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Studies on the Endocrine Glands of the Salmonoid Fish, the Ayu, *Plecoglossus altivelis* Temminck et Schlegel—VII.

The Hypothalamic Neurosecretory System of the Koayu exposed to the Artificial Photoperiods

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Abstract The annual, land-locked salmonoid fish, the Koayu, *Plecoglossus altivelis*, reared in the outdoor hatchery ponds and exposed to short-(8 hours daily), long-photoperiodic regime (16 hours daily) and natural day-length (control) were examined to elucidate the activities of hypothalamo-hypophysial neurosecretory complex and a possible interrelationship between the hypothalamic nuclei and maturation of the fish. The period of experiment extended from July 2, 1966 to January 22, 1967. Five females and five males collected at monthly intervals were supplied to inspect the growth, maturity and histological feature of the neurosecretory system. High mortalities were encountered between the months September and November in the short photoperiodicity, October and December in the control, and December and January in the long photoperiodicity, respectively, in parallel with the highest level of gonadal maturation and of cyanophilic gonad stimulating cells. Untill each prespawning season, the perikarya and juxta-somal axons of the preoptico-nucleic cells heavy loaded with AF-stainable neurosecretory material have been observed in each experimental group. Early in each spawning season, fine droplets of material in smaller amount are scattered around the nuclei of the cells. After that, a notable depletion of the material from the perikarya and juxta-somal axons is detected. Recovery phase of the neurosecretion is seen in the female fish survived beyond each spawning time and tided over the winter. On the contrary, all of the males were deceased untill the next year. Changes in the amount of the storage material in the neurohypophysis appear to be parallel with those of neurons. During each breeding time, on the other hand, the highest activity is reached by the nucleus lateralis tuberis which were stained with acidic dyes. These results suggest that there is a role of the light rhythm upon the maturation of the Koayu via hypothalamic neurosecretory system, and the possibility of artificial control of the breeding time in the fish.

It has been reported by the several investigators that the artificially controlled light upon the pond-cultured Ayu is largely concerned with the rate of maturation (Shiraishi and Takeda, 1961). If the Ayu, one of the typical annual and diadromous fishes, are kept under the short photoperiodic regime, a rapid gonadal development can be induced one to two months in advance of normal time. The long photoperiodic regime, on the other hand, brings about the delay of maturation and prolongation of the life-span of the fish. In such a case, the pituitary and also other endocrine glands showed notable histologic variations (Honma, 1966). In the Japanese char, a possible relationship between the secretory activity of the hypothalamo-hypophysial neurosecretory system and the maturation of gonads was suggested (Honma and Tamura, 1965 and 1967 a).

In order to examine the activity of cranial neurosecretory system of the Ayu that were exposed to short or long photoperiod, the histological and cytological changes of this system, growth rate and maturity of the fish were investigated with emphasis on the inter-

relationship among them. It appeared that the proper photoperiodicity provokes the function of gonadal cycle via hypothalamic neurosecretory system.

Material and Methods

The fish used in this study were supplied from the natural stocks of juvenile land-locked fish, "the Koayu", of Lake Biwa (Honma and Tamura, 1962 and 1963). On June 3, 1966, 1,500 individuals of fish, about 6 cm in body length and 2 g in body weight, were transferred to each outdoor pond of the hatchery attached to the Inland Water Fisheries Experiment Station of Niigata Prefecture in the suburbs of Niigata City. During one month, the fish were placed and exposed to natural water temperature and illumination. Three long hexagonal ponds, each extending about 36 m^2, were alloted to each experiment. One of them was covered with vinyl-made black sheet to adjust the length of daylight to 8 hours every day. The second one was equipped with two 40-watt fluorescent tubes to maintain the duration of exposure time for 16 hours every day. The third one was served as control group and exposed to natural illumination. The onset of artificially controlled lights was then on July 2, 1966. Three times per day, the fish were fed with the paste of commercially prepared powder for Ayu adding the chopped fresh fish and pupae of silk-worms.

To examine the bodily condition and histological changes of the cranial neurosecretory system of the fish, 10 specimens consisting of 5 females and 5 males were chosen from each of the ponds at approximately monthly intervals. After immersion in Bouin's fixative, length and weight of the fish were measured, and then a block of the brain including the hypothalamo-hypophysial region was removed, dehydrated, embedded in paraffin (paraplast), cut serially at 5–8 μ thickness chiefly in sagittal direction, stained with paraldehyde fuchsin (AF)-azan trichrome or impregnated with protalgol to discriminate the neural fibers, and observed under the light microscope. The histologic features of the gonads, pituitary, thyroid and adrenal glands of the Koayu under the natural condition at Lake Biwa have been described previously (Honma and Tamura, 1962 and 1963).

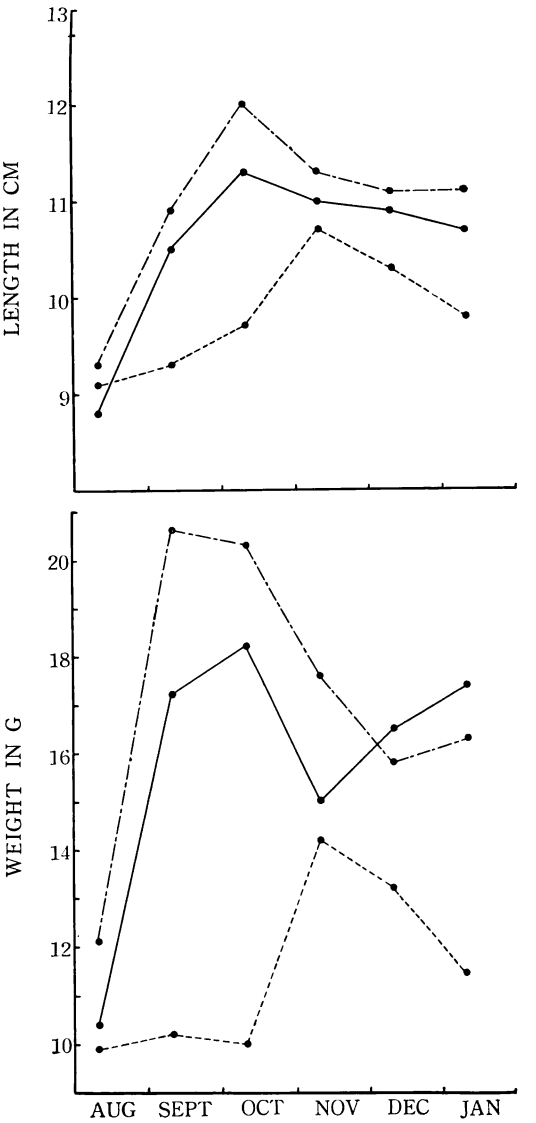

Fig. 1. Graph comparing growth rate of the Koayu, *Plecoglossus altivelis* (land-locked form), reared under the artificially controlled photoperiodic regime throughout the experment. The specimens illustrated include both sexes. Short periodic regime of 8 hours a day (dashed line), long periodic regime of 16 hours (stroked and dashed line) and the control (solid line) are shown.

Results

As indicated in the text-figures, the rate of growth, maturity of gonads, and mortality of each experimental series are satisfied in general to explain the effects of artificial photoperiods (Figs. 1-3).

At the time of beginning of the experiment (July 10, 1966)

The cyanophils regarded roughly as gonad stimulating cells (GS-cells) in the proximal pars distalis of the adenohypophysis of young Koayu are very meager (Pl. 1, 1), only a trace of differentiation of the cells is present (Pl. 2, 1). The AF-positive material stored in the neurohypophysial digits is not so large quantities. The nucleus preopticus as a group is stained well with aldehyde fuchsin (AF), each of perikaryon of the cell also contains a lot of AF-positive materials (Pl. 3, 1). The cytoplasm of the nucleus lateralis tuberis shows a fairly smooth and homogeneous condition (Pl. 2, 5). The axons leaving the perikarya of the nucleus preopticus are detected in the region of infundibulum, but not yet in the dorsal region of the neurohypophysis.

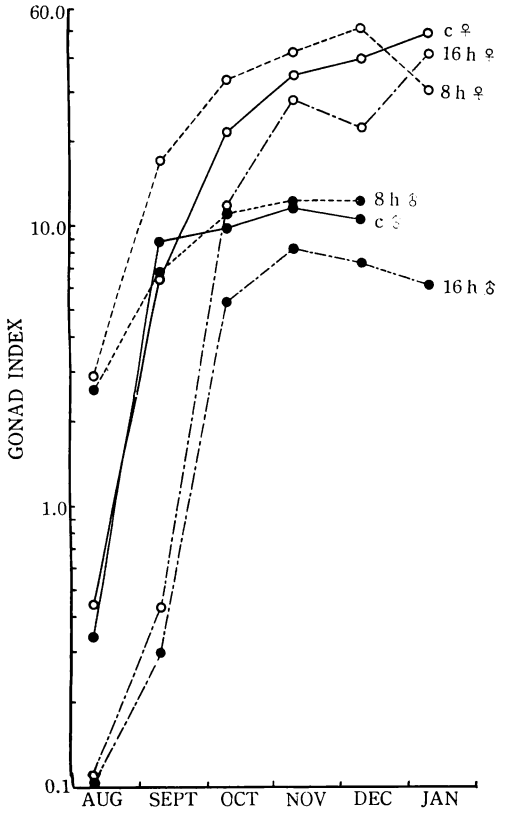

Fig. 2. Graph comparing gonad index (weight of ovary or testis/body weight × 100) of the Koayu reared under the artificially controlled photoperiodic regime. Short and long photoperiodic regime by sexes are shown.

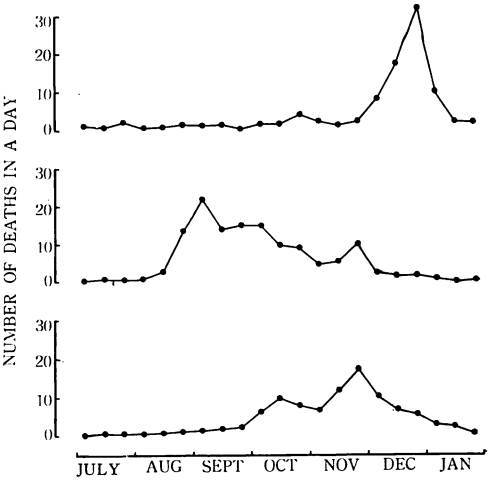

Fig. 3. Graph comparing the number of deaths of the Koayu reared under the artificially controlled photoperiodic regime, during the experiment. The upper line showing the long periodic regime of 16 hours a day, the middle short periodic regime of 8 hours, and the bottom control; counts were made on the two sexes combined.

One month after the onset of experiment (August 10, 1966)

Control

The differentiation of the GS-cells is distinct in this period (Pl. 1, 2). Although only the basal part of the cell indicates an affinity for dyes, nearly twice the number as compared with the preceding period is seen (Pl. 2, 2). An increase in the amount of storage of neurosecretory material in the neurohypophysis is remarkable. Most of the cells in the nucleus preopticus contain the large AF-stainable granules scattered over the perikarya (Pl. 3, 2). No marked change is detected in the nucleus lateralis tuberis.

Short photoperiodic regime

A remarkable increase in the number of GS-cells in the proximal pars distalis is seen accompanying no enlargement of their dimension (Pl. 1, 3). The cytoplasm of the cell is stained entirely with basic dyes (Pl. 2, 3). Rich storage material consisting of comparatively large granules is in the neurohypophysis. AF-positive material of the nucleus preopticus is found in the state of dot or bar, and a slightly indication of depletion is accompanied in the periphery of the cell nucleus (Pl. 3, 3). The perikarya of the nucleus lateralis tuberis show a homogeneous condition.

Long photoperiodic regime

Even one month after the onset of illumination, there is no detectable change in the cyto-histologic figure of the hypothalamo-hypophysial system of the 16 hours-exposure fish (Pl. 2, 4; Pl. 3, 4).

Two months after the onset of experiment (September 10, 1966)

Control

A large number of GS-cells are now prominent, cytoplasm of which are well dyed with basic stains (Pl. 1, 4). The amount of AF-positive storage material in the neurohypophysis reached the highest level (Pl. 1, 4). The perikarya and juxta-somal axons in the thickened appearance of the cells of the nucleus preopticus are filled with rough granules (Pl. 3, 5 and 6). Depletion of the granules is detected in some of the cells indicating somewhat the empty condition. Beaded but fine fibers are recognized in the infundibulum. Just beneath these AF-positive fibers, the cells of the nucleus lateralis tuberis stained strongly with acidic dyes are seen (Pl. 4, 8).

Short photoperiodic regime

Most of the proximal pars distalis are occupied with dilated GS-cells forming the complicated islands (Pl. 1, 5). A few cells in larger size appeared to be the castration cells. There is no detectable difference in the amount of storage materials in the neurohypophysis between the present and preceding periods (Pl. 3, 7). Because the affinity of the nucleus preopticus for AF is too weak, the depletion of the neurosecretory material from the perikarya is prominent. Besides this releasing picture, the juxta-somal and infundibular axons, as compared with control group, are not so heavily loaded with AF-stainable material. In some of the parikarya of the nucleus lateralis tuberis moderate number of vacuoles are seen (Pl. 2, 6).

Long photoperiodic regime

A distinct differentiation of the GS-cells is not yet begun in this period, and dense neurosecretory material is stored in the neurohypophysis (Pl. 1, 6). Although the cells and juxta-somal axons of the pars magnocellularis are stained well, those of the pars microcellularis are occupied with rather large granules acattered (Pl. 3, 8). The tract near the infundibular stalk to dorsal neurohypophysis is distinct by having AF-stainable material (Pl. 4, 7). No marked change is found in the nucleus lateralis tuberis.

Three months after the onset of experiment (October 2, 1966)

Control

The differentiation of the GS-cells is remarkable, and the coarse granules are recognized in the cytoplasm. The amount of the neurosecretory material in the neurohypophysis is not so large as that of the preceding period. The granules located nearer to the periphery of the cell nucleus of the nucleus preopticus are larger than those more eccentric to the nucleus (Pl. 4, 1). As a result, the marginal area of the cell was light without stainable materials.

Short photoperiodic regime

Although the number and amount of the GS-cells with rich granular cytoplasm now reach the highest level, the material in the neurohypophysis is not so dense. In spite of a few amount of AF-positive material in the perikarya of the nucleus preopticus, the material in the cell of larger size is more distinct than that in smaller one (Pl. 4, 2). There are no noticeable axons with secretory product. On the other hand, a fairly granular condition can be observed in the perikarya of the nucleus lateralis tuberis.

Long photoperiodic regime

The differentiation of the GS-cells is noticed at present, though a nearly half of

the basal part of the cell is stained with dyes. The neurohypophysial digits include a dense neurosecretory material. A considerable number of the perikarya and juxta-somal axons of the cells of nucleus preopticus contain a fairly large granules suggesting the active transportation of the neurosecretory product (Pl. 4, 3). The cells of the nucleus lateralis tuberis take acidic dyes strongly (Pl. 2, 7). These pictures are very similar to those of the control fish one month after the onset of experiment.

Four months after the onset of experiment (November 5, 1966)

Control

As compared with preceding period, there is only a slightly change in the amount of AF-stainable cells in the proximal pars distalis, except a considerable decrease in the storage neurosecretory material of neurohypophysis. With regard to the activity of the nucleus preopticus, no sign of significant difference between this and preceding periods was observed (Pl. 4, 4). However, vacuoles in the perikarya of the nucleus lateralis tuberis are evident.

Short photoperiodic regime

As shown in the text-figure, from September to November, a high mortality was encountered in this experimental group (Fig. 3). Although the survivors examined, which delayed in their maturity, still maintain the ripe gonads, the present period is equivalent to post-spawning one. A marked decrease in the dimension of the GS-cell islands and in the amount of storage neurosecretory material of neurohypophysis is evident. The cytoplasmic contents of some of the GS-cells are condensed into several large colloid droplets. On the other hand, an early indication of increase in the amount of neurosecretory products in the perikarya and juxta-somal parts of the nucleus preopticus and in the nucleus lateralis tuberis can be easily observed (Pl. 2, 8).

Long photoperiodic regime

The highest activity of the GS-cells may be now reached in this period. However, the feature of the nucleus preopticus is not so different from that in the preceding period, in spite of the progress of activity in having some vacuoles in the cells of the nucleus lateralis tuberis.

Five months after the onset of experiment (December 4, 1966)

Control

From October to December, in the control group there was seen a high mortality. It seems that this month corresponds to the postspawning period. Even in the survivors, a decrease in the number and amount of the GS-cells and neurosecretory material in the hypophysis is evident. Condensed, large colloid-like droplets are seen in the cytoplasm of a few GS-cells. A considerable number of the lacunae, varying in size, are developed in the rostral pars distalis of the adenohypophysis. Generally, both the nucleus preopticus and nucleus lateralis tuberis are stained well with dyes. Unless silver impregnation is applied, all axons projected from the neurosecretory cells are not so well defined (Pl. 4, 6).

Short photoperiodic regime

The individuals tided over their natural life-span are very few. Except a slightly increase in the amount of AF-stainable material in the perikarya of the nucleus preopticus, it is difficult to discriminate the cytohistologic picture of the present specimen as compared with that of preceding one.

Long photoperiodic regime

The number of deaths rises rapidly in this month (Fig. 3). Roughly speaking, nearly a half of the dimension of proximal pars distalis is still occupied with GS-cells, accompanying a slight indication of release of the cell contents. The affinity for dyes of the cells of both preoptic and latero-tuberal neurosecretory neurons is fairly strong.

More than a half year after the onset of the experiment (January 22, 1967)

Control

Normally, all male fish were deceased untill the next year, and if the fish could survive for considerably long time beyond spawning time, we have named them as "Etsunen-Ayu" or "Otsunen-Ayu". In this control group, only six females have survived

at the end of the experiment. Although the amount of the GS-cells and neurosecretory material in the hypophysis and in the neurosecretory cells are not so exceedingly large, the pictures seem to attain a certain recovery phase. However, the gigantic cyanophils (GS-cells) in small number, diagnosed as the dilated castration cells, are encountered.

Short photoperiodic regime

We could only examine the six females which indicate a low gonadal index. The cyto-histological pictures of this group are very similar to those of the control one. The dilated cells containing colloid-like substance are also found in the proximal pars distalis.

Long photoperiodic regime

A decrease in the GS-cell islands is not so striking, and the cytoplasmic condition of each cell is heterogeneous containing some vacuoles. In spite of moderate amount of storage neurosecretory material in the neurohypophysis, rather much material is demonstrated in the perikarya of both neurosecretory cells (Pl. 4, 5).

Discussion

There are a considerable number of papers on the seasonal or experimentally induced changes in the hypothalamo-hypophysial neurosecretory system of the osteichthyan fishes. Little is known about this system of fish or fish-like animals (cyclostomes) exposed to artificially controlled light under the laboratory condition (Öztan and Gorbman, 1960; Sathyanesan, 1965; Öztan, 1966), and much less is under the outdoor ponds for the aim of propagation. The role of the light on the hypophysis-gonadal function via cranial neurosecretory system is extensively discussed and postulated by Critchlow and Wolfson (1963), and Wurtman (1967). If the vertebrate animals are subjected to externally continuous or intermittent illumination in various manners, excessive depletion of AF-stainable material from the perikarya of the cells of the nucleus preopticus or nucleus supraopticus is resulted (Kumamoto and Shimizu, 1955; Oksche *et al.*, 1958; Fiske and Greep, 1959, *etc.*). In the case of the Koayu that is considered as the short term photoperiodic fish, the neurosecretory system and the gonadal maturation are highly stimulated by the short photoperiodic regime. On the contrary, the long photoperiodic regime brought about a pronounced delay of the reduction of the materials produced in the neurosecretory cells and of hypophysis-gonadal activity. These results are in good accordance with the aim of the fish-culturists who want to obtain the ripe eggs of the Ayu or Koayu whenever they like.

In his serial experiments on the maturation of the Ayu influenced with photoperiodicity, Shiraishi (1965 a, b, c, d and e) reported an appropriate day-length for exhibition or inhibition of maturation, maximum or minimum intensity and wave length of artificial lights, and time of the onset of effective treatment. He also mentioned that removal of eye upon the maturation of the fish that are exposed to short or long day-length cannot be produced any significant difference as compared with the maturation of intact fish. This result suggested that any organ or tissue other than ophthalmus responds to light rhythm, and then transmits the stimuli to the central nervous system. It is therefore imagined by us that the supposed receptors may be the pineal body and skin. It would be of value to test whether pineal and skin are more responsive or sensitive to the photoperiodicity than other organs or tissues.

A fairly reasonable evidence is demonstrated experimentally and histologically on the role of the cranial neurosecretory system of the lower vertebrates, such as frogs and freshwater fishes. The nucleus preopticus seems to be much concerned with the ovulation or osmoregulation, and the nucleus lateralis tuberis plays a possible function to control the gonadotropic activity of the hypophysis (von Brehm, 1958; Fridberg and Olsson, 1959; Billenstein, 1962 and 1963; Stahl and Leray, 1962; Öztan, 1963; Dierickx, 1965, 1966 and 1967; Szabo and Molnar, 1965; Honma and Tamura, 1967 a, *etc.*). The present investigation on the Koayu is also inclined toward the hypothesis mentioned above.

Despite a typical annual fish, seasonal changes in the cranial neurosecretory complex of the Koayu under the photoperiodicity are evidently ascertained by the present histolo-

gical techniques like those of other fishes reported, but none were confirmed in the caudal neurosecretory one which is peculiar to the actinopterygian fishes (Honma and Tamura, 1967 b). The pattern and typical appearance of AF-stainable neurosecretory complex under electric stimulated and different external conditions were represented as diagrams (Jasinski, *et al.*, 1966; Jasinski and Gorbman, 1967). From the cytological criterion, cyclic changes in this complex described by the present time seem to be comparable to these designs.

Anyhow, much information on the precise interrelationship between hypothalamic neurosecretory activity and maturity of commercially important fishes is wanted to control the breeding season and maintain the seeds and fry of the proper fish at any time.

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アユの内分泌腺に関する研究—Ⅶ. 光周期を統御したコアユの視床下部神経分泌系　本間義治・鈴木淳悦. 魚類における視床下部—下垂体神経分泌系の活動，ならびにこの視床下部神経分泌核と成熟との相関関係を解明するために，ビワ湖産コアユを材料として選び，1966 年 6 月 3 日に新潟県内水面水産試験場の屋外飼育池へ収容した．そして，人工的に光周期を調整し，短日処理区（8 時間照射/日），長日処理区（16 時間照射/日），対照区に分け，7 月 2 日から実験を開始して 1967 年 1 月 22 日まで続けた．この間，毎月 10 日頃に 1 回，大体♀♂各々 5 尾を取りあげ，固定のうえ生長度と成熟度をしらべ，さらに組織標本を作って視床下部下垂体神経分泌系を観察した．8 時間区では 9 月から 11 月の間に，対照区では 10 月から 12 月，そして 16 時間区では 12 月から 1 月の間にもっとも死亡率が高く，これと平行して生殖腺の成熟度ならびに塩基（青色）好性の生殖腺刺激細胞の活動も最高に達していた．また各実験群共それぞれの産卵前期までに，視束前核細胞の胞体ならびに起始円錐とその付近の軸索中には，AF 陽性の神経分泌物が充満しているのがみられる．しかし，産卵の初期にはこの分泌物は，神経分泌細胞の核のまわりに小滴として少量認められるに過ぎない．引続き，胞体と軸索起始部において神経分泌物の顕著な放出枯渇がおこるが，産卵後も生延びて冬を迎えることができた少数の雌魚の視束前核細胞には，再び神経分泌物の生産蓄積がうかがえる．これに反し，♂魚はことごとく斃死し，翌年まで生存したものはなかった．この視束前核で作られた分泌物（後

葉ホルモン）を貯蔵している神経葉のAF陽性物質の量も，全く視束前核神経元の像を追い平行して変動している．一方，酸好性色素で染まる隆起部外側核の細胞の活動像も，それぞれの実験群の産卵期には最高に達する．上述した結果は，コアユの成熟に視床下部神経分泌系を介して，光のリズムが役割を果していることと，したがって魚類の産卵期を人工的に統御できる可能性とを示している．

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