Prespawning and Spawning Migrations of the Southern Greenling *Pleurogrammus azonus* (Mathematical Model)

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Abstract

Prespawning and spawning migrations of the southern one-finned greenling Pleurogrammus azonus in the bay are considered on the basis of the author's and literary numerical material. Peter the Great, in the summer-autumn period. As part of the spatio-temporal model building, the pre-spawning and spawning migrations were formalized. The dynamics of diurnal displacements is made in terms of transport equations. The recording of their representations follows the modified Patlack-Keller-Segel equations, according to which the flow of objects/substance is directed along the gradients of the stimulus zone functions introduced here. It is believed that in the pre-spawning period, morphophysiological and behavioral adaptations to a rather long and energy-consuming spawning occur. It is shown that the intensity of daily movements is proportional to their linear size (the larger the fish, the faster it moves). The equations for the spawning stage take into account the spatial competition of males, which under natural conditions is observed only in the vicinity of spawning areas. For females, clusters of males act as an incentive for movement. The simulation results turn out to be close to the observed migration regime.

Key words: Fish Migration, Spawning, Patlack-Keller-Segel Equations, Adaptation Zone

Introduction

Greenling fish Hexa grammidae spawn near rocky shores in the zone of currents. Males guard the laid eggs. Hatched larvae are carried by currents to the open sea. When migrating, the fish often form dense concentrations, making them easily accessible to catch. At the same time, they form commercial accumulations near the coast. During this period, the physiological state of fish is characterized by various changes, which, as a rule, are adaptations to changing environmental conditions. In greenling fish, the first adaptations appear in large males, which begin their pre-spawning migration. They are followed by females [1-3].

In the relevant publications, only a general phenomenological picture of the intrapersonal variability of greenling distributions in the summer-autumn period is given, which does not take into account the dynamics of fish movements. Due to the discrepancy between the temporal discreteness of natural measurements and the mobility of fish movements, difficulties are noted in understanding the dynamics of their movements. In this connection, the construction of such a numerical model is an urgent task, the solution of which allows us to present a picture of displacements. The results obtained can be presented in a discrete form (say, with a weekly step), which may be useful for short-term forecasting of the fishing situation.

The purpose of the work is to assess the intensity of migrations of the greenling, as well as to assess the heterogeneity of the distribution density and formalize incentive stimuli based on the development of a compact 1D numerical model.

Material

The material for the research is selective data collected on research and fishing cruises, which are supplemented by materials from the fish processing plants of the Primorsky Territory (Sea of Japan) in 1978–2018. Processed 1212 catches of the southern greenling. Of particular value are 59 commercial catches in the search for commercial concentrations of greenling. 7155 specimens were taken for a complete biological analysis. 18092 specimens were measured.

Mathematical model

The quantitative basis for constructing the model here is the Patlack-Keller-Segel (PRS) equations system [4, 5]. The essence of the provisions for its mechanism consists in the adoption of a po-

sition on directed mass movements of individuals in the field of a heterogeneous distribution of a certain function, which in terms of works is called a stimulus or the so-called slow taxis. In particular, the stimulus for insects is the distribution of the concentration of their food substrate, and for bacteria in aquifers, the distribution of the concentration of their nutrients [4, 6, 7]. It is assumed that the flow of the objects themselves is proportional to the distribution of the stimulus. A different situation underlies the models, where the intensity of movements is proportional to the stimulus gradient [8, 9]. In a similar way, this gradient "controls" the nature of the daily averaged speeds of the objects of study.

In PKS systems, it is assumed that the object is endowed with taxis to some environmental characteristics (such as temperature, salinity, terrain, etc.), that is, it is able to perceive some external signal [10]. Here, 4 types of such distributions are considered, by means of which the directed mass movement of spawning fish is modeled: the gradient of the adaptation zone, the gradient of the spawning zone and the distribution of males already immediately before the spawning areas (during this period, the females move after the males and, moreover, in these areas Males compete with each other to fertilize the caviar.

When building the model, the following assumptions are made:
1. The dynamics of fish density distribution follows the transfer equation, where the diffusion of their density and natural mortality are additionally taken into account.
2. The concepts of the zone of adaptation and the zone of action of stimuli are introduced.
3. The dynamics of movement speed is proportional to the gradient of the stimulus zone and the viscosity of the medium.
4. The duration of the pre-spawning adaptation stage is t^*; after its completion, the fish rise to the spawning zone.
5. Since, before spawning, males drive away other fish from spawning clutches, at this stage, males compete with each other for areas of clutch sites.
6. Compared to males, females have a slightly different transition from the adaptation zone to spawning, after which they follow the males.
7. There are no flows of system components at the boundaries of the environment.
8. Initial distributions are given for dynamic variables.

According to the accepted assumptions, the model equations take the form

$$
\begin{cases}
\partial_t M = \partial_x(U_M M) - \beta_M M + D_M \partial_{xx} M \\
\partial_t F = \partial_x(U_F F) - \beta_F F + D_F \partial_{xx} F \\
\partial_t U_M = \partial_x(k_{11} R - k_{12} M) + D_M^{(U)} \partial_{xx} U_M \\
\partial_t U_F = \partial_x(k_{21} R + k_{22} M) + D_F^{(U)} \partial_{xx} U_F \\
\partial_x M|_{a,b} = \partial_x F|_{a,b} = 0 \quad \text{и} \quad \partial_x U_M|_{a,b} = \partial_x U_F|_{a,b} = 0 \\
M(x,0) = M_0(x), F(x,0) = F_0(x), U_M(x,0) = U_F(x,0) = U_0(x)
\end{cases} \quad , \text{(1)}
$$

where x, t are spatial and temporal coordinates; $M(x,t)$, $U_M(x,t)$, $F(x,t)$, $U_F(x,t)$ distribution densities, speeds of males and females; β_M, β_F natural mortality rates; $R(x,t)$ stimulus zone function; D_M, D_F, $D_M^{(U)}$, $D_F^{(U)}$ diffusion coefficients (the first subscript indicates the corresponding variable: M - male, F - female); $\{k_{ij}, i,j=1,2\}$ time dependent non-negative coefficients of proportionality. Their time dependence reflects the uneven contribution of stimuli to the dy-

namics of system (1). The coefficients k_{11} and k_{21} characterize the degree of "attractiveness" of stimuli, and k_{12} and k_{22} - the spatial competition of males for spawning areas and the directed movement of females after males already immediately during spawning. The functions of the stimulus zone $\{R_i, i=1\div3\}$ are defined by such representation

$$
R(x) = \begin{cases}
R_1(x). \quad \text{при} \quad t < t^* \\
R_2(x), \quad \text{самцы при} \quad t > t^* \\
R_3(x) = [R_1(x) + R_2(x)]/2, \quad \text{самки при} \quad t > t^*
\end{cases}
$$

where the nature of the distribution of each of them most closely matches the observations; $R_1(x)$ characterizes the stimulus zone common for males and females at the adaptation stage, $R_2(x)$ and $R_3(x)$ characterize their stimulus zones for transitions to the spawning stage. The non-zero initial movement of fish $U_0(x) \neq 0$ is

due to the hormonal background of their organism, which is usually expressed in the color of individual parts of the fish body. In particular, the greenling has a black mask resembling a raised visor [1].

The detailing of the functions and coefficients of system (1) is made here on the basis of averaged long-term observations of pre-spawning and spawning migrations of the greenling. The observed conditions of its life cycle are also taken into account. Thus, $R(x)$ from (2) in the adaptation zone $[x_1, x_2]$ turns out to be close to the normal distribution, and in the coastal spawning zone $[x_0, x_3]$ it is close to the lognormal distribution [11, 12]. With regard to $R(x)$, it is appropriate here to emphasize the semantic nature of these distributions: in the first case, this distribution is due to the influence of many weakly interdependent random variables (rv), each of which makes a small contribution relative to the total sum; the basis for the formation of the log-normal distribution of rv constitutes a process where the action of each additional factor on the rv. proportional to its additional level [13]. Apparently, this situation reflects the cycle evolution of fish. According to what has been said, here we accept the following approximation of these functions

$$R(x,t) = \begin{cases} R_1(x) = A_1 exp[-a \cdot (x - x_1)^2 (x_2 - x_1)^{-2}]. & \text{при} \quad t < t^* \\ R_2(x) = A_2 x exp(-bx), \text{самцы при } t > t^* \\ R_3(x) = [R_1(x) + R_2(x)] /2, & \text{самки при} \quad t > t^* \end{cases}, \quad (3)$$

Where coefficients A_1, A_2 and a are calculated based on observations. In particular, for the greenling: the interval of the zone of feeding and adaptation of fish x_1=40 m, x_2=90 m,, and the spawning zone x_0=5 m, x_3=25 m; coefficients A_1=1 units and a =0.25 were estimated by selection; coefficients A_2 =14.8147 units · m^{-1} and b=0.085 m^{-1} A_2 =14.8147 units · m^{-1} and b=0.085 m^{-1} were estimated by the least squares method based on a linear relationship, which is obtained after taking the logarithm of both sides of the expression for $R_2(x)$ [2]. To represent $R_2(x)$, instead of the lognormal representation of the function of the stimulus zone, a simpler Ricker curve is used, which is similar in its form in many respects [14].

In subsequent calculations, for each of the distributions $\{R_i(x), i=1÷3\}$, unit normalization is performed (the sum of its terms is reduced to one). The normalized distributions of the stimulus zones of the model (1) are shown in Figure.1.
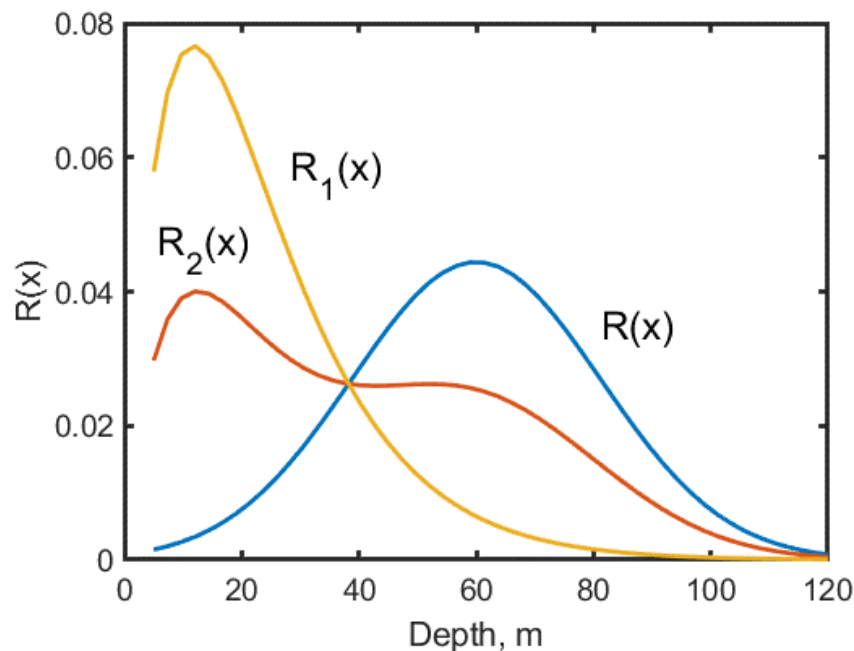

Figure 1: Normalized distributions of stimulus zones of the model (1)

The boundaries of the change in the arguments of the functions of the stimulus zones are extended to the entire range of depths, which does not correspond to the ideas accepted in practice (specific values are usually indicated [1]). This situation is due to insignificant differences of these functions from zero outside the specified intervals, as well as the presence of fish in other deep waters. So a certain proportion of mature fish do not participate in spawning, which is associated with pathologies of reproductive products. The numerical values of the model parameters (1) are presented in Table 1

$\Delta t = 1\ day$	$D_M = 0.95$ $m^2 day^{-1}$	$D_M^{(U)} = 2.1$ $m^2 day^{-1}$	$k_{11} = 9.8\ day^{-1}$
$\Delta x = 5\ m$	$D_F = 0.9\ m^2 day^{-1}$	$D_F^{(U)} = 2.1$ $m^2 day^{-1}$	$k_{21} = 9.8\ day^{-1}$
$\beta_M = 10^{-3}\ day^{-1}$	$\beta_F = 10^{-3}\ day^{-1}$	$k_{12} = 10^{-5}\ day^{-1}$	$k_{22} = 0.7$ day^{-1}

The densities of model distributions and movement velocities corresponding to individual days of simulation are shown in figure. 2.
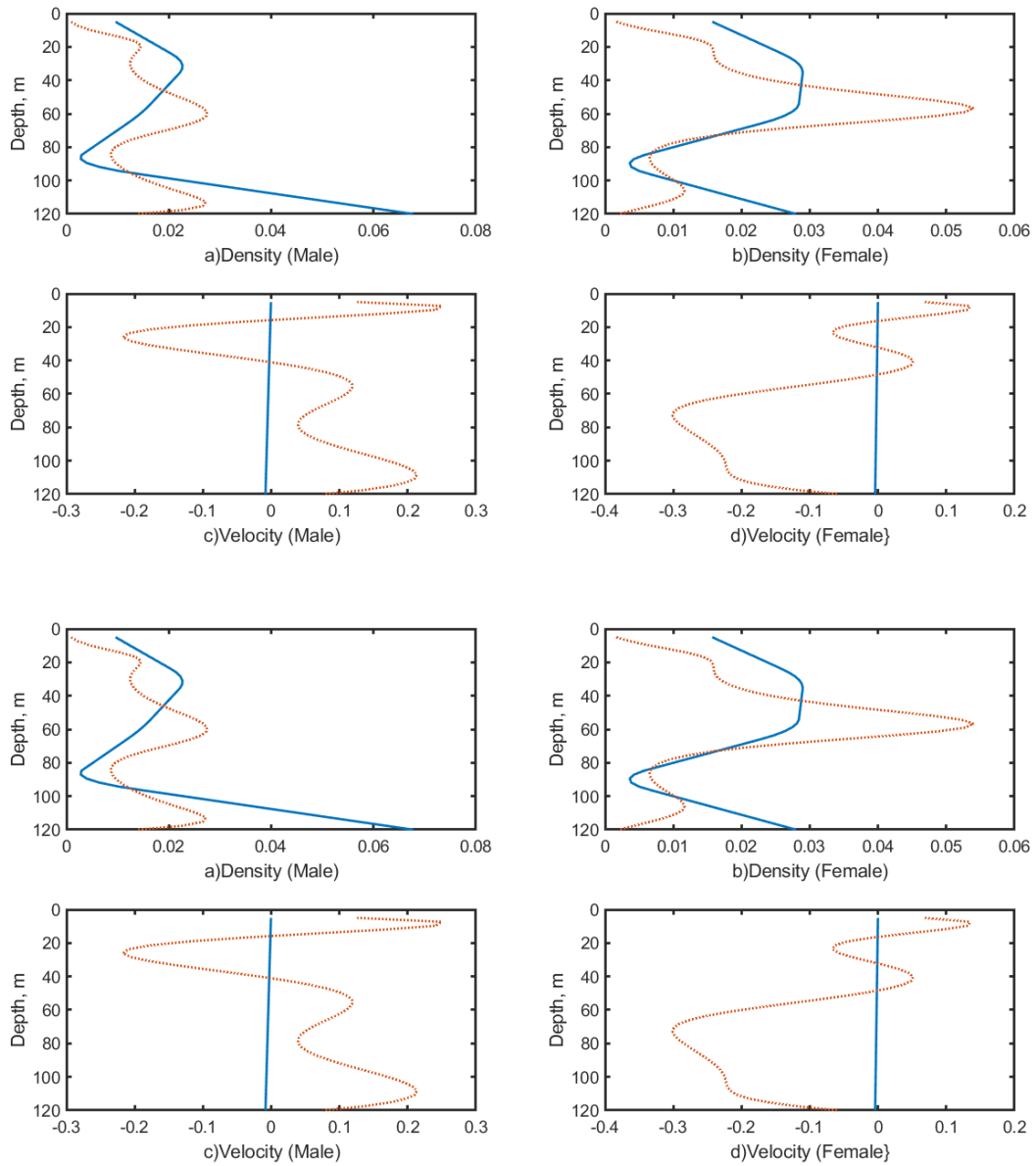

Figure 2

The analysis of the curves presented in the graphs has such a substantive interpretation. For males, the 60th day (cases a-d) is a continuation of their movement from the adaptation zone to the spawning zone, as indicated by an increased density value in the region of 20 m and the direction of daily movements/velocities of males. On the 60th day, the females mostly remain in the zone of their pre-spawning adaptation. Then their movement to the spawning zone begins. On the 110th day (cases d-h), the main part of the males is in the range of spawning depths, where their low speed of movement is noted. For females, a similar picture is noted. There is also a certain delay in the time for the females to spawn.

A comparison of the curves in Fig. 2 shows that the duration of the adaptation stage introduced here for females is 20–30% longer than for males. It seems that this is due to the peculiarities of the formation of reproductive products of females, the mass of the gonads of which is several times greater than the mass of the gonads of males [3].

The change in diurnal velocity directions (from plus to minus and back) in Figs. 1 and 2 reflects the yaw of fish in the zones of their adaptation and incentives, which is caused by the heterogeneity of the marine environment and the heterogeneity of the population structure.

Conclusion

A compact 1D numerical model of pre-spawning and spawning migrations of fish, which is based on the equations of the Palatka-Keller-Segel system, has been developed, a stage of pre-spawning adaptation of fish has been introduced, and zones of action of stimuli have been introduced. In the model, within the framework of a single mechanism, the following processes are performed: pre-spawning adaptation of fish; male competition for spawning grounds; at the spawning stage, the females follow the males (taxis). A communication mechanism has been developed, according to which males are the first to go to spawning sites, which stimulates the subsequent movement of females.

Following the provisions of the model, the mass movements of fish are due to the gradients of the zone of action of stimuli fixed in the water depths, which are depths that are comfortable for pre-spawning adaptation, well-aerated and convenient for spawning ledges of bottom areas, and distribution of males. An analysis of the results shows that during spawning migration, males move faster than females, although they do not spend longer in spawning grounds; the slowest movements are noted for the intermediate zone where adaptation takes place; continuity of transitions between stages; the duration of the adaptation stage introduced here is 20–30% longer than in males. The results of numerical experiments showed the continuity of transitions between the stage of pre-spawning adaptation of fish and the stage of spawning.

According to the construction of the model, the functions of the adaptation zone and zones of spawning incentives are determined over the entire depth interval. Such an assumption leads to multidirectional diurnal velocities, which integrally determine the main direction to the spawning zone. The adoption of such an assumption turns out to be a reflection of the natural fact of skipping spawning of a part of mature fish [15-23].

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