

Modeling of the Population Density Flow for Periodically Migrating Organisms

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Received May 9, 2008

Abstract—The Patlak–Keller–Segel population density flow equation was derived based on the hypotheses concerning the way of movement of the benthic organisms with periodic appearance in the water mass differing from the commonly used assumptions [12, 14, 15]. On the basis of these hypotheses, a time-discrete and space-continuous individual-based model of the population distribution in the environment with the continuous stimulus distribution was built. Using this model, we have shown that the analyzed taxis mechanism (i.e., the decrease of the migration frequency of the individuals from the bottom to the water mass with the increase of the stimulus concentration) leads to the aggregation of the organisms in the places with a high concentration of the stimulus. The population dynamics is well approximated by the continuous model in which the obtained Patlak–Keller–Segel flow equation is used. The numerical modeling has shown that the form of the dependence of the individual migration frequency to the water mass on the stimulus concentration (hyperbolic, exponential, linear, and sigmoid) slightly influences the pattern of the individuals' distribution.

DOI: 10.1134/S000143701001008X

1. INTRODUCTION

A striking example of the spatial and temporal heterogeneity of living systems is the harpacticoida (*Harpacticoida: Copepoda*) copepods' distribution, which are one of the main components of the sea benthos on soft sediments. For most harpacticoids, their marked patchy (aggregated) distribution is typical and their clusters' size can vary from microaggregations 0.5–1 cm² in area to large spots several meters in area [1, 9, 16–18]. On the whole, the microscale heterogeneity observed even in the quite homogeneous biotopes prevails. However, the reasons for this heterogeneity remain unclear [8, 16].

This is the first paper devoted to the analysis of the structure formation at the population level in harpacticoid and diatoms systems. The interaction in the system will be described using a population model of the taxis-diffusion-reaction type. The classical Patlak–Keller–Segel equation of the population flow is commonly used in such models. The equation is based on the assumption that the individuals are in permanent movement and the movements' type is the tumbling frequency, i.e., the frequency with which the individuals change their direction with the different stimulus concentrations. This flow equation doesn't describe the case when the individuals can be in relative quiescence for some time. For harpacticoids, these are the periods when the individuals are in the sediment. Consequently, strictly speaking, the application of the

Patlak–Keller–Segel flow equation when modeling organisms with similar movement types needs to have an additional basis. Considering the experience of constructing the taxis models in [12, 14, 15], we present the derivation of an equation of the population density flow of organisms with periodic migrations. The individual movement was considered to consist of two events: the appearance in the bottom layer of the water and making the spatial movement. The separation of these events allowed constructing the equation of the population density flow, which indirectly takes into account the periods of the relative quiescence, when the individual is in the soil column.

2. DESCRIPTION OF THE BENTHON AND THE MAIN SUGGESTIONS

Vertical migrations are typical for harpacticoids. They are caused by the daily and flood and ebb cycles. Some species move into the sand's deep layer when there is a flood, while others, on the contrary, actively move into the water mass and are able to move there a distance of tens of meters with the watercourse as well as actively swim [5, 7, 10, 11]. In doing so, up to 50% of the individuals appear in the benthic water [6]. Migrations can also occur at the time of the ebb (in the soil column). However, they happen with much less intensity and for shorter distances [5]. At the same time, harpacticoids' migrations with their appearance

in the mid-water are shown when there are no obvious floods and ebbs. Similar periodic migrations with appearance in the mid-water are also typical for some other groups of meiofauna and macrofauna [6, 7]. Thus, if we neglect the movements in the soil column, the horizontal movement of these organisms can be shown as an alternation of the periods when the individuals are in the soil column and the periods of movements to the new spatial position.

The main hypotheses and idealizations are enumerated below. We will hold to them during the construction of the mathematical model:

(1) We won't explicitly take into consideration the flood and ebb periods, considering that the individuals appearing on the bottom surface appear in the water environment.

(2) We will consider that, when the copepods appears in the water, then they will be to move for sure; all directions of movement are equally probable.

(3) We consider that the time of the copepods being in the soil column is defined by the frequency of the individuals appearance in the water, which, in turn, depends on the local concentration of some stimulus in the environment. The stimulus influences the copepods spatial activity determining the intensity of the individuals' vertical migration. The stimulus's nature is not specified beforehand (the possible variants will be briefly described in the Discussion).

3. ESTIMATION OF THE HARPACTICOID'S POPULATION DENSITY FLOW

Let us examine the individual movements during the finite time interval $(t - \tau, t)$. We will consider that the τ parameter is so small ($\tau \ll 1$) that the probability of the fact that, during the time interval $(t - \tau, t)$, the copepod appears in the water several times is almost zero. The τ value defines the minimal spatial resolution of the model. All the events with their typical time scale less than τ are considered to be microscopic and are not taken into account by this model.

The environmental state at the point x at the time moment t is characterized by the $S(x, t)$ concentration of some stimulus, whose level influences the intensity of the individual vertical migrations. Let $P(\overline{S(x, t)})$ be the probability that the individual being at the point with the coordinate x will appear in the water during the time interval $(t - \tau, t)$ depending on the value of the stimulus concentration at the point x averaged over the time interval $(t - \tau, t)$:

$$\overline{S(x, t)} = \frac{1}{\tau} \int_{t-\tau}^t S(x, s) ds.$$

If it is known that the individual appeared in the water, then the functions $P^+(r, \tau)$ and $P^-(r, \tau)$ describe its spatial movements. Namely, $P^+(r, \tau)$ and $P^-(r, \tau)$ are the probabilities of the fact that the individual will move

right or left a distance longer than r during the time period τ . As it is assumed that the individuals movement to the right or to the left is equally possible, $P^+(r, \tau) = P^-(r, \tau)$. Accordingly, the individuals movement is practically due to two events, i.e., their appearance in the water and movement to a certain distance.

The population density flow at the point x at the time moment t , $J_N(x, t)$, is the difference between the number of individuals moving in the positive direction during the time interval $(t - \tau, t)$ (the first summand) and the number of individuals moving in the negative direction during the same period of time (the second summand):

$$J_N(x, t) = \int_0^\infty \overline{N(x-r, t)} P(\overline{S(x-r, t)}) P^+(r, \tau) dr - \int_0^\infty \overline{N(x+r, t)} P(\overline{S(x+r, t)}) P^-(r, \tau) dr. \tag{3.1}$$

Here, the multipliers $\overline{N(x, t)}$ and $\overline{S(x, t)}$ are the values of the population density and the stimulus concentration at the point x averaged for the time interval $(t - \tau, t)$. The product of $\overline{N(x-r, t)} P(\overline{S(x-r, t)})$ is the expected number of individuals that will leave the point $x - r$ during the time interval $(t - \tau, t)$. The products $\overline{N(x-r, t)} P(\overline{S(x-r, t)}) P^+(r, \tau)$ and $\overline{N(x+r, t)} P(\overline{S(x+r, t)}) P^-(r, \tau)$ – are the expected number of individuals that will leave the points $x - r$ and $x + r$ during the time interval $(t - \tau, t)$ and will move right or left a distance longer than r (Fig. 1).

Let us suggest that the functions $N(x, t)$ and $S(x, t)$ are rather smooth in time and the probability $P(S)$ is in S . Then, as $\tau \ll 1$, the $P(\overline{S(x, t)})$, $\overline{N(x, t)}$, $\overline{S(x, t)}$ mean values for the time period $(t - \tau, t)$ almost coincide with the $P(S(x, t))$, $N(x, t)$, and $S(x, t)$ values, and the flow equation (3.1) can be represented in the following way:

$$J_N(x, t) = \int_0^\infty N(x-r, t) P(S(x-r, t)) P^+(r, \tau) dr - \int_0^\infty N(x+r, t) P(S(x+r, t)) P^-(r, \tau) dr. \tag{3.2}$$

Let us examine the movements that the copepods make when they appear in the water. Let the random value $\xi(\tau)$ indicate the distance that the individual moved during the period of time τ . The probabilities $P^+(r, \tau)$ and $P^-(r, \tau)$ will be evaluated through the

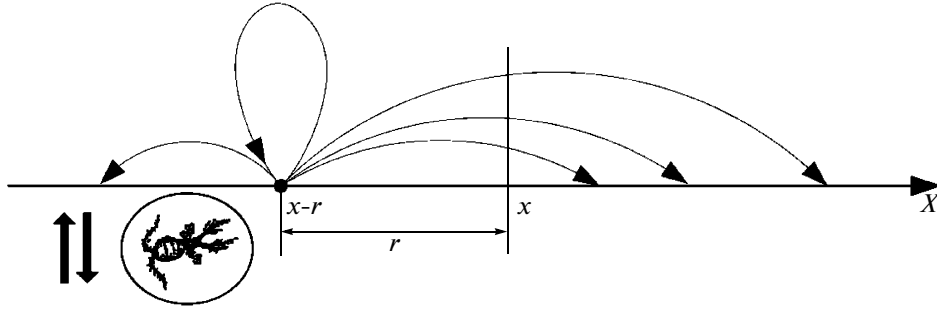


Fig. 1. Harpacticoid's behavior during the flow. With some probability the individual appears in the water and moves in the horizontal direction.

probability distribution of the random value $\xi(\tau)$, $\rho(\xi(\tau))$:

$$P^-(r, \tau) = \int_{-\infty}^{-r} \rho(\xi(\tau)) d\xi, \quad P^+(r, \tau) = \int_r^{\infty} \rho(\xi(\tau)) d\xi.$$

We will consider that the individuals movement to the new spatial positions depends on a large amount of stochastic factors. Then, according to the central limit theorem of the probability theory, $\xi(\tau)$ follows the normal distribution law with the zero mathematical expectation and variance depending on the time interval duration when the movement is examined: $\xi(\tau) \in \mathcal{N}(0, \sigma^2(\tau))$. As the fixed period of time τ is considered to be small ($\tau \ll 1$), the variance value will also be considered to be small: $\sigma^2(\tau) = \sigma_\tau^2 \ll 1$.

As $\xi(\tau)$ obeys the normal distribution law, $\xi(\tau) \in \mathcal{N}(0, \sigma_\tau)$, the following estimation is valid:

$$\forall \varepsilon > 0 \quad \exists c = \text{const}: \quad \forall r > c\sigma_\tau$$

$$P^+(r, \tau) = \left| \int_r^{\infty} \rho(\xi(\tau)) d\xi \right| < \varepsilon. \quad (3.3)$$

Using estimation (3.3) and the equality of the probabilities $P^+(r, \tau)$ and $P^-(r, \tau)$ allows in the flow equation $J_N(x, t)$ (3.2) to be integrated in a finite region:

$$J_N(x, t) = \int_0^{c\sigma_\tau} [N(x-r, t)P(S(x-r, t)) - N(x+r, t)P(S(x+r, t))] P^+(r, \tau) dr. \quad (3.4)$$

From the characteristics of the normal distribution, it follows that the most probable movements are concentrated in the rather narrow region close to the mathematical expectation. For example, according to the three sigma rule, for $\varepsilon = 0.003$, the estimation (3.3) is valid at $c = 3$, while, for $\varepsilon = 6 \times 10^{-8}$, at $c = 5$. Since high accuracy in practical calculations is not required and $\sigma_\tau \ll 1$, it can be considered that the $c\sigma_\tau$ value is also much less than one, and the Taylor formula near

the point x can be applied to each of the two summands in the right part of expression (3.4):

$$\begin{aligned} N(x \mp r, t)P(S(x \mp r, t)) &= N(x, t)P(S(x, t)) \\ &\mp r \left(\frac{\partial N(x, t)}{\partial x} P(S(x, t)) \right. \\ &\left. + N(x, t) \frac{dP(S)}{dS} \frac{\partial S(x, t)}{\partial x} \right) + o(r). \end{aligned}$$

After the truncation of the remainder term, the flow equation (3.4) acquires the following form:

$$J_N = - \left[\int_0^{c\sigma_\tau} r P^+(r, \tau) dr \right] \left(P(S) \frac{\partial N}{\partial x} + \frac{dP(S)}{dS} N(x, t) \frac{\partial S}{\partial x} \right). \quad (3.5)$$

Having calculated the integral in (3.5) using the permutation of the limits of the integration and estimation (3.3),

$$\begin{aligned} \int_0^{c\sigma_\tau} r P^+(r, \tau) dr &= \int_0^{c\sigma_\tau} r \int_r^{\infty} \rho(\xi, \tau) d\xi dr \\ &= \int_0^{c\sigma_\tau} \rho(\xi, \tau) \int_0^\xi r dr d\xi + \int_{c\sigma_\tau}^{\infty} \rho(\xi, \tau) \int_0^{c\sigma_\tau} r dr d\xi \\ &\approx \int_0^{c\sigma_\tau} \frac{\xi^2}{2} \rho(\xi, \tau) d\xi = \frac{\bar{l}^2}{2} \end{aligned}$$

(as

$$\int_{c\sigma_\tau}^{\infty} \rho(\xi, \tau) d\xi \int_0^{c\sigma_\tau} r dr \frac{c^2 \sigma_\tau^2}{2} \int_{c\sigma_\tau}^{\infty} \rho(\xi, \tau) d\xi < \frac{c^2 \sigma_\tau^2}{2} \varepsilon \approx 0),$$

the flow equation (3.5) can be represented as the following:

$$J_N = -\mu(S)\frac{\partial N}{\partial x} + \chi(S)N\frac{\partial S}{\partial x}, \quad (3.6)$$

$$\mu(S) = \frac{\bar{l}^2}{2}P(S), \quad \chi(S) = -\frac{\bar{l}^2}{2}\frac{dP(S)}{dS},$$

where $\mu(S)$ is the diffusion constant; $\chi(S)$ is the taxis constant; and \bar{l}^2 is the mean value of the squared movement distance, which coincides with the variance σ_τ^2 .

Accordingly, we obtain the flow equation of Patlak–Keller–Segel on the basis of assumptions different from those in [12, 14, 15].

3.1 The Frequency of the Individuals' Appearance in the Water $f(S)$

3.1.1. The individuals' appearance in the water is an stochastic Poisson process. Let us examine the harpacticoids' vertical movements. The order of the animals' appearance in the water is the flow of events satisfying the following conditions:

(1) At every space point, for every two disjoint time intervals, the number of vertical migrations, i.e., the appearances in the water, during one interval of time doesn't depend on the number of migrations during the other period.

(2) The probability that, during the time interval $(t - \tau, t)$, an individual will appear in the water more than once is an infinitesimal of higher order in comparison with τ and can be considered equal to zero.

The fulfillment of these conditions means that the studied flow of events is an ordinary stream without a consequence and can be classified as an elementary Poisson flow with a variable parameter [2–4]. Subsequently, the probability that, during the time interval $(t - \tau, t)$, there will be k events of the individuals appearance in the water can be calculated using the Poisson distribution:

$$p_{x,k}(t - \tau, t) = \frac{\varphi_x^k}{k!} e^{-\varphi_x \tau},$$

$$\varphi_x = \int_{t-\tau}^t \lambda(x, u) du = \int_{t-\tau}^t f(S(x, u)) du, \quad (3.7)$$

where φ_x is the number of events taking place during the period of time $(t - \tau, t)$ at the spatial position x , and $\lambda(x, t)$ is the momentary value of the parameter of the Poisson distribution. As the given flow is elementary, the $\lambda(x, u)$ parameter is at the same time the average number of events taking place at the time moment t at the spatial point x , or the flow's instantaneous intensity [4]. Concerning the harpacticoids, we consider

that $\lambda(x, t) = f(S(x, t))$, where $f(S)$ is the frequency of the harpacticoids' appearance in the water.

As we suppose that both S and the $f(S)$ function are sufficiently smooth, and $\tau \ll 1$, it can be considered that, for every value $u \in (t - \tau, t)$, $f(S(x, u)) \approx f(S(x, t))$. According to (3.7) the average number of events is $\varphi_x = f(S(x, t))\tau$. Thus, the probability that, at point x during the time interval $((t - \tau, t) k)$, the individuals' appearance in the water will occur k times is expressed by the formula

$$p_{x,k}(t - \tau, t) = \frac{[f(S(x, t))\tau]^k}{k!} e^{-f(S(x, t))\tau}.$$

3.1.2. The association of the coefficients of the diffusion $\mu(S)$ and the taxis $\chi(S)$ with the frequency of the individuals' appearance in the water $f(S)$. Let us find the correlation between the probability that the individual at point x will appear in the water during the time interval $(t - \tau, t)$, $P(S(x, t))$ and the frequency of this event $f(S(x, t))$. Let us examine the random value:

$$\zeta_x(t - \tau, t) = \begin{cases} 1, & \text{the individual at point } x \\ & \text{appears in the water during } (t - \tau, t); \\ 0, & \text{the individual at point } x \\ & \text{is in the soil during } (t - \tau, t). \end{cases}$$

Let the probabilities that $\zeta_x(t - \tau, t) = 1$ and $\zeta_x(t - \tau, t) = 0$ expressed through the probability that the individual at point x will appear in the water k times during the time interval $(t - \tau, t)$, $p_{x,k}(t - \tau, t)$ be expressed by the following expressions:

$$P(\zeta_x(t - \tau, t) = 1) = \sum_{k=1}^{\infty} p_{x,k}(t - \tau, t) = 1 - e^{-f(S(x, t))\tau}, \quad (3.8)$$

$$P(\zeta_x(t - \tau, t) = 0) p_{x,0}(t - \tau, t) = e^{-f(S(x, t))\tau}.$$

The smallness of the time interval τ allows representing the Taylor formula representing the right part of expression (3.8) as the following:

$$P(\zeta_x(t - \tau, t) = 1) = 1 - (1 - f(S(x, t))\tau + o(\tau)) \approx f(S(x, t))\tau. \quad (3.9)$$

Hence, the probability that the individual that is at point with the coordinate x will appear in the water during the time interval $(t - \tau, t)$ is related to the frequency of the individual's appearance in the water by the following expression:

$$P(S(x, t)) = f(S(x, t))\tau. \quad (3.10)$$

Then, the coefficients of the diffusion $\mu(S)$ and taxis $\chi(S)$ are expressed as the following:

$$\mu(S) = \frac{\bar{l}^2 \tau}{2} f(S), \quad \chi(S) = -\frac{\bar{l}^2 \tau}{2} \frac{df(S)}{dS} = -\frac{d\mu(S)}{dS}. \quad (3.11)$$

3.1.3. The probability to move a distance longer than r and the frequency of the individuals' appearance in the water $f(S)$. Let us examine the spatial movements of the individuals. Let $\eta_{x,r}(t - \tau, t)$ be the random value describing the process of an individual's movement in the horizontal direction with the distance l , which is longer than the fixed distance r :

$$\eta_{x,r}(t - \tau, t) = \begin{cases} 1, \text{ the individual moved} \\ \text{from } x \text{ in} \\ l > r, \text{ during } (t - \tau, t); \\ 0, \text{ the individual did not} \\ \text{move from } x \text{ in} \\ l > r, \text{ during } (t - \tau, t). \end{cases}$$

Let us calculate the probability that an individual won't move from the point x a distance longer than r during the time interval $(t - \tau, t)$. This probability is equal to the sum of the probabilities that, at the point x , the individual's appearance in the water will happen k times but, at the same time, the individual will move distances shorter than r :

$$\begin{aligned} P(\eta_{x,r}(t - \tau, t) = 0) &= \sum_{k=0}^{\infty} P \left\{ \begin{array}{l} \text{there will be } k \text{ events of the} \\ \text{individual's appearance} \\ \text{in the water at point } x \\ \text{during } (t - \tau, t) \end{array} \right\} (1 - P^+(r, \tau))^k \\ &= \sum_{k=0}^{\infty} p_{x,k}(t - \tau, t) (1 - P^+(r, \tau))^k \\ &= e^{-f(S(x,t))\tau} \sum_{k=0}^{\infty} \frac{((1 - P^+(r, \tau))f(S(x,t))\tau)^k}{k!} \\ &= e^{-f(S(x,t))\tau + (1 - P^+(r, \tau))f(S(x,t))\tau} \\ &= e^{-P^+(r, \tau)f(S(x,t))\tau} \end{aligned}$$

Subsequently, the probability that the individual will move from the point x a distance longer than r during the time interval $(t - \tau, t)$ is expressed by the formula

$$\begin{aligned} P(\eta_{x,r}(t - \tau, t) = 1) &= 1 - P(\eta_{x,r}(t - \tau, t) = 0) \\ &= 1 - e^{-f(S(x,t))P^+(r, \tau)\tau} \end{aligned}$$

As $\tau \ll 1$, let us use Taylor's formula and, throwing away the remainder term, we will have

$$\begin{aligned} P(\eta_{x,r}(t - \tau, t) = 1) &= 1 - (1 - f(S(x,t))P^+(r, \tau)\tau + o(\tau)) \\ &\approx f(S(x,t))P^+(r, \tau)\tau. \end{aligned} \tag{3.12}$$

When modeling the population density flow, the probability $P(\eta_{x,r}(t - \tau, t) = 1)$ was expressed by the following formula:

$$P(\eta_{x,r}(t - \tau, t) = 1) = P(S(x,t))P^+(r, \tau). \tag{3.13}$$

Comparing formulas (3.12) and (3.13), we reach the conclusion that

$$P(S(x,t))P^+(r, \tau) = f(S(x,t))P^+(r, \tau)\tau.$$

Let us note that this correlation can be obtained by the formal substitution of (3.10) into (3.13); i.e., the assumption that the individual's movement to the water is an accidental Poisson process doesn't contradict the main hypothesis of the model.

4. THE INDIVIDUAL-BASED MODEL OF THE DISTRIBUTION OF THE HARPACTICOID'S POPULATION

Let us illustrate the distribution of the individuals in the environment with the continuous distribution of the stimulus using the individual-based model. The model is discrete in time with the time step τ and continuous in space. The assumptions used when deriving the flow equation underlie the model. Let us change them a little.

- (1) The individual's movement in each time step is determined by two events: the appearance in the water and the movement.
- (2) During the step of the simulation model, the time interval $(t - \tau, t)$, the individuals have time to appear in the water and make a movement no more than once.
- (3) Whether the copepod that is at the point x appears in the water depends on the stimulus value at this point $S(x)$.
- (4) When the copepod appears in the water, it necessarily makes a movement and goes back to the soil.
- (5) The random value describing the individual's movements complies with the normal distribution law: $\xi \in N(0, \sigma_\tau)$.

The coordinate of the copepod at the step $i + 1$ is expressed by the formula

$$x_{i+1} = x_i + \zeta_{x_i}(t_{i+1} - \tau, t_{i+1})\xi,$$

where x_i is the individual's location at the i th step; $\zeta_{x_i}(t_{i+1} - \tau, t_{i+1})$ is the random value describing the process of its appearance in the water during the $i + 1$ th step: $\zeta_{x_i}(t_{i+1} - \tau, t_{i+1}) = 0$ (the copepod is in the soil), $\zeta_{x_i}(t_{i+1} - \tau, t_{i+1}) = 1$ (the copepod moves into the water; and the random value ξ specifies the direction and distance of the individual's movement during the time period τ , $\xi \in N(0, \sigma_\tau)$ (Fig. 2). The random value $\zeta_{x_i}(t_{i+1} - \tau, t_{i+1})$ is formed in such way that equality (3.9) is satisfied; i.e., $P(\zeta_{x_i}(t_{i+1} - \tau, t_{i+1}) = 1) = f(S(x_i))\tau$, where $f(S)$ is the dependence of the frequency of the copepod's appearance in the water on the stimulus value.

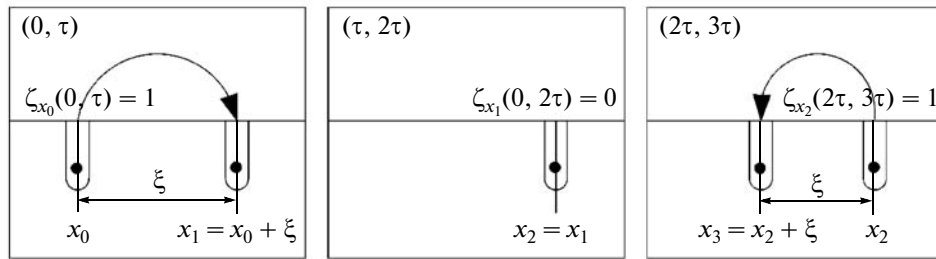


Fig. 2. Harpacticoid's movements (3 iterations of the imitation model): (1, 3)—the periods when the individual appears in the water and makes movements, (2)—the period when the individual is in the soil column.

The frequency of the copepod's appearance in the water was suggested to decrease with the increase of the stimulus value. The better the conditions, the more time the individual spends at the given point. In unfavorable conditions, in an environment with a low stimulus level, the animals frequently appear in the water and move there. As the mechanisms of the individuals' reaction to the stimulus, four types of $f(S)$ dependences satisfying this condition were examined: hyperbolic, exponential, linear, and sigmoid.

The model of the harpacticoids' movement was realized for the cases of one-dimensional and two-dimensional spaces in the MATLAB development environment. Examples of the population distribution in environments with different stationary stimulus distributions for the exponential dependence $f(S) = \exp(-S/2)$ are shown in Fig. 3 and Fig. 4.

5. CONTINUOUS MODEL OF THE HARPACTICOID'S POPULATION DISTRIBUTION

According to the widespread Euler approach [13, 14], let us describe the harpacticoid population's distribution using the following differential equation:

$$\frac{\partial N}{\partial t} = f_N - \frac{\partial}{\partial x} J_N, \quad (5.1)$$

where $N(x, t)$ is the population density, f_N is the function describing the processes of the individuals' birth and death, and J_N is the population density flow. As when formulating the individual-based model, we will assume that, during the analyzed period of time, the demographic processes act rather slowly and don't considerably influence the total population number, $f_N = 0$. We will take the earlier obtained Patlak–Keller–Segel flow equation (3.6), (3.11) as J_N . In this case, the equation will take the following form:

$$\frac{\partial N}{\partial t} = a_0 N + a_1 \frac{\partial N}{\partial x} + a_2 \frac{\partial^2 N}{\partial x^2}, \quad (5.2)$$

$$a_0 = \frac{\bar{l}^2 \tau}{2} \left(\frac{d^2 f(S)}{dS^2} \left(\frac{dS}{dx} \right)^2 + \frac{df(S)}{dS} \frac{d^2 S}{dx^2} \right), \quad (5.3)$$

$$a_1 = \bar{l}^2 \tau \frac{df(S)}{dS} \frac{dS}{dx}, \quad a_2 = \frac{\bar{l}^2 \tau}{2} f(S). \quad (5.4)$$

$$N|_{x=a,b} = 0.$$

This equation was reduced by the net method with the central finite-difference scheme to a system of ordinary differential equations, which was then solved by the fifth order Runge–Kutta method with automatic step-size control.

The harpacticoids' population distribution obtained using the individual-based model and the solutions of equations (5.2)–(5.4) are shown in the right upper corner in Fig. 3. The values of a and b for the different parameter values were estimated each time all over again. Firstly, we observed how the individuals would distribute in the case of the individual-based model; then, the $[a, b]$ segment was chosen so that it was sufficiently wide and included the whole range of values of the individuals' coordinates. For the above-listed parameter values, $[a, b] = [-200, 200]$.

The coincidence of the harpacticoids' distribution picture obtained using the individual-based model with the solution of the differential equation (5.2)–(5.4) testifies that the set up hypotheses concerning the way of the harpacticoids' movement are true and allow describing the individuals' aggregation in the places with a high stimulus concentration. In addition, it was shown that the population dynamics are well approximated by differential equation (5.2)–(5.3) when the number of individuals is high.

DISCUSSION AND CONCLUSIONS

In this paper, the dynamics of the movement of the periodically migrating organisms in the environment with the spatially heterogeneous stimulus distribution were analyzed using the example of the harpacticoids living in the bottom layer. Based on the hypotheses about the individuals' movement, which were different from the suggestions made in other works [12, 14, 15], the validation of the Patlak–Keller–Segel equation of

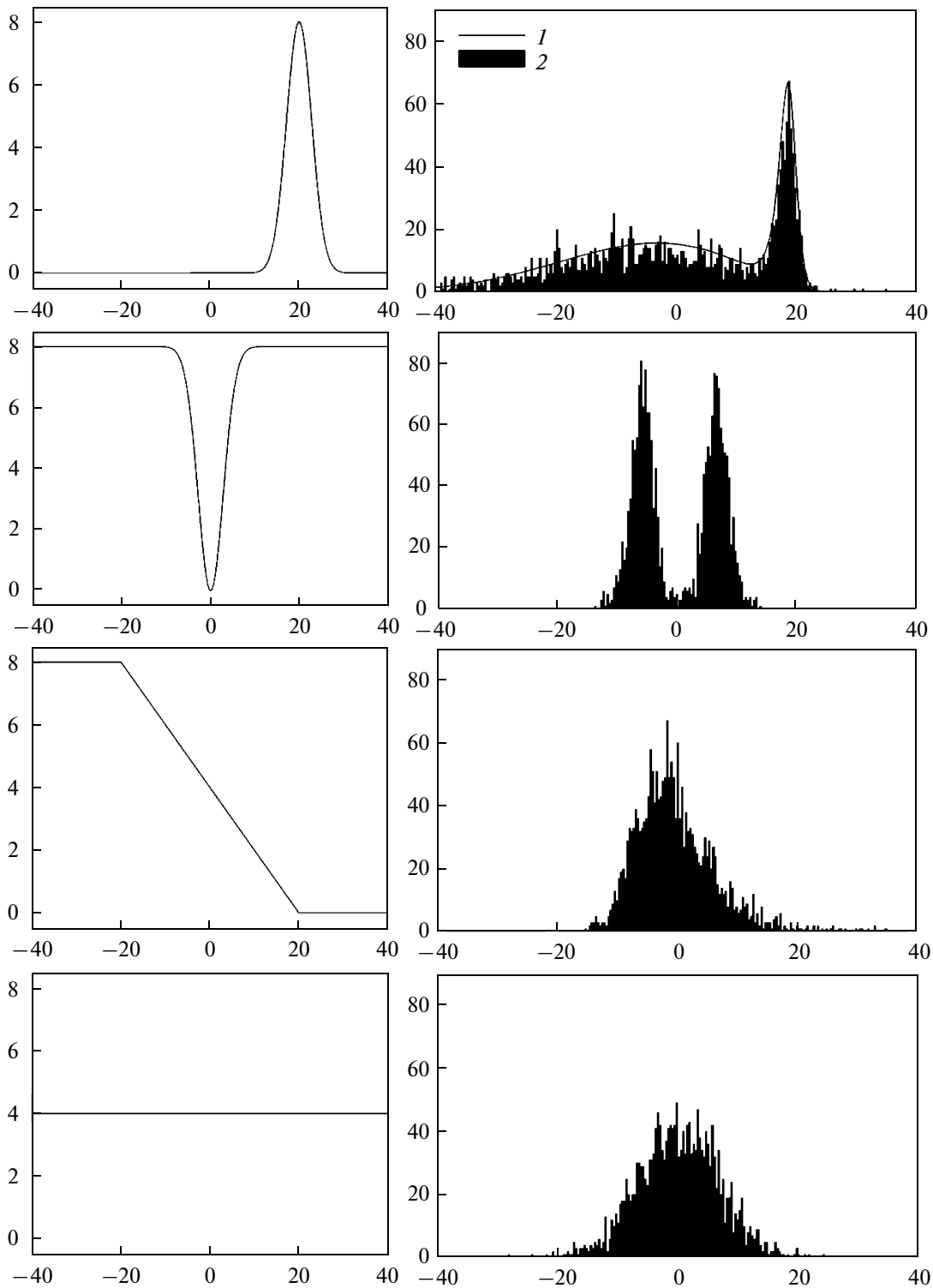


Fig. 3. 1-D distribution of the harpacticoids' population (on the right) in an environment with a continuous stimulus distribution (on the left) at $t = 325$. Abscissa—the horizontal coordinate; ordinate—the stimulus concentration (on the left) and the number of individuals (on the right), rel. units.

(1)—obtained using the continuous model, (2)—obtained using the individual-based model. The parameters: the frequency of appearance in the water is $f(S) = \exp(-S/2)$, the time period is $\tau = 1$, the number of steps is $T = 325$, the number of individuals is $M = 2000$, the average value of the traveled square is $\bar{l}^2 = \sigma_\tau^2 = 1$, and the stimulus distribution in case of the continuous model is $S(x) = 8\exp(-(x - 20)^2/16)$. At the starting time, all the individuals were at the central point.

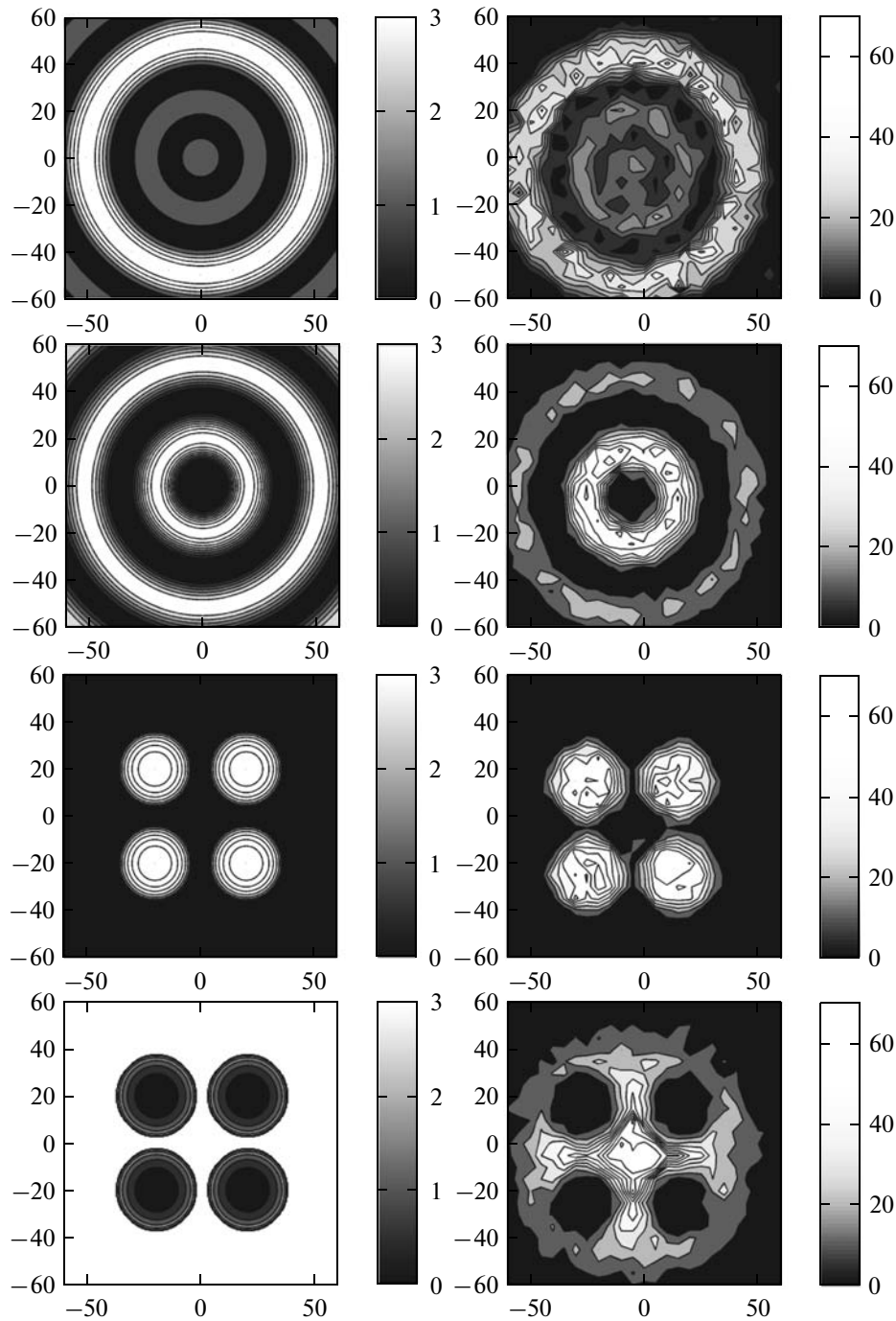


Fig. 4. 2-D distribution of the harpacticoids' population (on the right) in the environment with the permanent stimulus distribution (on the left). The parameters: the frequency of appearance in the water is $f(S) = \exp(-S/2)$, the time period is $\tau = 1$, the number of steps is $T = 5000$, the number of individuals is $M = 10000$, and the variance is $\sigma_t^2 = 1$. At the starting time, all the individuals were at the central point. The datum lines are the spatial coordinates. The filling shows the stimulus concentration (on the left) and the number of individuals (on the right), rel. units.

the population density flow was given. The obtained result confirms the universality of the Patlak–Keller–Segel model and its applicability for the description of the taxis phenomenon in different situations. Note that the accepted hypotheses seem to be quite natural

and the distributions involved in them normal and Poisson due to the extremality in the entropy index often observed in biological systems.

The taxis response of the organisms to the changes in the stimulus concentration lay in the changes in the

individuals' appearance in the water with varying of the stimulus value. We suggested that, in a favorable environment with a high stimulus concentration, an individual spends almost all its time in the soil column and rarely appears in the water and makes movements. With unfavorable conditions with a low stimulus level, the individual tries to leave them, appears in the water more often, and more actively makes occasional undirected movements.

Based on the hypotheses used when forming the population flow equation, we formed the individual-based model of the harpacticoids' distribution in the environment with a distribution of stimulus concentration. Using the model, we illustrated the fact that the analyzed taxis mechanism, i.e., the decrease of the frequency of the copepods appearance in the water with an increase of the stimulus concentration, leads to the organisms' accumulation in places with a high stimulus content. When the number of individuals is big, the system's dynamics is well approximated by the continuous model of the reaction-diffusion-taxis type (5.2)–(5.4). The numerical modeling showed that the type of dependence of the frequency of the copepod's appearance in the water on the stimulus concentration (hyperbolic, exponential, linear, and sigmoid) doesn't significantly influence the individuals' distribution.

The presented model can also be used to describe the distribution of other organism populations whose movement is considerably different from the way of movement of harpacticoids. For example, instead of the probability of the appearance in the water, the probability that the individual will make a movement in a random direction can be analyzed. However, the individual-based model used to illustrate the taxis phenomenon was constructed assuming the stationarity of the stimulus distribution. In truth, of course this is not the case. Moreover, even when the stimulus is permanently distributed in infinite space and time, the individuals' distribution after the temporary aggregation in the favorable conditions will tend to become homogenous.

The received flow equation naturally enters into the balance equation of the harpacticoids' population density. To close the model system, it is necessary to set an equation describing the taxis stimulus dynamics. Note that here we don't fix what the stimulus is exactly that provides the directional movements and generates the dynamic spatial structures in the harpacticoids and diatom system. As possible candidates for this role, different factors and mechanisms, for example, the population density of the food objects (microalgae), the concentration of the microalgae excreted exometabolites, the extent of the individual satiation, etc. can be viewed. In our opinion, a correct model of the spatio-temporal harpacticoids' dynamics should reproduce the stable spatially heterogeneous regimes under minimal assumptions about the spatial and feeding behavior of the copepods. The investigation and the comparison of the dynamic characteristics of correspond-

ing alternative models of the predator–prey type will be the subject of our future investigations.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research (project no. 06-04-48106) and by the internal SFU grant.

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