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HISTOPHYSIOLOGY OF HYPOTHALAMO-HYPOPHYSIAL SYSTEM OF SOME MARINE FISHES IN RELATION TO SPAWNING TYPES

By E. S. Moiseeva

At the present time the peculiarities of hypophysial regulation of gametogenesis have been quite fully studied in a series of the freshwater, diadromous and semi-diadromous species of fish which have been the traditional objects of fish breeding. The majority of these belong either to the monocyclic species, or to those which spawn only once during the reproductive season (Gerbil'skii, 1947; Barannikova, 1965, 1969). The number of works concerning those species of fish which spawn intermittently is not high (Kazanskii, 1949; Barr, 1968; Hoar, 1969). Many facets of the regulation of intermittent spawning remain unexplained.

In recent years there has appeared in the literature persuasive data on the importance of the neuro-hormones of the hypothalamic region of the brain in the regulation of the hypophysial functions in vertebrates, including fish (Polenov, 1968; Jorgensen, 1968; Aleshin, 1971). Taking this into consideration, it is extremely important to elucidate the peculiarities of

*Nos. in the right hand margin indicate corresponding page nos. in the original. Trans.
the functioning of the hypotalamo-hypophysial complex in the course of the sexual cycle of fish.

Since a great variety of morphophysiological adaptations occur in the reproductive system of fish, and it is often possible to find within a single order or even a family species with very different reproductive peculiarities (Ball, 1960; Hoar, 1969), there is a great interest in comparing the hypothalamo-hypophysial system of closely related species of fish, which possess many traits of ecological similarity, but differ in spawning patterns. In our view, such an ecological-histophysiological approach would permit the exposure of those functional peculiarities of the basic regulatory endocrinal centres in fish, which condition the development and course of such important species adaptations as total and intermittent types of spawning. The solution to these questions is also of considerable interest in connection with the working out underway in recent years of the biological principles of artificial breeding of marine fish.

Representatives of the Gobiidae family, plentiful in the Azov-Black Sea basin, are suitable objects for conducting work on the plan indicated. Among them are species with a brief total spawning (toad-goby, *Gobius batrachocephalus*) and others with protracted and repeated intermittent spawning (*"round goby",* *Gobius melanostomus*). The work was executed in two stages: in the first stage the morphology of the hypophysis of gobies and partially of the hypothalamus was studied and the morpho-functional modifications of the hypothalamo-hypophysial system during the sexual cycle of fish were analyzed. In the second
phase an attempt was made to characterize quantitatively the level of gonadotropic activity of the hypophysis of the intermittently spawning "round goby" at various stages of sexual ripening and spawning.

Since the gonadotropic hormone of the "round goby" evidently differs qualitatively from the gonadotropines of other fish species, as the determination of its activity by biological testing methods showed (Goncharov, 1971, and our own data), we attempted to conduct a quantitative evaluation of the functional state of the hypophysis by means of an immunological investigation of the gland. In recent years immunological methods have been ever more widely employed in investigations of hormones in the hypophysis of fish (McKeown, van Overbeeke, 1971; Breton et al., 1972). In addition, since it is well known that modifications of the mass of endocrinal glands in the process of vital activity can be reliable indicators of their activity (Kabak, 1968), we also conducted an analysis of changes in the average mass of endocrinal glands taken at various stages of sexual ripening.

Males and females of Gobius batrachocephalus and G. melanostomus of various ages and sizes, which were collected in all seasons of the year in the regions of Kerchensk strait (Kerchenskii proliv) and Kazantip gulf (Kazantipskii zaliv) of the Sea of Azov, served as the material.

Immuneological investigation of the hypophysis of the "round goby" during the reproductive cycle was conducted with the direct collaboration and under the direction of V.S. Apekin, in connection with which we offer him our sincere thanks.
For the histological analysis, material from 148 specimens of "round goby" (77 females and 71 males) and 175 toad-goby individuals (114 females and 61 males) was used; the method of treatment was expounded in a previous work (Moiseeva, 1973).

The immunological and gravimetric analyses were conducted on the acetone-dry glands of the "round goby". The nature of the material and the method of weight analysis has been described earlier (Moiseeva, 1972; Apekin, Moiseeva, 1971, 1973).

For the immunological analysis of the hypophysis of rabbits, breeds of chinchilla were immunized at the age of 8-9 months with glands of sexually immature and sexually mature females and males with gonads at IV, IV-V, and VI-III stages of maturity. Immune serum, obtained in the hypophysis of females at the IV, IV-V stages, was chiefly used in the work.

Analysis of the antigenic composition of the hypophysis was carried out in experiments of immuno-diffusion, based on Ouchterlony, as modified by V.S. Apekin (Apekin, 1967). Both hypophysial extracts and also isolated glands were analyzed. The working method was given in detail in an article (Apekin and Moiseeva, 1973).

The study of the overall morphology of the hypophysis in the toad-goby and in the "round goby" indicated that it is similar in both goby species. The hypophysis of fish consists of four morphologically distinctly differing sectors, which in the terminology of Pickford and Atzl (Pickford, Atzl, 1957), we have
designated as pro-, meso- and meta-adenohypophysis (illus. 1). We distinguish six basic types of cells in the adenohypophysis of gobies (illus. 2). In addition, in the hypophysis of sexually immature fish there are present in large quantities small chromophobe or slightly acidophilic cells, which are found singly in sexually mature gobies. We surmise that these cells are the poorly differentiated components from which afterwards develop definite types of cells. Therefore, we do not consider them as independent types.

The proadenohypophysis is in area the smallest of the sectors of the hypophysis. In it can be distinguished two different types of cells: the acidophilic, which are extremely sensitive to azo-carmine and orange G, and the barely-stainable, conventionally so-called due to their poor colourability by all the dyes used in the work, with the exception of lead haematoxylin. The acidophilic cells predominate in the proadenohypophysis. They are of varying shape, the cytoplasm often being filled with acidophilic granules. The barely-stainable cells bound the anterior parts of the roots of the neurohypophysis, and have an elongated shape and distinct cellular boundaries (cf. illus. 2, a, b).

The mesoadenohypophysis occupies the greatest area in goby hypophysis sections. It contains two types of basophilic cells (primary and secondary) and a single type of acidophilic. Both types of basophilic are equally well coloured by para- and Schiff's reagent, but they are clearly distinguished from one another by a number of morphological and functional features.
Illus. 1. Diagram of the arrangement of cellular elements in the hypophyses of the toad-goby and "round goby".

1 – proadenohypophysis, acidophilic cell zone; 2 – proadenohypophysis, zone of barely stainable cells (accepting only lead haematoxylin); 3 – mesoadenohypophysis, region of location of basophilic cells of secondary type (thyrotropic); 4 – mesoadenohypophysis, acidophilic cell zone; 5 – mesoadenohypophysis, region of location of basophilic cells of primary type (gonadotropic); 6 – meta-adenohypophysis, acidophilic cell zone; 7 – neurohypophysis (objective 10X, ocular 4X).

Illus. 2. Basic goby adenohypophysis cell types:

a – proadenohypophysis, acidophilic cells; b, b1 – barely stainable cells (b- paraldehyde-fuchsin, azo-carmine, b1 – lead haematoxylin); c, d, e – mesoadenohypophysis cells [c – basophilic primary type (gonadotropic), d – basophilic secondary type (thyrotropic), e – acidophilic]; f – meta-adenohypophysis acidophilic cells (paraldehyde-fuchsin, azo-carmine) (objective 90X, ocular 10.5X).
Primary type basophilic cells predominate in the meso-
adenohypophysis. They are located in the middle and peri-
pheral sections of the hypophysis, and envelop the meta-adeno-
hypophysis zone in a "dipper" (cf. illus. 1, 2, c). They are
large, polygonal cells with big rounded or oval nuclei
and well defined cytoplasmic processes.

Secondary type basophilic cells form a comparatively
small and compact cluster on the boundary of the pro- and meso-
adenohypophysis, near the large roots of the neurohypophysis.
They are small, angular cells, with barely discernible cellular
boundaries. The cell nuclei often have an elongated ellipsoidal
shape (cf. illus. 1, 2, d).

Acidophilic cells of the mesoadenohypophysis are easily
stained by azp-carmine and orange. These cells are arranged
in one or two rows along the roots of the neurohypophysis (cf.
illus. 1, 2, e).

In the meta-adenohypophysis we distinguish a single type
of palely staining acidophilic cells. The cell cytoplasm does
not accept Schiff's reagent or paraldehyde-fuchsin (cf. illus.
2, f).

A comparison of the histological pictures of the hypophysis
of sexually immature and sexually mature gobies indicated that
in the sexually immature fish, the zone of mesoadenohypophysis
basophilic cells of the primary type is practically undefined,
(toad-goby) or defined extremely poorly ("round goby").
Since, as is generally known, the thyrotopic elements are first
to form and to begin to function in ontogeny (Yakovleva, 1970; Ball and Baker, 1969), we assumed that the basophilic cells of the mesoadenohypophysis, equally well developed in sexually immature and sexually mature gobies, are connected with the thyrotropic function, and that basophilic cells of the primary type, differentiated only in sexually mature fish, fulfil the gonadotropic function. Staining of sections of goby hypophysis with lead haematoxylin showed that this dye is accepted selectively by only a single type of cell in the hypophysis, namely the barely stainable cells of the proadenohypophysis. On this basis we supposed that these cells in the goby adenohypophysis are connected with the production of the adrenocorticotropic hormone (Olivereau, Ball, 1963; van Oordt, 1968).

The hypothalamo-hypophysial neurosecretionary system of the toad- and "round" goby is in its general morphology indistinguishable from those described for the majority of bony fish species (Polenov, 1968). It consists of two nuclei (lateral and preoptic ), conforming to the tracts which unite the nuclei with the hypophysis and the neurohypophysis. The cells of these nuclei are easily distinguished among themselves by the ability of the cytoplasm to be stained by paraldehyde-fuchsin. Cells of the lateral nucleus do not accept paraldehyde-fuchsin, while cells of the preoptic nucleus are clearly coloured. In both species of fish neurosecretionary cells of the lateral morphological nucleus did not manifest any noticeable changes during ripening or spawning of the gobies. Cells of the preoptic nucleus did not change substantially in the course of the sexual cycle, as will be shown below.
CHANGES IN THE GONADOTROPIC ELEMENTS OF THE HYPOPHYSIS AND NEUROSECRETIONARY CELLS OF THE PREOPTIC NUCLEUS DURING THE GOBY SEXUAL CYCLE

Prespawning period. In gobies of both species, caught in the prespawning period of the reproductive cycle (for "round goby" females, this means the period before the first spawning), changes in the mesoadenohypophysis basophilic cells of primary type, which fulfil the gonadotropic function, are of a similar nature and in outline consist in the following.

With the development and ripening of the sexual glands, the region of gonadotropic elements in the goby hypophysis markedly increases, and signs of their active functioning are observed. They are expressed in the growth of basophilic cells, in the appearance, accumulation and elimination from the cytoplasm of gomori- and PAS-positive granules, and also in the destruction of a part of the cells and their transformation into a basophilic secretion (illus. 3, a).

At the same time, a large quantity of gomori-positive granules are noted in the cytoplasm of cells of the preoptic nucleus of gobies (illus. 3, b). In fish caught immediately before spawning, it is possible to see the concentration of 110 granules in the processes of cells, and the patterns of migration of the neurosecretory substance along the fibres of the preoptico-hypophysial tract, which is indicative of the elimination of secretionary material from the cells. Evidently, the neurosecretory cells are found in the functional states of "filling" and "eliminating", described for the secretionary cycle of these cells by A.L. Polenov (1968).
The states of ovaries and testicles in toad- and "round" gobies in the prespawning period of the reproductive cycle are also very similar. In the period of growth and ripening, the gonads of gobies were discovered in the III, IV and IV-V stages of maturity, and the gonosomatic index was accordingly equal: for toad-goby females, 2.90 (variations from 0.7 to 5.4), 15.35 (8.6-24.8), 29.10 (21.5-34.8); while for the males, 0.70 (0.20-1.46), 1.93 (1.1-3.7), 3.83 (2.4-5.1); for "round goby" females, 2.74 (1.9-3.9), 6.27 (4.2-8.7), 17.70 (12.4-24.9), and for males, 0.97 (0.49-1.39), 2.07 (2.52-3.06), 2.82 (1.23-6.09).

Illus. 3. Gonadotropic elements of the hypophysis (a) and neurosecretionary cells of the preoptic nucleus (b) of gobies caught in the prespawning period (a—PAS-reaction, orange, b—paraldehyde-fuchsin, azocarmine; objective 90X, ocular 6X).
Postspawning period. The morpho-functional peculiarities of gonadotropic elements of the hypophysis, of neurosecretionary cells of the preoptic nucleus, and of the sexual glands, which are connected with differences in spawning types of toad- and very clearly "round" gobies, are revealed in the postspawning period of the sexual cycle.

In the toad-goby, the postspawning period is prolonged and extends for around five or six months. During this period the histological pictures of the hypophysis and the sexual glands substantially changes. On the basis of this we have provisionally divided the whole postspawning period into two stages - early and late, and designated the condition of the gonads correspondingly as early and late VI-II stages of maturity.

The early VI-II stage in males and females continues for one to one-and-a-half months from the moment of laying of the sexual cells. The gonosomatic index in gobies at this period is still quite high, and for females it is 2.67 (0.9-4.5), for males - 1.00 (0.6-1.6).

The ovary of fish caught in the first 10-20 days after spawning is very flaccid. The composition of the sexual cells is made up of a small quantity of oocytes of protoplasmic growth, which differ in size. In comparison with that noted immediately after spawning, there is observed, roughly from the middle of the early VI-II stage, some increase in the mitotic activity of the oogonia. In separated sections of the ovary are found "nests" of oocytes of the synaptic path. Their number varies from 12 to 26 per section in fish caught during the early postspawning period.
In the testicle at this period is observed a large number of spent tubules with thickened walls of connective tissue; in the narrow spaces it is possible to see negligible remains of unspent spermatozoa. However, the area of cells of interstitial tissue is at roughly the same level as in fish at the IV stage of maturity (855.09±92.24). The follicles of the seminal vesicles are also in the majority devastated, but the glandular epithelium is still high.

![Image of gonadotropic elements of the hypophysis of toad-goby with gonads in the early VI-II stage:](image)

**Illus. 4.** Gonadotropic elements of the hypophysis of toad-goby with gonads in the early VI-II stage:

- a - middle region of mesoadenohypophysis (paraldehyde-fuchsin, Helm's mixture);
- b - peripheral region of mesoadenohypophysis (paraldehyde-fuchsin, azo-carmine) (objective 90X, ocular 60X).
In the hypophysis of the toad-goby, there is still observed in the early postspawning period a very large number of gonadotropic elements, similar to those of fish at the IV-V stage of maturity (illus. 4, a). In the cytoplasm of these elements, the process of accumulation of secretory granules goes on. Certain cells contain such quantities of gomori- and PAS-positive granules that their nuclei lose their regular rounded shape and acquire angular outlines. In our view, the pictures described indicate a delay in the elimination of hormonal material from the hypophysis. Coincidental with this in the peripheral sections of the mesoadenohypophysis and on the border of the meta-adenohypophysis, it is possible to see vacuoles of varied size and shape, probably formed as a result of holocrine secretion of a part of the gonadotropic elements (illus. 4, b). Some vacuoles are filled with homogenous basophilic PAS-positive secretion.

The late VI-II stage lasts three or four months, from the end of May through August-September. In this period the gonads become more compact, and the gonosomatic index decreases: for females it is 0.57 (0.3-0.9), and for males, 0.50 (0.2-0.9).

By comparison with those in the early VI-II stage, the number of "nests" of developing oocytes in the ovaries of gobies in the late VI-II stage increases substantially, varying from 20 to 70 per section. Processes connected with the resorption of remaining spermatozoa and cells of the last stages of spermatogenesis, also go on in the testicles. The area of cells
of interstitial tissue decreases noticeably (260.52±34.48).
In addition, at this time the beginning of reproduction of spermatogonia is observed in the testicle.

In the hypophyses of fish caught during late postspawning period, a massive degeneration and destruction of glandular components connected with the gonadotropic function are observed. In the peripheral and middle regions of the mesoadenohypophysis, and also on the boundary of the meso- and meta-adenohypophysis, are noted "hollow" spaces, extremely varied in shape and size, and accumulations of a basophilic secretion. The remaining basophilic cells of the primary type are not numerous. They consist of deformed nuclei, surrounded by "scraps" of barely-stained and degranulated cytoplasm. The sizes of cell nuclei decrease, and the nuclei acquire an irregular elongated form with a striated depression along the long axis (illus. 5, a). The pictures described point to the depletion of gonadotropic elements.

![Image of gonadotropic elements and neurosecretory cells](image-url)
Simultaneously with the lysis and degeneration of the gonadotropic elements of the hypophysis, other cells of the adenohypophysis (barely-stainable cells of the proadeno-hypophysis, basophilic of the mesoadenohypophysis of secondary type and acidophilic cells of the meta-adenohypophysis, which fulfill different functions) also undergo substantial changes (table 1).

<table>
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<th>Месен, стадия зрелости</th>
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<th>3</th>
<th>4</th>
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<tr>
<td>5 ацетофильные</td>
<td>6 слабопигментированные</td>
<td>7 ацетофильные</td>
<td>8 базофильные 1 типа</td>
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<td>10,39 ± 0,70</td>
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<td>19,31 ± 0,92</td>
<td>18,67 ± 0,75</td>
<td>19,93 ± 0,88</td>
</tr>
</tbody>
</table>

Table 1.

Sizes of nuclei (in μm³) of various types of hypophysis cells of the toad-goby (females), caught in the prespawning period.

Legend: 1. Month, stage of ripeness (maturity)
2. Proadeno-hypophysis
3. Mesoadeno-hypophysis
4. Meta-adenohypophysis
5. Acidophilic
6. Barely stainable
7. Basophilic of primary type
8. Basophilic of secondary type
9. March
10. June
From table 1 it is apparent that, by comparison with those fish caught before spawning, the sizes of the nuclei of the types of cells indicated from the hypothysis of gobies caught in the post-spawning period, are certainly decreased.

In spent gobies with gonads in the early and late VI-II stage of maturity, the state of neurosecretionary cells of the preoptic nucleus differs materially from their condition before spawning. During the early postspawning period, degranulation of part of the neurosecretionary cells is observed. The arrangement of elements in the nucleus becomes looser, and hollow optical spaces arise between the cells. Not infrequently it is possible to see in these spaces bodies and "globes" of neurosecretionary substance. The condition of the cells of the preoptic nucleus which is described is evidently analogous to the "elimination" and beginning of "devastation" phase (Polenov, 1968).

In the preoptic nucleus of gobies with gonads in the late VI-II stage of maturity, the looseness of the arrangement of cellular elements becomes even more pronounced. Granules are not revealed in the cytoplasm of the majority of neurosecretionary cells. Many cells consist of "bare" bubble-like nuclei. Close to the neurosecretionary cells, and sometimes among them, is observed a large number of globular formations which vary in size (illus. 5, b). In separate preparations it is possible to see pictures of the formation of gomori-positive "globes" in the cytoplasm of neurosecretionary cells. The described condition of neurosecretionary cells of the preoptic...
nucleus during the late stage of the postspawning period indicates that processes which correspond to the "devastation" or "high activity" phase, predominate in these cells.

In the "round goby", the postspawning state which corresponds to that of the toad-goby begins only after laying of the last batch of eggs, and does not last long (about a month). In males, this condition is somewhat more prolonged (around two months). In the "round goby", the spawning season is drawn out and continues for three or four months (Il'in, 1949; Trifonov, 1955). During this period the same females lay up to five or six batches of eggs, while the males participate in spawning only once in the reproductive season (Il'in, 1949; Rashcheperin, 1967; Kulikova and Fandeeva, 1974).

From the beginning to the end of the spawning season, the gonosomatic index in males decreases; however, the histological picture of a fish caught after laying the first, second, and subsequent batches of eggs, is practically unchanged. In sections of the gonads, besides the burst follicles and the oocytes of protoplasmic growth, it is possible to observe oocytes in the phase of vacuolation and and beginning of yolk accumulation, and also ova with a large quantity of yolk, which form the next batch of eggs. In definitively spawned-out gobies, the composition of the sexual cells consists of oocytes at the period of protoplasmic growth and the beginning of trophoplasmic growth (vacuolation phase).
In the spawned-out males (VI, VI-II stage of maturity), the matrix of the sexual cells is eliminated from the testicle. The majority of tubules have collapsed walls. In isolated cysts, which lie in the peripheral regions of the gonad, are observed cells catching up to the wave of spermatogenesis. Cells of interstitial tissue are small, their nuclei wrinkled. The seminal vesicles are characterized by the almost complete release of the majority of follicles from the colloid (Moiseeva and Ponomareva, 1973).

In order to observe the condition of the hypophysis of "round" goby females during the spawning season through their laying of egg batches, we investigated the glands of fish caught in April (average GSI* - 4.65, stage of maturity of gonads, VI-III₁), May (average GSI - 3.97, stage of maturity - VI-III₂), June (average GSI - 1.24, stage: - VI-III-II), July (average GSI - 1.71, stage, VI-III...ₚ), and September (average GSI - 0.91, 0.87, stages of maturity - VI-II-III, VI-II).

The analysis conducted showed that the morphological pictures of the hypophysis of gobies caught at the beginning, middle and end of the spawning period, differ very little one from the other. Typical for the postspawning condition of the hypophysis of females is the picture observed after the laying of the first batch of eggs. In the zone of gonadotrophic elements once can see a small number of "hollow" spaces; most often they are found on the border of the meso- and meta-adenohypophysis and on the periphery of the mesoadenohypophysis. The nuclei

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*GSI - gonosomatic index. Trans.
of certain cells are wrinkled, striated, and reminiscent of nuclei of degenerating gonadotropic elements in the hypophysis of spawned-out toad-gobies. However, on the whole, despite a certain depletion of basophilic cells of primary type, their zone in the mesoadenohypophysis remains still quite large, and, judging from morphological features, functionally active.

![Image of gonadotropic elements of the hypophysis](image)

**Illus. 6.** Gonadotropic elements of the hypophysis (a) and neurosecretory cells of the preoptic nucleus (b) of "round goby" females after spawning of egg batch (paraldehyde-fuchsin, Heidenhain's azan; objective 90X, ocular 6X).

Large quantities of secretionary gomori- and PAS-positive granules are observed in the cytoplasmic processes of many middle and peripheral elements and in the cells themselves (illus.6, a). These pictures evidently indicate quite a high activity of gonadotropic elements in female "round goby" hypophyses after spawning of the first batch of eggs.
The condition of gonadotropic elements of the hypophysis which has been described remains practically unchanged throughout the entire spawning season. However, after laying of the last batch of eggs, the signs of depletion of mesoadenohypophysis basophils of primary type increase.

In comparison with the prespawning state, no substantial changes are observed in the region of the preoptic nucleus neurosecretory cells in female "round gobies", caught at the beginning, middle and end of the spawning season. As before, it is possible to see a considerable quantity of secretionary gomori-positive granules in the cytoplasm of the neurosecretory cells (illus. 6, b). However, in fish captured at the end of the spawning season, predominant are accumulations of cells with a light cytoplasm, probably analogous in their constitution to the "lightly-staining" cells of A.L. Polenov (1968). Very granulated elements are found singly in the nucleus. The state of preoptic nucleus neurosecretionary cells described is also preserved in the fully spawned-out females.

The hypophyses of spawned-out males (GSI* varies from 0.82 to 1.52) are somewhat reminiscent of the glands of spawned-out toad-gobies caught in the late postspawning period. The cells of the hypophysis are loosely arranged. It is possible to see numerous small "vacuoles" in the zone of gonadotropic elements. In isolated fish, a large cavity with the remains of the basophilic secretion is formed on the site of cells forming the "dipper". The cytoplasm of the gonadotropic elements is much

* Text has "GMI". Trans.
more faintly stained by paraldehyde-fuchsin and Schiff's reagent. The large granules and their aggregates, which are observed in the cytoplasm of cells in the hypophysis of fish caught before spawning, disappear. The nuclei of many gonadotropic elements also undergo noticeable changes. They decrease in size, and become striated and lumpy (illus. 7, a, b).

Illus. 7. Gonadotropic elements of the hypophysis (a, b) and neurosecretionary cells of the preoptic nucleus (c) of spawned-out "round goby" males (a—middle, b—peripheral regions of the mesoadenohypophysis; paraldehyde-fuchsin, Heidenhain's azan; objective 90X, ocular 6X).
The pictures described indicate a considerable depletion of gonadotropic elements of the hypophysis in spawned-out males. It should be noted, however, that depletion and degeneration are far from affecting all the cells which produce gonadotropin, as does occur in toad-gobies with gonads in the late VI-II stage of maturity. In the mesoadenohypophysis can be seen an even greater quantity of little changed (judging by morphological features) basophils of primary type. In addition, the degree of degenerative changes in gonadotropic elements is to a considerable extent of an evidently individual nature, since the morphological signs of these processes are very poorly expressed in separate males.

In the hypothalamic region of the brain in spawned-out noticeable males are observed traces of depletion of neurosecretory elements (illus. 7, c). Besides the degenerating cells in the preoptic nucleus are also found those with secretionary granules in the cytoplasm. On the whole, signs of depletion of preoptic nucleus neurosecretionary cells are manifested considerably more weakly in "round goby" males than in the toad-goby.

DATA ON THE QUANTITATIVE EVALUATION OF GONADOTROPIC ACTIVITY OF THE "ROUND GOBY" HYPOPHYSIS

In attempting to describe the level of activity of the "round goby" hypophysis by biological testing methods, we used males of as test objects the amphibians Rana temporaria and Rana ridibunda (Alpatov, Stroganov, 1950), and females of the loach

Experiments with the lacustrine frog were carried out by a laboratory co-worker, A.P. Zolotnits
**Misgurnus fossilis** (Kazanskii, Nusenbaum, 1947). Not in a single variant of the experiments with "round goby" hypophyses was a positive result observed, although in a parallel administration of synonymous doses of carp hypophyses, the test-animals indicated responded positively. Attempts to evaluate the activity of "round goby" hypophyses were also made by B.F. Goncharov (1971) by a system of ripening amphibian oocytes in vitro, and by G.L. Travkina (private communication) on female ruffes in vivo. In their experiments as well no positive result was obtained. On the basis of the data cited we postulated that the gonadotropic factor of the "round goby" hypophysis possesses zoological specificity.

The mass of the hypophysis as an indicator of its functional state at different stages of sexual ripening and spawning. As has been indicated above, in the glands of sexually immature gobies, the zone of cells performing the gonadotropic function is very poorly developed. Proceeding from this, we assumed that an increase in size of the hypophysis (and consequently, of its mass) in the process of gonad ripening, would occur chiefly due to the development and active functioning of the gonadotropic elements.

It was established during the investigation that the values of the average mass in sexually immature gobies of the same size, but caught in different seasons of the year, were practically indistinguishable one from the other, while in females of the same size with gonads at different stages of ripeness, they were very different (Moiseeva, 1972).
As the sexual glands develop the mass of the hypophysis increases and reaches its highest values at the IV and IV-V stages of sexual maturity. In ripe females and gobies who have spawned a batch of eggs, the average mass of the gland is reduced; its furthest reduction is observed in completely spawned-out gobies with gonads in the VI-II stage. In an analogous manner, the indicator of the degree of development of the zone of gonadotropic elements in the hypophysis also changes (table 2).

A comparison of the average mass of the hypophysis and of the degree of development of its zone of gonadotropic elements in fish caught at the beginning and middle of the spawning season showed that during the spawning period the gonadotropic zone in the hypophysis remains high and makes up 50-60% of the mass of the entire gland.

Thus, an analysis of the change in mass of the hypophysis of the "round goby", and a comparison of data on weight with data from histological research, allows the conclusion that the average mass of the acetone-dry hypophysis, taken from fish at a determined stage of sexual ripening and spawning, and the indicator of the degree of development of its zone of gonadotropic elements, can serve as quantitative characteristics of the functional state of the gland at a given stage in its sexual cycle.
The immunological examination of the "round goby" hypophysis at different stages of sexual ripening and spawning. The fish hypophysis as an object of immunological research has a number of specific peculiarities, connected in part with the size of the gland, the storage life of the material, etc. Taking this into consideration, it is first of all necessary to elucidate certain methodic features of the immunological analysis of the "round goby" hypophysis, namely the possibility of the antigenic composition of a single gland, and also to determine the conditions which it is important to observe in the comparative examination of the hypophyses.

As a result of the experiments conducted, it was established that an extraction of hypophyses in immune condition can with success be replaced by the individual hypophysis; the precipitation picture does not change if the fish whose hypophyses are taken for the experiment differ from each other in size by 10-30 mm; the stability of the antigenic composition of the hypophysis to storage life depends on the physiological state of the gland and on the period of storage of the material. With storage for over a year the spectrum of the hypophyses of sexually mature gobies undergoes substantial changes (Apekin, Moiseeva, 1971).

The comparative experiments conducted showed that the two precipitates which compose the interior part of the spectrum are characteristic for fish hypophyses at all stages of gametogenesis. The outer part of the spectrum is revealed only in
<table>
<thead>
<tr>
<th>№</th>
<th>Стадия зрелости гонад</th>
<th>Размерная группа 80—85 мм</th>
<th>Размерная группа 90—95 мм</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td>1</td>
<td>Месц сбора материала, год</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>3 Размерной группа 80—85 мм</td>
<td>4 Размерной группа 90—95 мм</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Среднее значение</td>
<td>Число гипофизов в измерении, шт.</td>
</tr>
<tr>
<td>October</td>
<td>Октябрь, 1969</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Самцы неполовозрелые</td>
<td>—</td>
<td>50</td>
</tr>
<tr>
<td>10</td>
<td>Самки</td>
<td>0,7</td>
<td>50</td>
</tr>
<tr>
<td>March</td>
<td>Март, 1970</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Самцы неполовозрелые</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>10</td>
<td>Самки</td>
<td>8,3</td>
<td>50</td>
</tr>
<tr>
<td>July</td>
<td>Июль, 1970</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Самки</td>
<td></td>
<td></td>
</tr>
<tr>
<td>IV—V</td>
<td>10,5</td>
<td>50</td>
<td>56,6</td>
</tr>
<tr>
<td>V</td>
<td>15,9</td>
<td>50</td>
<td>62,0</td>
</tr>
<tr>
<td>VI—III</td>
<td>18,2</td>
<td>50</td>
<td>54,0</td>
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<tr>
<td>September</td>
<td>Сентябрь, 1970</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Самцы неполовозрелые</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>10</td>
<td>Самки</td>
<td>0,7</td>
<td>50</td>
</tr>
</tbody>
</table>

Table 2

Change in the average mass of the hypophysis and in degree of development in it of the zone of gonadotropic elements (indicator A) in groups of "round gobies" of the same size at various stages of the sexual cycle.

Legend: 1 Month of collection of material, year
2 Stage of ripeness of gonads
3 Size group 80—85 mm
4 Size group 90—95 mm
5 Average value of GSI, %
6 Number of hypophyses in weighed quantity, pieces
7 Average weight of single hypophysis, mg.
8 Indicator A, %
9 Sexually immature males
10 Females
sexually mature gobies with gonads at III, IV, IV-V, V, and VI-III stages of maturity. This fact allows the assumption that the antigens of the outer part of the precipitation spectrum of the hypophysis are connected with the processes of ripening and spawning. In order to confirm this supposition, 118 experiments with depleted antiserum were conducted.

The antiserum was exhausted by the glands of sexually immature gobies at a rate of 1 ml in 100, 150 glands. The completeness of the depletion was judged by the absence of visible reaction with the hypophyses of sexually immature fish.

Experiments with depleted antiserum indicated that, after removal from the analysis of the antigens common to the hypophyses of sexually immature and sexually mature fish, there were revealed one or two more specific antigens in the hypophysis of females with gonads in the III-VI-III stages of maturity. This fact permitted us to assume that the antigens revealed are connected with the degree of development of the sexual glands, and consequently reflect the gonadotropic function of the hypophysis.

A quantitative analysis of the indicated antigens was conducted through reactions of the precipitation of individual hypophyses with the depleted antiserum (table 3). Since the hypophyses of fish in the initial stages of sexual ripening do not present a visible precipitation with the antiserum, we considered it advisable in the quantitative evaluation to compare between themselves the values of the mass of the entire densitogram, taking into account the mass of its active part in those cases when it was to be found.
### Table 3

Результаты количественной оценки реакции прессинга гипофизов бычка-кругляка на разных стадиях полового цикла в опытах с истощенной антисывороткой

<table>
<thead>
<tr>
<th>№</th>
<th>Место сбора материала, г.</th>
<th>Стадия зрелости гонад</th>
<th>Средний гоносоматический индекс ГСИ, %</th>
<th>Число опытов прессинга</th>
<th>Масса всей денситограммы M, м.г</th>
<th>Масса прессингатов (активная часть денситограммы), мг</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>July Июль, 1970</td>
<td>Самцы неполовозрелые</td>
<td>—</td>
<td>6</td>
<td>23,3±2,2</td>
<td>0,0</td>
</tr>
<tr>
<td>2</td>
<td>October Октябрь, 1969</td>
<td>II—III</td>
<td>0,8</td>
<td>6</td>
<td>28,8±3,5</td>
<td>0,0</td>
</tr>
<tr>
<td>3</td>
<td>March Март, 1970</td>
<td>III</td>
<td>8,0</td>
<td>12</td>
<td>35,1±1,7</td>
<td>10,7±1,4</td>
</tr>
<tr>
<td>4</td>
<td>May Май, 1970</td>
<td>IV</td>
<td>13,0</td>
<td>6</td>
<td>49,5±4,8</td>
<td>25,1±1,7</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>IV—V</td>
<td>14,5</td>
<td>6</td>
<td>48,7±3,9</td>
<td>24,2±2,1</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>V</td>
<td>16,2</td>
<td>6</td>
<td>33,1±1,1</td>
<td>17,8±1,2</td>
</tr>
<tr>
<td>7</td>
<td>December Декабрь, 1970</td>
<td>VI—III</td>
<td>2,8</td>
<td>6</td>
<td>30,5±1,8</td>
<td>16,3±1,9</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>VI—II</td>
<td>0,7</td>
<td>6</td>
<td>29,1±1,4</td>
<td>0,0</td>
</tr>
</tbody>
</table>

1 Размерная группа 90-95 мм.

Results of quantitative evaluation of precipitation reaction of hypophyses of "round gobies" at various stages of the sexual cycle in experiments with depleted antiserum

Legend: 1 Month of collection of material, year  
2 Stage of ripeness of gonads  
3 Average gonosomatic index, GSI, %  
4 Number of precipitation experiments  
5 Mass of entire densitogram M, mg  
6 Mass of precipitates (active part of densitogram, mg)  
7 Sexually immature males  
8 Females

As seen from table 3, the mass of the densitogram of the hypophyses of sexually immature gobies is at the level of the control. For females with gonads at the II-III stage, it is somewhat increased, although we do not note a visible E-precipitation at this stage. In gobies at the III stage of ripeness,
the mass of the densitogram without doubt increases by comparison with that of females in the II-III stage of maturity \( (t_d = 2.32, \gamma = 16) \). About 30\% of this increase occurs in the active part of the spectrum. The densitogram of the reaction of hypophyses of fish in the IV stage of maturity is characterized by a substantial change in mass. With this also occurs a change in the ratio of background and active parts of the spectrum, the latter already composing 50\% of the mass of the densitogram. The relatively low value of the active part of the hypophysis of fish in the IV stage of maturity is characterized by a substantial change in mass. With this also occurs a change in the ratio of background and active parts of the spectrum, the latter already composing 50\% of the mass of the densitogram. The relatively low value of the active part of the hypophysis of fish in the IV stage of maturity is characterized by a substantial change in mass. With this also occurs a change in the ratio of background and active parts of the spectrum, the latter already composing 50\% of the mass of the densitogram. The relatively low value of the active part of the hypophysis of fish at the III stage as compared with those at the IV stage (10.7 as opposed to 25.1), apparently indicates the elimination of those antigenic factors from the hypophysis in connection with the actively ongoing processes of vitellogenesis; the sharp increase in their value at the IV stage of maturity probably testifies to the accumulation in the hypophysis of the gonadotropic factor at that stage. Further characteristic of the hypophyses of fish beginning to spawn (V stage) is the positive decrease both in the mass of the entire densitogram, and of its active part. In gobies caught soon after spawning (VI-III stage), is noted the furthest reduction of the mass of the densitogram and its active part, which is, however, unreliable by comparison with that at the V stage. The decrease in the values of the mass of the densitogram and its active part in spawnsed-out gobies and fish which have laid an egg batch, is evidently connected with the participation of the antigens revealed in the processes of spawning and formation of subsequent generations of ova.
The hypophyses of completely spawned-out gobies (VI-II stage of maturity) do not give a visible precipitation in the interaction with the antiserum. Apparently this is explained by the low level of the antigenic factor which is connected with the gonadotrophic function in completely spawned-out gobies.

Thus, results of experiments with depleted antiserum confirmed the suppositions put forward on the connection of the antigens of the outer part of the spectrum with the gonadotrophic factor of the hypophysis, and allowed their quantitative characterization at various stages of the sexual cycle.

DISCUSSION OF RESULTS

The histological study of the hypophysis of sexually immature toad- and "round" gobies showed that their characteristic feature is the extremely weak development of mesoadenohypophysis basophilic cells of primary type, which fulfil the gonadotrophic function. The solitary basophilic cells in the hypophyses of sexually immature gobies are the thyrotropic elements. An analogous picture was noted by Knowles and Vollrath (Knowles, Vollrath, 1966) in the hypophyses of immature eels, by Leatherland (Leatherland, 1970) in the three-spine stickleback, and by other authors. The hypophyses of sexually immature fish possess the structure indicated, irrespective of the season of the year. The results of gravimetric and immunological analyses of the glands also show the similarity of the functional state of the hypophysis of sexually immature gobies caught in different periods of the annual life cycle.
With the development of the gonads the zone of basophilic cells of primary type in the mesoadenohypophysis substantially increases, and the signs of active functioning of the cells mount. In addition, at this period is also noted a considerable increase in the mass of the hypophysis and in the degree of development of the zone of gonadotropic elements in it (cf. table 2). The outer precipitates which characterize the level of hypophysis antigens (connected with the gonadotropins) are discovered in 100% of the experiments, and their mass makes up almost half the mass of the entire densitogram (cf. table 3). Fontaine, Callamand and Vibert (Fontaine, Callamand, Vibert, 1950), and Woodhead (Woodhead, 1971) also noted an increase in ratio of the mass of the hypophysis to the body mass in salmon and cod in the prespawning period.

The morpho-functional peculiarities of the hypophysis of toad- and "round" gobies, which are connected with peculiarities of their types of spawning, are clearly revealed in the postspawning period.

During the early stage of the postspawning period, there is noted in the toad-goby a delay in the elimination of secretionary substances from the cytoplasm of the gonadotropic elements, which results in its heavy loading with gomori- and PAS-positive granules and in degenerative changes of cells. A possible reason for this phenomenon might be the high level in the organism of sexual hormones, which, as is well known, are antagonists of the gonadotropic hormones (Aleshin, 1971). Indirectly that fact shows that during the early postspawning
period the size of the area of cells of interstitial tissue is still quite high (855.09±92.24 \( \mu m^2 \)), and is at the level of that in males of the IV stage of maturity (838.48±34.55 \( \mu m^2 \)). It is generally known that interstitial tissue is the site of production of the steroid hormones in male sexual glands of vertebrates (Turdakov, 1972; Lofts, 1968). Stanley, Chieffi, and Botte (Stanley, Chieffi, Botte, 1965) established this histochemically for the closely-related toad-goby species - Cobius paganeleus L.

Another reason for the observed retention of secretionary material in the gonadotrophic elements of the hypophysis could be the increase in the quantity of steroid hormones in the blood of the fish due to the strengthening of the activity of the adrenal gland in the early postspawning period. In the literature there is information on the rise in the concentration of corticosteroids in the blood of spawned-out fish: in carp (Bondy, Upton, Pickford, 1957), salmon (Robertson, Wexler, 1959; Idler, Ronald, Schmidt, 1959; Fagerlund, 1967). Idler and his co-workers connected the great rise in the level of corticosteroids in the blood of spawned-out O. keta (at the 17th time) with the postspawning death of the fish, i.e., with the stress tension of the organism, which has been reported in other works (Robertson, Krupp, Favour et al., 1961; Garlov, 1971). We postulate that the brief total spawning of the toad-goby also exerts on the fish the action of a type of stress, as a result of which there might occur an increase in the secretion of steroid hormones by the adrenal gland. Indirectly, it is
possible to judge this by the growth of the signs of activity of cells in the hypophysis, which are connected with the ACTH- (adrenocorticotrophic hormone) function; and of neurosecretionary cells of the preoptic nucleus observed in gobies during the early postspawning period (Moiseeva, 1973).

A characteristic feature of the hypophysis of fish with gonads in the late VI-II stage is the massive depletion and degeneration of gonadotropic elements. Parallel to this in the ovaries occurs an increase in the quantity of "nests" of oocytes in the prophase of meiosis. This fact permits us to suppose that the secretionary material of gonadotropic elements of the hypophysis in some manner participates in the development of ova in the early stages of oogenesis. The data of Sundararaj (Sundararaj, 1959), Barr (Barr, 1968), O.F. Sakun (1970), and G.L. Travkina (1971), point to the possibility of gonadotropic regulation of processes connected with replenishment of the stock of sexual cells.

Besides the indicated morpho-functional changes of gonadotropic elements in the hypophysis of toad-goby in the postspawning period of the sexual cycle, other types of adenohypophysis cells also undergo noticeable changes: the cells of the proadeno-hypophysis which fulfil the ACTH-function, thyrotropic elements, and cells of the meta-adenohypophysis. One recorded fact permits us to assume the participation in the reproductive processes of an entire complex of hormonal factors, which probably act as synergists. This assumption is confirmed by the works of a group of Indian scholars (Sundararaj and Coswami, 1966; Sundararaj, Nayyar, 1967; Sundararaj, Anand, Donaldson, 1972) in
which stimulation of the seminal vesicles in the hypophysectomized bullhead, *Heteropneustes fossilis*, was obtained by means of the action on the fish of a complex of hormonal preparations (testosterone-propionate, prolactin, growth hormone, sheep LH (luteinizing hormone) etc.).

If in toad-gobies the morphological pictures of the hypophysis of spawned-out males and females looks practically identical, then in the glands of male and female "round goby" individuals caught in the postspawning period, it is possible to see marked differences. Signs of the depletion of gonadotropic elements in male hypophyses are much more strongly expressed than in female glands. In females, both after spawning of the first and also after elimination of subsequent batches of eggs, small changes in the hypophysis are observed during the course of the entire spawning season, which indicates the high functional activity of that gland. The action of the gonadotropic elements evidently ensures the growth and ripening of the many successive developing batches of eggs. A.V. Zaitsev (1955) pointed out the differences in the histological pictures in the male and female pike, which are connected with peculiarities of their gametogenesis. The noted peculiarity of the "round goby" hypophysis is also characteristic for the glands of other examined species of intermittently-spawning fish (Gerbil'skii, 1947; Kazanskii, 1949; Sundararaj, 1959). The ability of the hypophysis to produce the gonadotropic hormone during an extended period is conditioned by the peculiarities of the secretionary cycle of mesoadenohypophysis basophilic cells of primary type.
A characteristic feature of their functioning is the asynchronous passing of successive phases of their secretory cycle.

Histophysiological data on the high activity of goby hypophysis during the entire spawning season is confirmed by results of gravimetric and immunological analyses of the condition of the gland.

Sundararaj (1959) tested the hypophyses of "sack-gill catfish" H. fossilis, and discovered that during the early post-spawning period when a large number of basophils is present in the hypophysis, the gonadotropic activity of the gland is high and at roughly the same level as that of fish with running sexual products.

As was shown above, the histological analysis did not reveal morphological changes of the cellular parenchyma in the hypophysis of a female "round goby" as they laid their egg batches. However, in spite of this, an analysis of the average mass of the glands indicates that during the spawning period there nevertheless occurs a certain depletion of the hypophysis. It must be noted that in a number of cases where the histologically functional changes of the "round goby" hypophysis are not revealed, an examination of the dynamics of the mass of the gland, and also the immunological analysis of the hypophysis, permits their capture and evaluation.

CONCLUSION

Thus, the investigation conducted permitted the revelation of the morpho-functional peculiarities of the hypotalamo-hypophysial system of two species of gobies, possessing different
types of spawning, and the evaluation of gonadotrophic activity of the "round goby" hypophysis at various stages of the sexual cycle through gravimetric and immunological analyses.

The chief functional feature of the hypothalamo-hypophysial system of the toad-goby is to a considerable extent the synchronous passing by the neurosecretionary cells of the preoptic nucleus and by the glandular elements of the adenohypophysis of the successive phases of the secretionary cycle. This peculiarity is evidently conditioned by the realisation of the brief total spawning peculiar to this species. The asynchronous passing of these phases by the neurosecretionary cells of the preoptic nucleus and by the gonadotropic elements of hypophysis in the "round goby" leads to the development of a prolonged intermittent spawning, characteristic for this species.

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Histophysiology of hypothalmo-hypophysis system of some marine fishes in relation with spawning types

E. E. Mosseva

SUMMARY

An ecologo-histophysiological approach has been used in the study of histophysiology of the pituitary gland, sex glands and partly hypothalamus of the two closely related species of gobies, having different spawning types: todd-goby Gobius batraccephalus (total-spawning species) and roost-goby Gobius melanostomus (intermittent-spawning species). Functional peculiarities of the hypothalmo-hypophysial system of gobies causing the development and course of intermittent and total spawnings in fishes have been elucidated.

The quantitative estimation of the gonadotropic activity of the pituitary gland of Gobius melanostomus at the different stages of the reproductive cycle has been conducted by means of analysis of the average weight dynamics of the acetone-dry hypophysis and immunological analysis of acetone-dry glands. It has been shown that the average weight of the pituitary gland and degree of development of its gonadotropic zone in equal size females with gonads at the different maturation stages, reach their highest values at stages IV, IV–V and decrease after spawning. The level of antigens of hypophysis, connected with gonadotropic activity, changes similarly.