Research Article

Participation of the Hypothalamic-Hypophysial Neurosecretory System in the Occurrence of a Migration Impulse on Fish

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ABSTRACT

The participation of the Hypothalamic-Hypophysial Neurosecretory System (HHNS) in the initiation of anadromic fish migration was discovered. It is based on the results of ecological-histophysiological studies, using light microscopy, including immunohistochemistry, electron microscopy with quantitative morphometry. At the beginning of migration, an activation of neurosecretory products synthesis in pericarions of Nonapeptidergic Neurosecretory Cells (NSC) and their transport to neurohypophysis where they accumulate occurs. The excretion of neurosecretory products from pericarions of NSC into the liquor of the III brain ventricle is shown at the same time. We assume that HHNS causes a complex synchronous effect, which first consists of the active neurotropic action of Nonapeptide Neurohormones (NP-Nh) to the behavioral centers of the Central Nervous System (CNS), causing a dominant state of its excitation, designated as a migration impulse. In contrast, the cessation of viscerotropic action of NP-Nh through the general blood flow in neurohypophysis causes both the violation of the longly adapted level of the marine pastured type of osmoregulation, and the interruption of the known anti-gonadotropic action of NP-Nh. And the latter contributes to the transition of the body to the energy-intensive energetically type of metabolism. In subsequent navigation mechanisms, widely covered in world literature, the leading role is played by the gonadoliberinergic forebrain centers.

Keywords: Hypothalamic-hypophysial; Neuroendocrine regulation; Salmon migrations; Migration impulse; Central nervous system

INTRODUCTION

Before our work it was known, that HHNS (or rather "preoptico-post-neuro hypophysial nonapeptidergic neurosecretory system", most powerful in the neuroendocrine complex of the brain), which produces 2 Nonapeptide Neurohormones (NP-Nh: Arginine-8-vasotocin, VT and isotonic, IT in bony fish), is responsible for regulation of the most important body functions: Water-salt metabolism, tone of the gonads smooth muscles, spawning behavior, and that it is involved in stress reactions [1]. It was initially assumed that the leading role in determining migration behavior in fish is performed by HHNS [2]. At the beginning of spawning migration in primary monocyclic forms-anadromous lampreys and catadromous eels, as well as in anadromous sturgeons, salmons, down-stream migration of salmon smolts, clear changes in osmotic and ion regulation were

established, but not in the functional state of HHNS [3-5]. However, during the period of spawning migrations, an inverse correlation was often noted in the content of Neurosecretory Material (NSM) in the central (Nucleus Preopticus-NPo, synthetic center) and distal (Neurohypophysis-NH, center of accumulation and extrusion of NSM) parts of HHNS, and also many large Neurosecretory Terminals (NT)-Herring's Bodies (HB, up to 50 μ m) appeared in NH. Since it was not stated any patterns of HHNS functional changes during fish migrations, nature of the trigger mechanism of migrations, the so-called migration impulse, is not clear to date. Therefore, the only leading mechanism of fish migrations is considered to be navigational processes of the geomagnetic field's impact on the body receptor systems [6] and olfactory imprinting and homing [7].

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Received: 03-Feb-2022, Manuscript No. FAJ-21-48579; Editor assigned: 07-Feb-2022, PreQC No. FAJ-21-48579 (PQ); Reviewed: 21-Feb-2022 QC No. FAJ-21-48579; Revised: 25-Feb-2022, Manuscript No. FAJ-21-48579 (R); Published: 04-Mar-2022; DOI: 10.35248/ 2150-3508.22.13.293.

Citation: Pavel EG (2022) Participation of the Hypothalamic-Hypophysial Neurosecretory System in the Occurrence of a Migration Impulse on Fish. Fish Aqua J.13:293.

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The purpose of the research is to find out the functional role of HHNS in the implementation of fish spawning migration. The main objective is to determine the degree of HHNS participation in the process of anadromous fish spawning migration based on the ecological-histophysiological study.

MATERIALS AND METHODS

Morph-functional state of HHNS was studied in sexually matured producers of passing anadromous fish: Spring-spawning Russian sturgeon acipenser gueldenstaedtii [6], stellate sturgeon A. stellatus from the lower reaches of the Volga river and autumn-spawning monocyclic pink salmon *Oncorhynchus gorbuscha* from the lower reaches and spawning grounds of the Naiba and Umba rivers (Southern Sakhalin island, Kola Peninsula).

For light microscopy, brain tissue with hypothesis (from 230 fishes of both sexes) was fixed in Bouen fluid, histological sections (5-6 μm thick), were stained with Paraldehyde-Fuchsin (PAF) according to Gomori-Gabe's method with Heidenhain's azan staining [8]. Functional activity of HHNS was determined by morphometric quantitative methods for assessing the degree of NSM content in NSC of Nucleus Preopticus (NPo) and in its accumulations in the proximal and distal parts of NH roots. Cytospetrophotometry of histological preparations was carried on the micro analyzers "Morpho-quant" and "Video-test", using the Programs "Ancell" and "Video-test".

For immunocytochemical research (17 fishes of both sexes) a peroxidase-ant peroxidase method for detecting unlabeled antibodies was carried out, and to detect Vasotocinergic (VT) and Isotocinergic (IT) structures were used antiserums to VT and mesotocin, which allows to identify VT- and IT-NSC.

Electron microscopical research was carried out on material (29 fishes of both sexes) fixed in glutaraldehyde (according to Sabatini), postfixed in tetroxide osmium and enclosed in araldite and epon. Ultrafine slices were contrasted (to Reynolds) in uranium acetate and lead citrate. The percentages ratios of NSC of dorsal part NPo (NPo magnocellularis) in different phases of their secretory and extrusion cycles (of neurosecretory terminals-NT of A1, A2, B types in NH) were analyzed. The results of quantitative morphometry of HHNS structures and ultrastructure's are processed statistically using the Microsoft excel program and presented in tables, histograms and diagrams [9].

The article applied an ecological-histophysiological approach, or method of scientific research in the form of the analysis adaptation mechanisms at various levels of organization, considered as the result of an experiment, set by nature itself, and its aim is to clarify the role of cellular and tissue structures in the implementation of the most important phylogenetic adaptations that ensure the biological progress of the spicy [10]. So, for a constructive analysis the mechanism of HHNS participation in fish migrations at different stages of gonadal

maturity is a formalized graphic method of comparative analysis ("cross-analysis" from the field of assessing the novelty of inventions, discoveries and literary sources) alternative functional states of HHNS was used [8-10].

RESULTS

At the beginning of spawning migration, most NSC are represented by hypertrophied active "light" forms in secretory phases of "excretion" and "devastation from the NSM", while the vessels in the NPo region are also hypertrophied (Figures 1a-1d and Table 1).

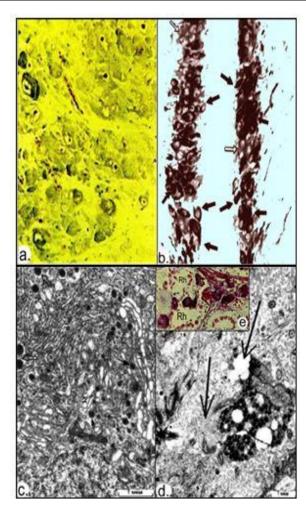


Figure 1: NSC in pink salmon NPo and NT in sturgeon NH at the beginning of river period of spawning migration. (a) Active light NSC forms predominate in NPo; (b) Predominant in number VT-NSC are in intimate contact with the cavity of the III brain ventricle (black arrows); (c) Neurosecretory granules are finally formed, but not accumulate in Golgi complex of NSC; (d) The destruction of Herring Body (HB) fragment in NH and the release of its fine-grained contents into the cavity of Recessus Hypophyseus (RH).

| Functional states of NSC | IV: Spawning migration (in the lower reaches of the river) | V: At the beginning of spawning (on spawning graunds) | |
|---|--|---|--|
| Rest | 8.2 ± 1.74 | 5.8 ± 1.77 | |
| Accumulation | 34.6 ± 8.0 | 12.8 ± 5.4 | |
| Extrusion | 45.8 ± 9.4 | 57.7 ± 3.1 | |
| Exhaustion | 11.4 ± 4.7 | 23.8 ± 7.3 | |
| The width of the vessels lumen (degree of NPo hyperemia, µm) | 7.6 ± 0.57 | 8.7 ± 0.88 | |

Table 1: Morphometric characteristics of NSC in pink salmon NPo at the process of spawning migration and at the beginning of spawning in light microscope.

By immunocytochemical study of NPo morpho-functional state it was revealed a significant predominance of VT-immunopositive NSC over IT-immunoreactivity NSC (light arrows). In symmetrical parts of the NPo, many VT-NSC apical surfaces are closely adjacent to cavity III of brain ventricle, forming a network of somato-ventricular (and dendroventricular) neurosecretory contacts in relation to IT-NSC 5:1. Electron microscopically, pictures of the mass formation of Elementary Neurosecretory Granules (ENG) and their direction to dendrites and axons are observed in Golgi complex. In NPo prevails NSC in a state of high secretory activity, of 51-56% (Figures 2a and 2b) and (Table 2).

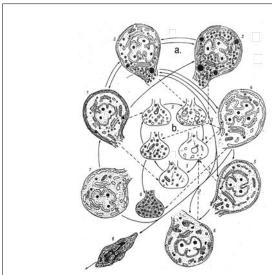


Figure 2: Scheme of the secretory cycle of NSC in the dorsal part of NPo and the extrusion cycle of NT in fish NH. (a) The secretory cycle phase; (b) The extrusion cycle phase.

The secretory cycle phases of the type-I NSC are represented by the following functional states:

- 1. Low or moderate activity
- 2. High activity
- 3. Deposit of neurosecretory material
- 4. Hyperactivity
- 5. Reparations of cell organelles
- 6. Massive degradation of organelles

The state of type-II NSC is represented by the following functional state:

1. Rest or deep braking functions

The state of type-III NSC is represented by the following functional state:

1. Degeneration of NSC (that is not revealed in pink-salmon)

The extrusion cycle phases of NT are represented by the following states:

- 1. Deposit of Elementary Neurosecretory Granules (ENG)
- 2. Start of neurohormones excretion
- 3. Active extrusion of neurohormones
- 4. Exhaustion after extrusion of neurohormones
- Accumulation of ENG
- Overflow of polymorphic neurosecretory granules (dark NT). NSC perikaria are connected with NT of their axons by broken arrows.

| Phases of NSC secretory cycle | IV Spawning migration | V At the beginning of spawning | |
|-----------------------------------|-----------------------|--------------------------------|--|
| Low or moderate activity | 8 ± 0.81 | 3 ± 0.24 | |
| High activity | 42 ± 5.43 | 59 ± 8.53 | |
| Deposit of NSM | 30 ± 4.9 | 10 ± 4.05 | |
| Hyperactivity | 9 ± 1.92 | 21 ± 3.47 | |
| Reparations of cell organelles | 4 ± 0.78 | 1 ± 0.17 | |
| Mass organelles degradation | | , | |
| Rest or deep braking functions | 7 ± 1.22 | 6 ± 1.34 | |

Table 2: Morphometric characteristics of NSC in pink salmon NPo at the process of spawning migration and at the beginning of spawning in electron microscope.

During period of active river spawning migration, mass accumulation of NSM occurs in NH, which is clearly consistent with the morpho-functional state of all its ultrastructure's (Figures 3a and 3b). NT sinusoid capillaries and pituicytes in NH are in an inactive functional state, indicating unidirectional to a low level (or absence) of NP-Nh excretion into the general bloodstream (Tables 3 and 4).

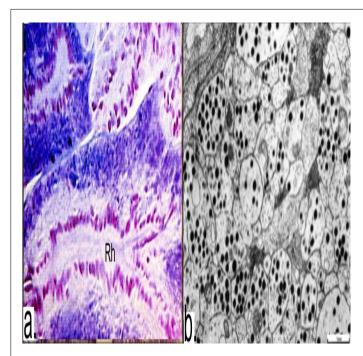


Figure 3: The states of Russian sturgeon NH, (a) Stellate sturgeon; (b) Pink salmon.

| NH, state of NH r structures (according 1 | V: Spawning migration (in the ower reaches of iver) | V: At the beginning of spawning | | | | |
|---|---|---------------------------------|--|--|--|--|
| NSM concentration in Cytospetrophotometry res | | NH divisions on the | | | | |
| NSM (in units of optical density) | 0.151 ± 0.06 | | | | | |
| NSM concentration in the distal NH divisions on the visual results (according to 5-point scale) | | | | | | |
| NSM (points): ♀ | 4.0 ± 0.12 | 2.4 ± 0.26 | | | | |
| ð | 3.8 ± 0.13 | 2.8 ± 0.28 | | | | |
| Q+3 | 3.9 ± 0.09 | 2.6 ± 0.18 | | | | |
| Diameter of pituicyte nuclei (µm) | 4.73 ± 0.10 | 6.24 ± 0.17 | | | | |
| Width of the capillaries lumen (µm) | 15.94 ± 0.45 | 16.64 ± 1.51 | | | | |

Table 3: Characteristics of structures and ultrastructure's in distal parts of pink salmon NH at the process of spawning migration and at the beginning of spawning in light microscope.

| Phases of the extrusion cycle NT | IV: Spawning migration | | beginning | V: At the beginning of spawning | |
|--|------------------------|-----------|-----------|---------------------------------|--|
| | A1 | A2 | A1 | A2 | |
| Deposit of eng | 17 ± 2.35 | 7 ± 0.53 | 7 ± 2.86 | 2 ± 1.05 | |
| Start of NP- Nh excretion | 58 ± 4.62 | 70 ± 1.45 | 54 ± 3.97 | 45 ± 1.70 | |
| Active extrusion of NP-Nh | 20 ± 3.58 | 20 ± 1.94 | 33 ± 8.44 | 47 ± 2.87 | |
| Exhaustion after extrusion of NP-Nh | 4 ± 1.20 | 2 ± 0.38 | 4 ± 1.56 | 6 ± 0.17 | |
| Accumulati on of ENG | 1 ± 0.18 | 1 ± 0.22 | 2 ± 1.31 | - | |

Table 4: Characteristics of structures and ultrastructure's in distal parts of pink salmon NH at the process of spawning migration and at the beginning of spawning in electron microscope.

A cluster of HB in the roots of NH often occurs near the cavities of Recessus Hypophyseus (RH), many of which is emptied from NSM and penetrates into it (Figure 1a). Pictures of destruction of the Herring Body (HB) fragment by the type of macroapocrine secretion, the disintegration of neurosecretory granules and the output of a fine-grained product into Rh (brain liquor) are revealed there (Figure 1a). Figures 3a and 3b indicates the active excretion of neurosecretory products from NSC into the liquor of the III ventricle not only in NPo region, but also in NH, in which, however, their excretion into the vessels of the general blood flow is absent.

To verify our observations and in order to more objectively clarify the functional role of the HHNS in the implementation of migrations on more material, we used the method of comparative analysis of own and literary data. Specifically, in this work:

- First of all, we formalized 2 alternative extreme states of the HHNS, according to the directions of NP-Nh excretion (and their unstable intermediate form).
- Then identified them in the literary sources.
- Analyzed in each work their sequence in ontogenesis.
- Generalized all of them in a single histogram, based on their manifestation at the main stages of ontogenesis.

Accordingly, a comparative analysis of the HHNS function in alternative states (devastation, or accumulation of NSM in NPo and in NH, and significant variations in its content) at different

stages of ontogenesis was produced, and the results are presented on histogram (Figure 4).

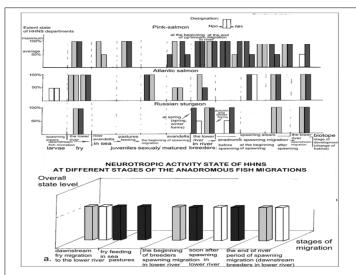


Figure 4: Morpho-functional states of HHNS at different stages of ontogenesis of the studied anadromous fish species.

Note: (\blacksquare) Sturgeon, (\blacksquare) Salmon, (\blacksquare) Pink Salmon

This simplified, but clear dynamics of morpho-functional changes in the HHNS shows that the state of devastation of NPo from NSM, with its accumulation in NH, dominates during the process of spawning migrations of anadromous fish.

DISCUSSION

The extreme morpho-functional states of HHNS in natural and experimental conditions, are mostly expressed either in the inverse correlation of the NSM content in its central (NPo) and distal (NH, neurohemal) parts Figure 1a, or in the devastation of NH from the NSM (Tables 3 and 4) Accordingly, it is possible to distinguish 2 main states of HHNS functional activity, differing in the direction of the NP-Nh action and the achieved physiological effects [11].

The state of neurotropic activity of HHNS is characterized by NPo devastation from NSM and its accumulation in NH, which expresses the process of active synthesis of neurohormonal products in the NSC pericarions, their transport and excretion into the liquor of the III brain ventricle, where NP-Nh cause a neurotropic effect on the behavioural centres in the CNS.

State of viscerotropic activity of HHNS: In the form of NH devastation from NSM, which expresses the excretion of neurosecretory products from NT into the general blood circulation, where NP-Nh causes a viscerotropic effect on targetorgans. Such an activation of HHNS (at the organism level, in stress especially) has a generalized (multifunctional) and prolonged character [12].

Previously, an increase the synthetic activity of NP-NSC in the dorsal part of NPo in females from the beginning of spawning migration and to spawning, especially VT-NSC at the pre-estuaries, and also of IT-NSC in the rostro-ventral part of NPo in males before spawning was found in anadromic salmon species However, the state of NH in the majority of these works was not considered. In teleost, NP-Nh affects centres of behaviour regulation in the amygdala and hippocampal regions of the

brain limbic system, causing spawning reflex, where VT is more active than IT. Thus, HHNS plays a key role in determining migration behaviour, causing the dominant state of CNS excitation the form of migration impulse, which we consider as a social form of behaviour [13-15].

Another important part of the complex synchronous mechanism of HHNS participation in the anadromic migration is a significant decrease of its viscerotropic activity in the form of accumulation NSM in NH, above the three-point norm of moderate functioning in natural conditions. This causes the violation of the long-term adapted marine-pastured hypotonic type of osmoregulation, due to the cessation of the active NP-Nh antidiuretic action, VT especially. The violation of the water-salt metabolism mechanisms in connection with the external medium salinity changes is evidenced by the progressive watering muscles in passage fish during migrations, especially in salmons. It is also assumed that VT and IT are involved in the body's ionic balance regulation through the gill blood-flow, since 2 different receptors (type-V1) on the chloride-secreting cells of the gills respiratory epithelium in Teleost were observed. Thus, the physiological stimulus of habitat change is a double effect caused by the HHNS, which consists in initiating persistent excitation of the behavioural centres of the CNS and in disrupting the long-adapted "pastured" hypotonic type osmoregulation and ionic balance of the body [8-13].

And a particularly important part of this starting neuroendocrine mechanism is the effect of violation antigonadotropic action of NP-Nh. It is carried out by direct inhibition of gonadoliberin (Gn-RH) secretion (synergy VT with dopamine), stimulation of adrenocorticotropic secretion in the adenohypophysis (synergy with corticoliberin), inhibition of endocrine and generative gonads functions, i.e. at all levels of the hypothalamic-hypophysial-gonadal axis. It is assumed, that the complex mechanisms of NP-Nh influence on reproductive processes are largely ensured by their interaction (VT, mainly) with adenohypophysiotropic hormones. The results of comparative tests of gonad-stimulating effects of the isolated anterior and posterior hypophysial lobes on sexual maturation and ovulation of sturgeon, sevruga and rotan (Perccottus glenii) showed, that NP-Nh extracts in physiological or slightly increased doses inhibit or disrupt ovulation process. The prolonged delay processes of ovulation and resorption sexual products of fish-producers in brackish water of critical salinity (4-8%) at spawning temperatures is also the effect of an increased content of NP-Nh in the blood. Thus, HHNS, simultaneously with the starting neurotropic action, participates in triggering the activation functions all links of the hypothalamic-hypophysial-gonadal axis. At the same time, the effects of viscerotropic NP-Nh action are generalized, since VT and IT receptors (type-V1) are detected in many organs of Teleost: pituitary, kidney, liver, ovary, gills, heart, muscles, spleen, lateral line, bladder, intestines. VT may be directly involved in the carbohydrate metabolism regulation, since its receptors (V1) are detected in fish hepatocytes and it was stated that NP-Nh stimulate glycogenolysis in trout and eel livers.

Therefore, we assume that this (the third, also synchronous) metabolic effect of NH-Nh, also generalized and prolonged, is the leading physiological mechanism for changing the plastic

energy-saving metabolism to energy-intensive energetically [14,15].

CONCLUSION

One of the leading functions of HHNS is the generalized and prolonged effect of the synthesized NP-Nh on target organs, on which they have a stimulating action in small doses, and inhibitory in large doses. The physiologically dosed NP-Nh secretion and their functionally differentiated, specialized pathways excretion, determine their alternative effects-neurotropic and viscerotropic, especially metabolic, generalized and prolonged.

Thus, the functional role of HHNS in fish migrations is to initiate migration processes in the form of Migration impulse is a complex synchronous effect of excitation brain behavioural centres, changing ion-osmotic body equilibrium and plastic metabolism to energise.

Further navigational mechanisms of fish migrations are provided by the close interaction of HHNS and diffuse accumulations of gonadoliberinergic (GnRH) NSC, in which, for example, 2 forms of GnRH (salmon and chicken) in the ventral (small-cell) part of the NPo (Nucleus parvocellularis preopticus) modulate the electrical activity of VT-NSC in its large-cell part. The leading significance of each of them dynamically changes according to their functional role at different periods of reproduction. We suggest that the dominant state of excitation is possibly a trigger involving primary phylogenetic navigational mechanisms of effecting geomagnetic fields on receptor systems and CNS, which are still not completely understood. In the further specialized navigation processes olfactory imprinting and homing, the main role is executed by GnRH-neurosecretory formations, localized near the olfactory and visual brain regions, where, GnRH, synthesized in olfactory nerve, participates in the navigational processes of imprinting and homing, but which is synthesized in the preoptico region, provides the puberty and spawning processes in accordance with the biological significance of chemical and photoreception. The considered complex mechanism. determining migration behaviour is the main reason for the progressive decrease in the eurybiontity degree of migratory fish in the process of spawning migrations and spawning.

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