring and finishing in the summer. It began earlier in heated water in which the spawning period was also considerably longer (3 months in group III against 1 month in group I). At the beginning of spermatogenesis, pituitary and plasma GTH was low, but rose rapidly when spermatogenesis was initiated (appearance of type B spermatogonial cysts and meiosis). The highest GTH levels in the blood were recorded during the spawning period, with important fluctuations probably due to discharges from the pituitary.

Introduction.

In cyprinid fish, the temperature may enhance sexual activity (the perch, *Cymatogaster agregatta* Gibbons, Wiebe, 1968 ; the rainbow trout, *Salmo gairdneri*, Breton and Billard, 1977) or may be the most important environmental factor. However Bullough (1940) already reported that *Phoxinus laevis*, in natural temperature conditions under different photoperiods, exhibits an internal reproductive rhythm which acts independently of exogenous factors. This literature has been reviewed by de

Vlaming (1974). Most of the reported experiments lead to the conclusion that high temperature promotes the final stage of gonadal maturation (the goldfish, *Carassius auratus*, Kawamura and Otsuka, 1950 ; the lake chub, *Couescius plumbeus*, Ashan, 1966). The effects of temperature on the earlier phases of gametogenesis are more contradictory. Thus, Ashan (1966) considered that low temperature favored the meiotic phase of spermatogenesis, while de Vlaming (1975) found in *Notemigonus crysoleucas* that spermatocyte formation and multiplication, as well as the early phase of vitellogenesis, were quite independent of environmental factors.

Most of these experiments were performed in the laboratory under constant temperature and over short periods of time. But these short-term experiments can be highly criticized, as underlined by de Vlaming (1972).

We have studied the reproductive cycle of the male tench, *Tinca tinca*, in a natural pond (in fish farm conditions) over a 2-year period with different thermoperiod regimes under natural photoperiod. The same experiments were carried out on the female (Breton *et al.*, 1980).

Material and methods.

The experiments were conducted in Poland in the Heated Water laboratory at Siekierki near Warsaw. This laboratory uses warm water from an electrical power station. In heated ponds (300 $m^2 \times 1.3$ depth), the water temperature was continuously recorded during the experimental period. The fish were fed pelleted food and cereals

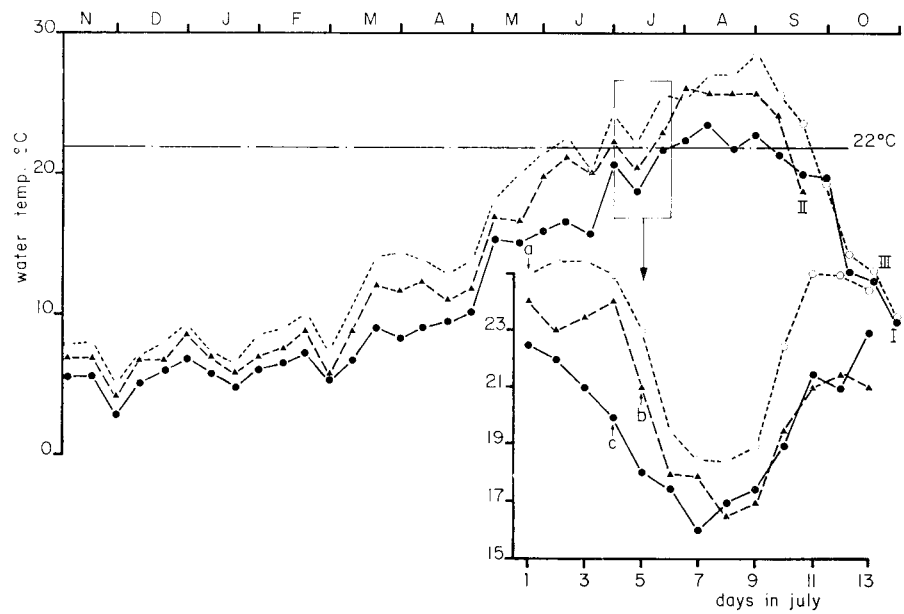

FIG. 1. — *Water temperature changes in the experimental ponds in* 1974 (mean weekly temperature) ; *a* : end of spawning n° 4, *b* : end of spawning n° 2, *c* : end of spawning n° 1.

Two experiments were carried out during two successive cycles from 1973 to 1975, using various temperature regimes by mixing natural water and warm water in different ratios :

Experiment A 1973-1974. This experiment extended from December 1973 to October 1974. Three ponds were supplied either with natural water (pond I) or with two different flow rates of heated water (ponds II and III) ; three different temperature regimes were obtained, as shown in figure 1. Each pond received about 200 3-year old male and female tench, supplied by a local fish farm. Seven males were killed monthly during the resting period, and more frequently during the spawning season (see table 1).

TABLE 1

Sampling dates in the 1974 *and* 1975 *experiments which ended on* 16/09 *in* 1974 *and on* 30/08 *in* 1975

	Experiment A (1973-1974)			Experiment B (1974-1975)	
	I	II	III	I	III
December				3	2
January	14	15	16	14	13
February	26	27	25	25	24
March					
April.....	8	9	10	7	8
May	20	21	22	20 bf_1	19 bf_1 dg_1 30 af_1
June		17 af_1 26 af_2	4 af_1 20 af_2	17 bf_1 dg_1	16 dg_2 af_2
July.....	3 af_1 17 af_2	4 af_3 18 af_4	4 af_3 16 af_4 25 af_5	7 af_1 25	10 af_3
August	7 af_3		13 af_6 17 af_7	9 30	8 af_4 29
September	16	16	16		

bf_n : before n spawning.
af_n : after n spawning.
dg_n : during n spawning.

Experiment B 1974-1975. This experiment extended from November 1974 to September 1975. Only two different temperature cycles were used : ponds I and III (fig. 2). Both ponds received between 220 and 260 2 or 3-year old male and female tench from the same source as experiment 1. A group of 10 males was tagged and continuously sampled once a month for plasma GTH measurement. These males were killed at the end of the experiment. Periodically (once a month or more, see

table 1), 6 males were killed for gonad and pituitary as well as blood sampling. When the fish had reached sexual maturity, they were inspected daily for reproductive behavior and spawning.

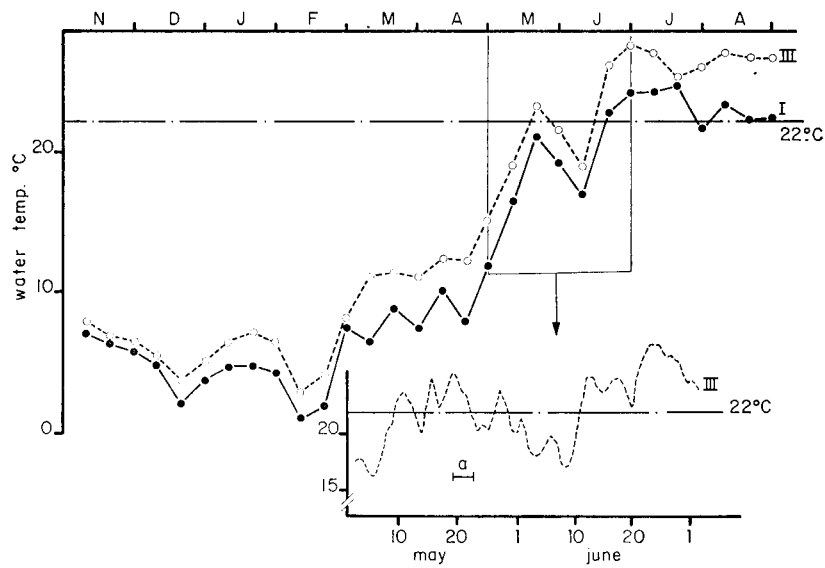

FIG. 2. — *Water temperature changes in the ponds in* 1975 (mean weekly temperature) ; *a* : spawning n° 1.

Blood was taken by caudal vessel puncture in a heparinized syringe. After centrifugation (3 000 g, 10 min, 4 °C), the plasma was stored frozen until GTH determination. Immediately after the fish was decapitated, the pituitaries were plunged into cold acetone where they remained for 24 hrs ; they were then dried at room temperature, weighed to the nearest 0.01 mg on a Mettler ME 22 microbalance, and homogenized in 0.025 M barbital buffer, pH 8.6, by 10 strokes in a glass teflon homogenizer. These homogenates were diluted just before use for GTH determination by radioimmunoassay (RIA). The system used was the carp gonadotropin RIA described previously (Breton *et al.*, 1971). Though the specificity of this system was demonstrated for cyprinid gonadotropin (Breton *et al.*, 1973), it was tested here for tench GTH measurement. The assay was conducted with 50 µl of one-third diluted plasma or 50 µl of a 1/2 000 dilution of the pituitary homogenates ; GTH concentration was expressed in ng équivalent of c-GTH per ml of plasma or per mg of dry pituitary.

To calculate the gonadosomatic index (GSI), the standard length of the dead fish was measured and its corporal, visceral and gonadal weights determined. Part of the testis was fixed in acetic Bouin Holland and spermatogenesis was analyzed by quantitative histology according to Billard *et al.* (1974). The following germ cell types were measured : spermatogonia A (G_A), spermatogonia B (G_B), spermatocytes (Spc), spermatids (Spt), spermatozoa (Spz).

Statistical analysis was carried out using the t-test and the analysis of variance.

Results.

I. — *RIA specificity for tench gonadotropin.* — The shift of ^{125}I-labelled c-GTH from its specific antibody, either by carp or tench pituitary extracts, gave parallel curves (fig. 3). A comparison of the regression line logit $\frac{B}{Bo}$: f (log. dose) by Snedecor and Cochran's method (1957) did not show any difference between the slopes of the two curves.

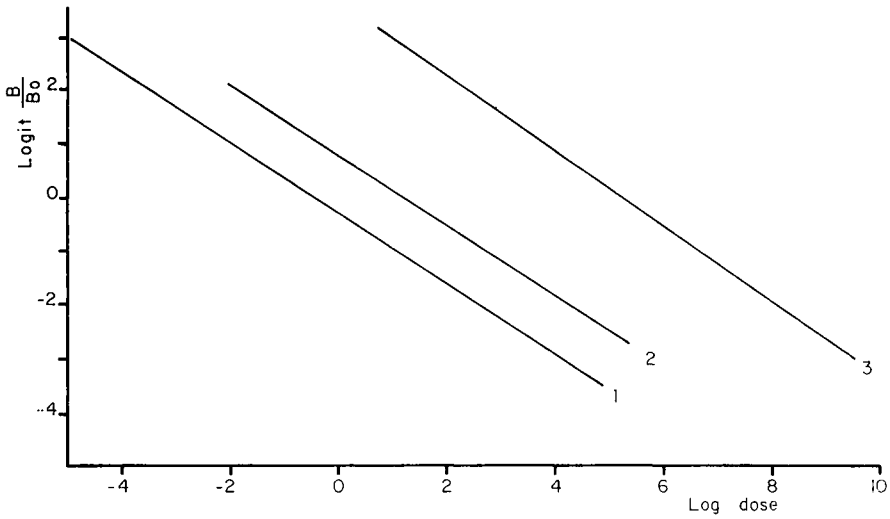

FIG. 3. — *Competition curves of* c-GTH *and total pituitary extracts from carp and tench in a specific radioimmunologic system for carp gonadotropin* 1 : pure c-GTH ; 2 : carp pituitary extract ; 3 : tench pituitary extract.

II. — *Temperature regimes and spawning periods.* — The temperature regimes were characterized by the total number of degree-days in each pond for the experimental period (fig. 3). The total thermal energy received by both the experimental ponds during the experiment B was lower than in experiment A in which the temperature rise was more pronounced, especially at the beginning of the year (until March-April) (fig. 4). During the experimental period, spawning was observed at various times and lasted several days (see top fig. 5) ; it occurred earlier and more frequently in heated ponds. The first spawning took place only when water temperature had reached 20 to 22 °C (1 565 degrees-days in experiment B pond II, 1712 in experiment B pond I, and 2 006 in experiment A pond III). The total duration of spawning was significantly increased by the highest temperature regimes ($P < 0.01$).

III. — The spermatogenetic cycle.

In *experiment A*, the maximum number of spermatogonia (G_A) was found from January to April, but it was higher in fish kept in pond I (1.88 ± 0.59) than in those kept in the heated pond (1.47 ± 0.17). During the rest of the cycle, G_A remained at

low level. Spermatogonial multiplication and meiosis started earlier in fish in the heated pond than in the controls. In the latter group, the spermatogenetic process was slower, and in July the total number of type B spermatogonia (G_B) + spermatocytes (Spc) was higher than in the heated-pond males. The same phenomenon occurred for spermatids : earlier appearance in the testis of heated-pond males, but precocious decrement in comparison with the control fish from pond I. The number of spermatozoa rose very rapidly in heated-pond fish in April, followed by earlier depletion in group II than in group III. The maximum number of spermatozoa was observed

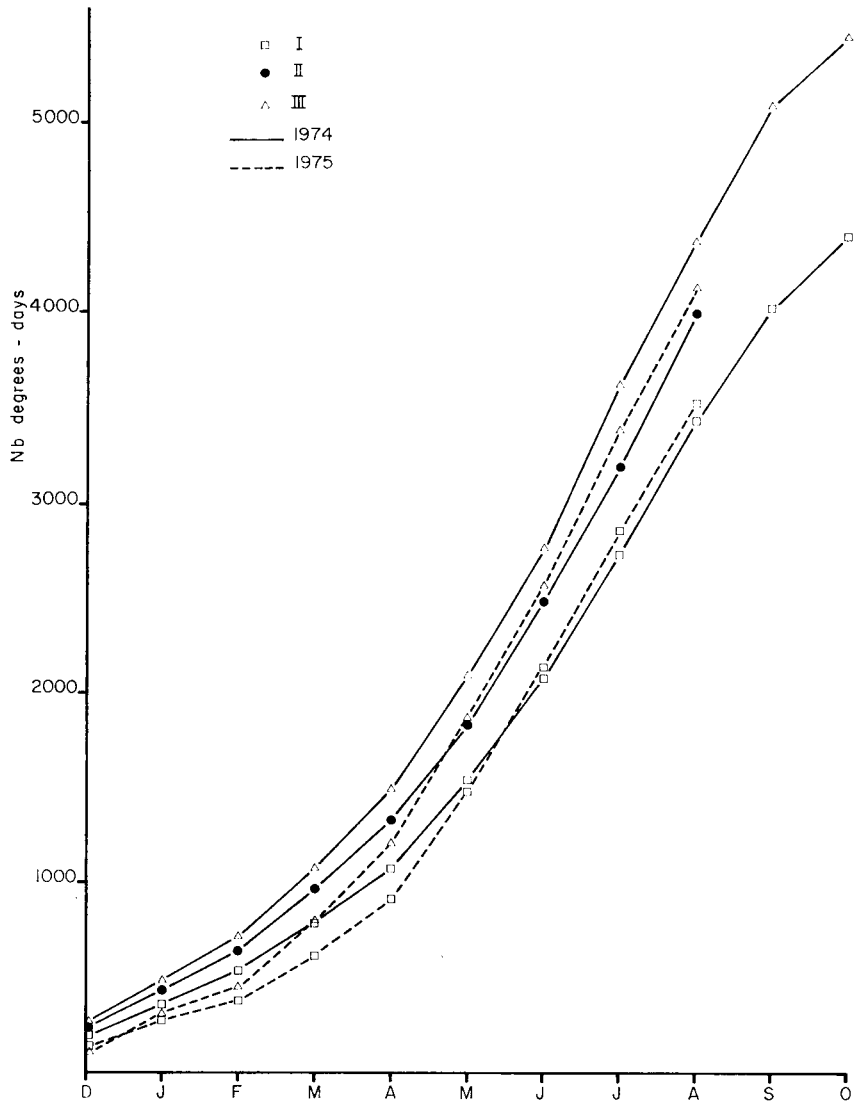

FIG. 4. — *Degrees-days used on the animals in 1974 and 1975. Monthly cumulation.*
Year 1974 —— ; 1975 ------

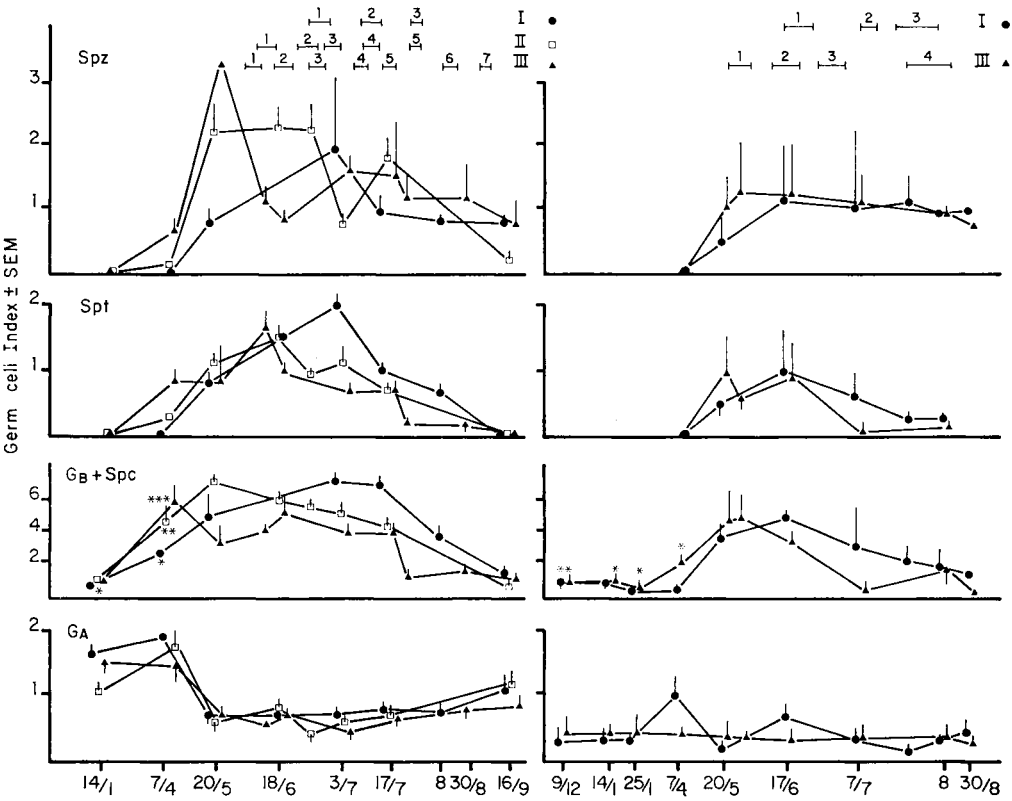

FIG. 5. — *Annual spermatogenetic cycle of tench kept under various temperature regimes* : pond I ●, II □, III ▲. Left : Experiment A (1973-1974) ; right : experiment B (1974-1975). Cell index corresponds to the total germ cell volume in the testis expressed by g body weight. G_A : type A spermatogonia, G_B ; type B spermatogonia, Spc : spermatocytes, Spt : spermatids ; Spz : spermatozoa. At the top of the graph : number and duration of spawning periods recorded in each experimental pond. * only G_B ; ** G_B only in 3 out of 7 males ; *** G_B only and no Spz in 2 out of 7 males.

before the first spawning in groups II and III, and after it in group I. At the end of the reproductive season, the number of spermatozoa was very low in the testis of all groups. The total number of spermatozoa recorded during the whole spermatogenetic cycle was significantly increased in the heated ponds ($P < 0.05$), pond III being significantly higher than pond II. The total number of G_B, Spc and spermatids was not significantly different among the three groups. The GSI rose more rapidly in groups III and II than in group I, but the maximum values reached in the three groups did not differ (fig. 6).

In *experiment B*, there was a rise of G_A in the control group in April but not in group III. Spermatogenesis was initiated earlier in group III, but ended sooner as in experiment A. The number of spermatozoa also increased earlier in the heated-pond fish but was significantly lower ($P < 0.01$) than in experiment A. The GSI reached a maximum value in May in group III and in June in groupe I (fig. 7).

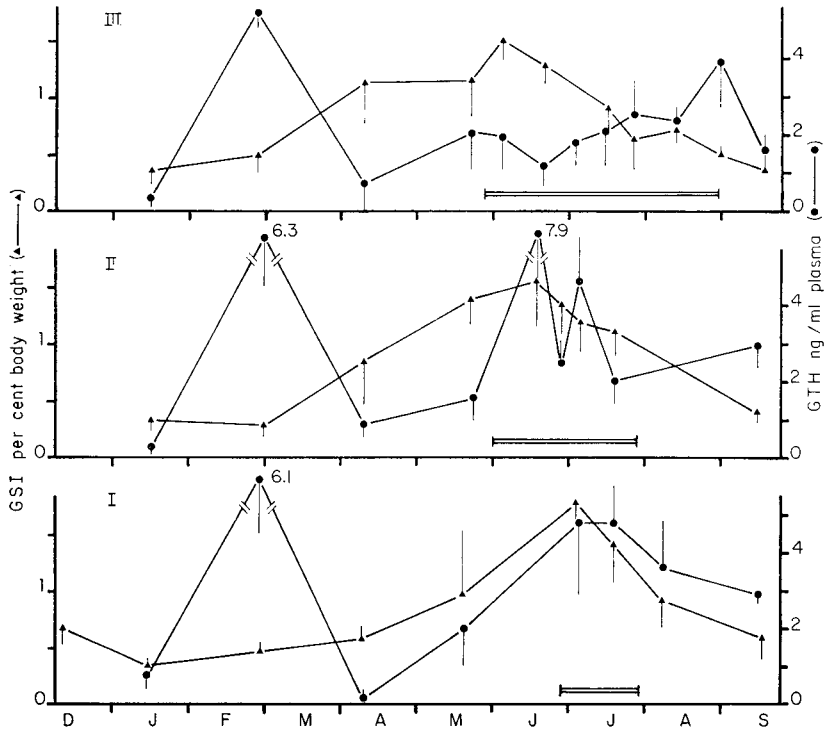

FIG. 6. — *Plasma gonadotropin pattern in relation to the gonadosomatic index (GSI) in the three experimental groups.* Experiment A 1973-1974. Horizontal line indicates the duration of the spawning period.

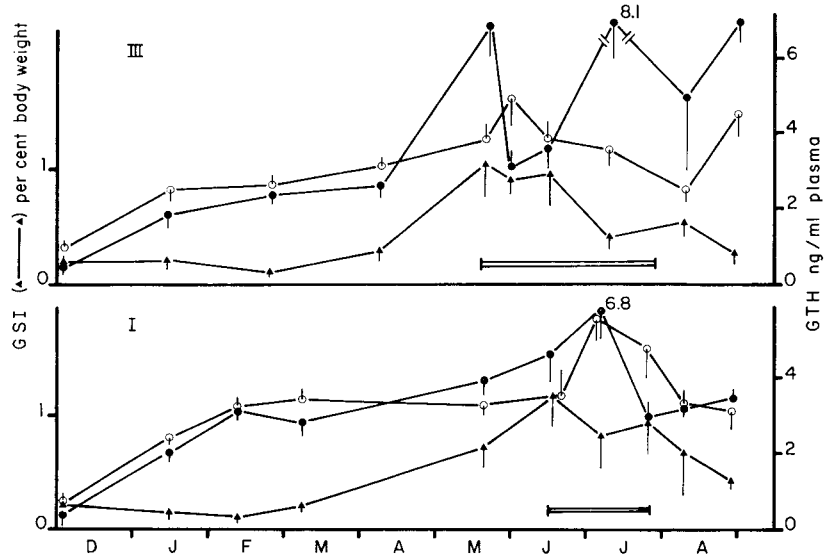

FIG. 7. — *Change in plasma gonadotropin and GSI in groups I and III (Experiment B* 1974-1975). GSI, GTH in continuously sampled animals, GTH in periodically killed animals.

Considering the number of degrees-days received by each group in the experiments A and B, it was found that under 700 degrees-days G_B did not appear since that stage of spermatogenesis occurred between 700 and 1 000 degrees-days, and spermiogenesis required more than 1 000 degrees-days.

TABLE 2

Date and duration of spawnings

Group	Spawning N°						
	1	2	3	4	5	6	7
I_{74}	2 006 (C) 27/6 (A) 6 (B)	2 092 12/7 6	2 601 27/8 2				
II_{74}.....	1 837 31/5 10	2 251 20/6 6	2 382 28/6 5	2 723 12/7 6	3 050 28/8 3		
III_{74}	2 006 18/5 16	2 249 8/6 12	2 585 24/6 7	2 959 9/7 4	3 165 18/8 3	3 865 10/8 6	4 202 26/8 4
I_{75}	1 912 19/6 9	1 446 13/7 5	2 695 24/7 13				
III_{75}	1 565 18/5 6	2 560 1/6 10	2 950 15/6 4	3 380 30/7 11	4 080 29/8 10		

(A) : date (first day of spawning) ; (B) : duration of spawning in days ; (C) : number of degrees-days since the beginning of December.

IV. — *Gonadotropin level in blood plasma.*

Experiment A (fig. 6). In 1974, the plasma immunoreactive GTH levels in the three groups increased significantly ($P < 0.05$) at the end of February, and then decreased later in April. A new, but less pronounced, rise of GTH appeared at the onset of active spermiogenesis, which was advanced with the temperature. In all groups the plasma GTH level rose continuously after April and was maximum just at the beginning of the spawning period.

Experiment B (fig. 7). At the beginning of the cycle, plasma GTH was identical in males which were sampled all the year round and in those killed monthly ; however, after May continuously sampled group III males usually had a lower GTH level ($P < 0.05$) than the periodically killed ones (sampled only once). This would suggest a harmful effect of repeated sampling.

V. — *Pituitary gonadotropin content.*

Experiment A (fig. 8). There was no significant difference among the groups until April 8th. On May 20th the situation remained unchanged in group I, but the immunologically reactive gonadotropin in the pituitary began to augment in group II and was higher ($P < 0.005$) in group III just before the first spawning. The same sharp rise in GTH concentration was also found in groups I and II when spawning started. On July 17th the pituitary gonadotropin content was low in all three groups after a drop in water temperature at the beginning of July. The temperature decreased to below 20 °C (mean decrease : 6 °C) at the end of this spawning period (fig.1). During the spawning period, the pituitary GTH content remained high but fell after the last spawning.

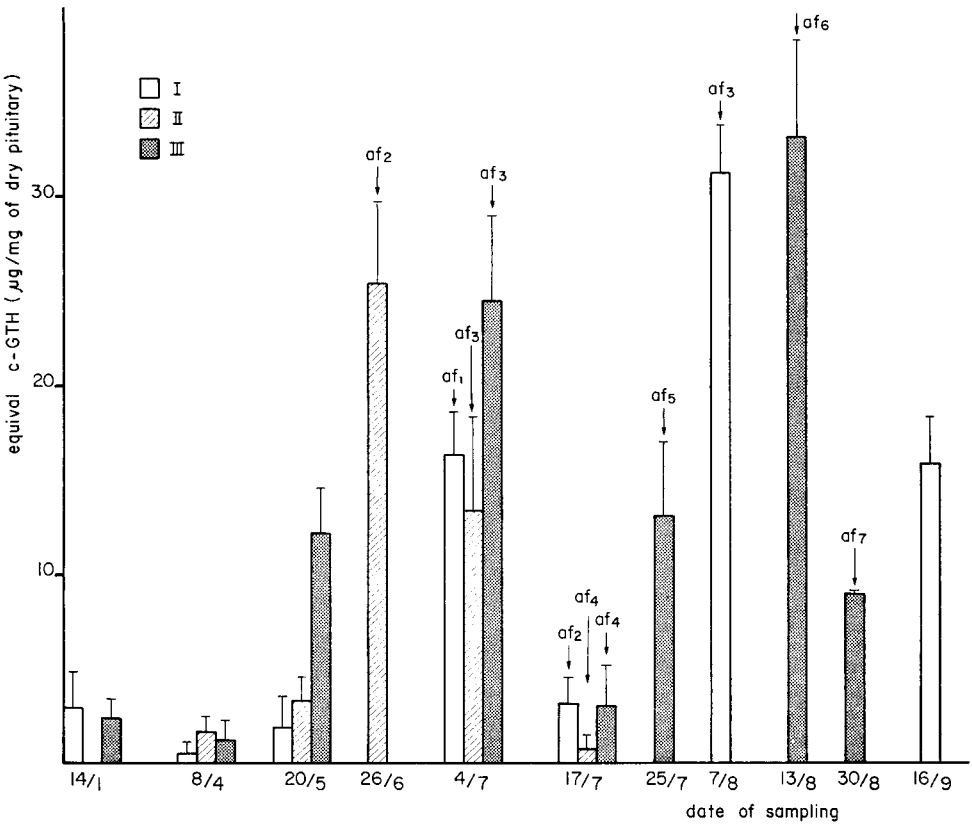

FIG. 8. — *Pituitary gonadotropin content in the different groups in* 1974. af_n : after n spawning.

Experiment B (fig. 9). The situation was the same in both groups until April 8th when pituitary GTH level augmented ; it remained significantly higher ($P < 0.005$) after spawning than before, suggesting a depletion of that content during spawning.

The values in I and III were always lower ($P < 0.005$) than those obtained in the corresponding groups in 1974.

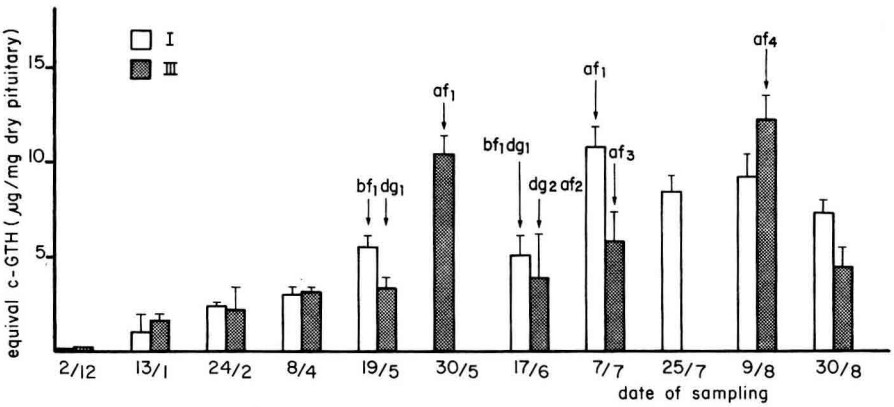

FIG. 9. — *Pituitary gonadotropin content in the* 1975 *groups.* af_n : after n spawning, bf_n : before n spawning, dg_n : during n spawning.

Discussion.

This work shows that the reproductive cycle of the tench is strongly influenced by the temperature regime. An increase of the rearing temperature induced an early onset of spermatogenesis and an extension of the spawning period. During the resting stage (end of the spawning season to April) there was no change in testicular activity ; the G_A remained at a maximum and began to form G_B only when the temperature rose above 10 °C, which level seemed to be critical for the initiation of type B spermatogonia multiplication. The same observation was reported by Burns (1976) studying *Lepomis gibbosus*. On the other hand, Ashan (1966) indicated that low temperatures were required to obtain a later stage of spermatogenesis (formation of primary spermatocytes in *Couescius plumbeus*). In the present experiment, there are indications that too a low winter temperature reduces the efficiency of pre-spermatogenesis. In groups II_{74}, III_{74} and III_{75} spermatogenesis was completed in May, but the number of spermatozoa in the testis was significantly higher in 1974 than in 1975. Similarly, the total number of all other types of germ cells was higher in 1974 than in 1975. The minimum temperature was much lower in winter 1975 (see figs. 1, 4). As most of the environmental condition were approximately similar between 1974 and 1975, it may be supposed that under prolonged low winter temperature, G_A multiplication was slowed down so that a limited G_A stock was accumulated. When the temperature rose above 10 °C in early spring, G_B multiplication was initiated. A larger stock of stem cells might also permit a larger number of spermatogenic waves. This was probably the case of the fish kept under the highest temperature regime, as shown in figure 5 ; spermatogenesis continued over a longer period of time in group III. At the end of the spawning season, all the germ cells, except G_A, disappeared from the testis of all groups before the drop in water temperature observed in autumn and when the level of circulating GTH as well as that

of pituitary GTH were still high. Therefore, the process of spermatogenes is stopped in mid-summer, although environmental conditions and gonadotropic levels still seemed favorable. In carp, the situation is quite different since new waves of spermatogenesis are seen after, or even during, the spawning season (Billard *et al*,, 1978 ; Weil, unpublished data). In tench, a lower temperature regime may be indispensable for reinducing a new spermatogenetic process, as discussed above.

Annual cyclicity may be needed in the temperature regime for a normal reproductive cycle. This has been suggested after some studies on cyprinids in which the spermatogenesis of fish kept under a constant temperature was inhibited or regressed (*Notemigonus crysoleucas*, de Vlaming, 1975 ; de Vlaming and Plaquette, 1977 ; *Carassius auratus*, Gillet *et al.*, 1977*a*, *b*). Spermatogenesis in the goldfish under a constant 30 °C temperature regime was inhibited, although the plasma GTH level remained high. Thus, temperature seems to act differently on the gonad and on the pituitary (Lofts *et al.*, 1968) ; the optimum temperature needed for the action of GTH on gonadal GTH receptors and for pituitary GTH secretion may be different.

In the present experiment, natural daily temperature cyclicity was also maintained. It has already been shown that this cyclicity is important for induction of spawning (Breton *et al.*, 1972) and possibly for the development of gametogenesis (Spieler *et al.*, 1977). Thermoperiod and photoperiod interaction should also be considered (Spieler *et al.*, 1977 ; Wiebe, 1968 ; Gillet *et al.*, 1978). Spawning occurred earlier and over a longer period of time at the highest temperature regime. There was no relation between the number of degrees-days and the time of the first spawning, which was recorded in a range of 1 565 to 2 006 degrees-days. Therefore, spawning depended more on a minimum water temperature ; in our experiment spawning never occurred below 20 °C, which corresponds to the normal spawning temperature in most cyprinid species. Baggerman (1969) made similar observations in the stickleback.

The pattern of GTH secretion was different in 1974 and 1975. The peak of plasma GTH in February 1974 in all the groups was quite similar to that described in trout (Billard *et al.*, 1978) where it was correlated with the onset of spermatogenesis. This correlation cannot be demonstrated in tench since the G_A had reached a maximum level and G_B multiplication occurred later. The sudden temperature elevation, inducing a rise in goldfish plasma GTH (Gillet *et al.*, 1977), cannot be shown in our experiment because the temperature rise was progressive and the peak was found in all the groups. Sampling may have coincided with a pulse of GTH secretion, but it is unlikely since the reproductive cycle was at a resting stage (Hontela and Peter, 1978). These pulses probably occurred during the spawning period, as shown by the fluctuation of plasma and pituitary GTH concentrations, and might correspond to the secretion peaks of a regular circadian rhythm, as observed in goldfish (Hontela and Peter, 1978 ; Gillet *et al.*, unpublished data). In some cases, (group III_{75}, figs 7 to 9), these drastic changes in plasma and pituitary GTH levels were obviously correlated with spawning, indicating that males may exhibit surges of plasma gonadotropin followed by a depletion of the pituitary content, as was observed in females of the same species (Breton *et al.*, unpublished data) and in other cyprinids (goldfish, Breton *et al.*, 1972 ; Stacey and Peter, 1978). The meaning of such surges is not known ; they may be involved in spermiation, sperm release, spawning behavior, or in the initiation of a new G_A cell population.

When spermatogenesis started, only low levels of GTH were measured, suggesting that GTH requirement was low at that stage. GTH level rose either in the blood or in the pituitary during active spermatogenesis, reaching a maximum level during the spawning period. Plasma GTH level rose earlier in fish reared in heated water, but pituitary GTH content did not differ significantly in the three groups, except in May 1974 (fig. 8). Enhancement of GTH secretion by temperature increase was probably due to higher pituitary responsiveness to hypothalamic neurohormone, as demonstrated in carp (Weil *et al.*, 1975).

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Résumé. Des tanches *Tinca tinca* mâles adultes ont été élevées pendant une période de 9 mois correspondant au déroulement du cycle reproducteur en étangs alimentés par des effluents de centrales thermiques. En 1974, les animaux ont été soumis à 3 régimes thermiques différents : groupe I à la température ambiante, groupe II température ambiante + 3 °C, groupe III température ambiante + 6 °C. L'expérience a été répétée en 1975 pour seulement les groupes I et III. Le cycle reproducteur et les effets des traitements thermiques ont été étudiés d'après l'analyse quantitative de la spermatogenèse, la durée de la période de fraie pendant laquelle les mâles ont présenté un comportement de reproduction et les mesures par radioimmunologie (RIA) de la gonadotropine (GTH) hypophysaire et plasmatique. Le RIA utilisant un système carpe s'est révélé suffisamment spécifique pour doser la GTH de tanche, laquelle est exprimée en équivalent c-GTH.

La spermatogenèse de la tanche est un processus discontinu qui débute au printemps et s'achève en été. Elle se déroule plus précocement dans les lots réchauffés. La période pendant laquelle des fraies se produisent spontanément dans les étangs d'élevage est considérablement allongée par le réchauffement des eaux (3 mois dans le groupe III contre 1 mois dans le groupe I).

En début de la spermatogenèse, les teneurs en GTH plasmatique et hypophysaire sont faibles, mais elles augmentent rapidement lorsque la spermatogenèse devient active (apparition des cystes de spermatogonies B et méiose). Les teneurs en GTH sont maximales au cours de la période de fraie où elles présentent des fluctuations importantes correspondant à des vidanges hypophysaires et des augmentations corrélatives dans le plasma.

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