A REMARK ON THE DISORIENTING OF SPECIES DUE TO FLUCTUATING ENVIRONMENT

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Abstract.  
In this article we study the stabilizing of a primitive pattern of behaviour for the two-species community with chemotaxis due to the short-wavelength external signal. We use a system of Patlak-Keller-Segel type as a model of the community. It is well-known that such systems can produce complex unsteady patterns of behaviour which are usually explained mathematically by bifurcations of the ‘basic’ solutions that describe simpler patterns. These bifurcations are always assumed to be a result of instability of the basic solution in the sense of Lyapunov. As far as we aware, all such bifurcations in the models of the Patlak-Keller-Segel type had been found for homogeneous (i.e. translationally invariant) systems where the basic solutions are equilibria with homogeneous distributions of all species. The model considered in the present paper does not possess the translational invariance: one of species (the ‘predators’) is assumed to be capable of moving in response to a signal produced externally in addition to the signal emitted by another species (the ‘prey’). For instance, the external signal may arise from the inhomogeneity of the distribution of an environmental characteristic such as temperature, salinity, terrain relief, etc. Our goal is to examine the effect of short-wavelength inhomogeneity. To do this, we employ a certain homogenization procedure. We separate the short-wavelength and smooth components of the system’s response and derive a ‘slow’ system governing the latter one. Analysing the slow system and comparing it with the case of homogeneous environment shows that, generically, a short-wavelength inhomogeneity results in an exponential decrease in the motility of the predators. The loss of motility prevents, to a great extent, the occurrence of complex unsteady patterns and dramatically stabilizes the primitive basic solution. In some sense, the necessity of dealing with intensive small-scale changes of the environment makes the system unable to respond to other challenges.  

Keywords: Patlak-Keller-Segel systems, prey-taxis, indirect taxis, external signal production, stability, instability, Poincare-Andronov-Hopf bifurcation, averaging, homogenization.

Introduction  

Taxis is usually defined as an ability of a biological substance to respond to another substance, called stimulus or signal, by directed motion on a macroscopic scale. The name ‘chemotaxis’ refers to taxis driven by chemical signals. The well-known Patlak-Keller-Segel (PKS) model assumes that the chemotactic flux of species is directed along the gradient of stimulus. The PKS approach is widely used for the modelling of the other forms of taxes. For example, the stimulus for one species (the ‘predators’) may be the density of another species (the ‘prey’).
Such interaction of species is known as prey-taxis. In the present study we consider so-called indirect prey-taxis when the stimulus for the ‘predators’ is not the ‘prey’ density itself but a signal emitted by the ‘prey’. The signal may be a chemical or something else which is either attractive or repellent for the ‘predators’. Various insights into the modelling of the taxes using the PKS systems and references on the subject can be found in recent articles [4, 5, 6, 7, 8, 9, 10].

It is well-known that the PKS-type systems can produce complex unsteady patterns which are explained mathematically by bifurcations of the ‘basic’ solutions describing simpler patterns. These bifurcations always assume the destabilization of the basic solution in the sense of Lyapunov. As far as we aware, all such bifurcations in the models of PKS type had been discovered for the homogeneous (i.e. translationally invariant) systems where the basic solutions are equilibria with homogeneous distributions of all species (e.g. [1, 2, 3, 8, 7, 6]). The model considered in the present paper does not possess the translational invariance: the ‘predators’ can move in response to a signal produced externally (in addition to the signal emitted by the ‘prey’). The external signal may arise, for instance, from an inhomogeneity in the distribution of an environmental characteristic such as temperature, salinity, terrain relief, etc. When the considered distribution is homogeneous, the model restores the translational invariance since such distribution produces no signal.

Our main goal is to examine the effect of a short-wavelength inhomogeneity of the environment. For this purpose, we employ a certain homogenization procedure. We separate the short-wavelength and smooth components of the system’s response and derive a ‘slow’ system governing the latter one. The slow system has almost the same form as the original system, but the inhomogeneity results in an additional contribution to the flux of the predators. This additional flux vanishes when a characteristic amplitude of the inhomogeneity is equal to zero; that is, the slow system includes the case of homogeneous environment as a particular case.

Analysing the slow system and comparing it with the case of homogeneous environment shows that a short-wavelength inhomogeneity results in an exponential reduction of the predator motility. The loss of motility prevents, to a great extent, the occurrence of complex unsteady patterns and dramatically stabilizes a primitive basic solution. This fact has an obvious interpretation: the necessity of dealing with intensive small-scale changes of the environment makes the system unable to respond to other challenges.

An inhomogeneous extension of a homogeneous PKS system can be obtained simply by adding an external source to the equation governing the signal production. We do this for the model originally proposed in [1, 2]. It is therefore useful to compare our results to those of [1, 2]. The key observations made in [1, 2] are: (i) if motility of the predators is beyond a threshold then the system responds to the prey deficiency by the destabilization of the homogeneous equilibrium accompanied by the excitation of wave motions; (ii) if the predator motility is below this threshold then the homogeneous equilibria are stable irrespective of the prey deficiency and the waves do not arise; (iii) the wave dynamics is more advantageous for the whole community than the equilibrium in the sense that the ‘predators’ may consume more than at the equilibrium, at the same time leaving greater stock of the ‘prey’.

The slow system derived in the present study formally reproduces the above properties (i) and (ii), but the motility of predators is replaced by an effective motility which depends on a characteristic amplitude of the short-wavelength inhomogeneity imposed onto the environment. If this amplitude is close to zero then the effective motility is almost the same as in the homogeneous environment but even a moderate increase in it causes the exponential loss of the effective motility while the threshold remains the same. Consequently, an inhomogeneous counterpart of the transition (i) becomes hardly attainable. Thus the predators lose their ability to pursue the prey effectively, and such effect can be treated as their disorientation due to the fluctuations of the environment. We note also that the analysis of [12] shows that a non-equilibrium state is in some sense necessary for living systems in order to adapt to a fluctuating environment.
The model proposed in [1, 2] is chosen as the basic one because it is perhaps the most simple model among those demonstrating the arising of unsteady patterns from their equilibria. Originally, this model had been formulated a slightly special way, and perhaps its connection with models of PKS type was insufficiently apparent. This connection has been clarified in the recent article [6].

The effect of spatial inhomogeneity is still rarely addressed in the literature. We know only of related results reported in [11] and in [13]. The former article is aimed to the modelling of the effect of the terrain relief on the spatially distributed living community. For this purpose, the authors perform a homogenization of a reaction-diffusion system with jumps of the coefficients across the points of some mesh, with this mesh being infinitely refined. The latter article written in the style of pure mathematics is aimed to the studying of the PKS systems with inhomogeneous reaction terms and contains several qualitative results concerning the global boundedness of solutions.

The averaging and homogenization methods are used very widely for constructing high-frequency or short-wavelength asymptotics for ODEs and PDEs, and we do not describe this area in any detail here. We only would like to mention two general phenomena underlying the results sketched out above. These are Stokes’s drift and the dynamical stabilization (similar to the stabilisation of the upside-down pendulum). Stokes’s drift typically arises from averaging over small-scale oscillations of an advective velocity, and the generation of ‘effective motility’ by short waves definitely resembles that. Further, the stabilizing effect of short waves resembles the dynamical stabilization due to high-frequency vibrations. Note that there are more or less regular procedures which enable us to analyze dynamical stabilization as well as Stoke’s drift under quite reasonable assumptions about the scales of pulsations. Further information on these methods can be found in [14, 15, 16, 17, 18, 19].

The article is organized into five section supplemented with two Appendices. In section 1, the governing equations and their relation to the chemotaxis models of Patlak-Keller-Segel type are discussed. In section 2, we consider the homogeneous case and describe the results of the stability analysis of the homogeneous equilibria. In section 3, we discuss the inhomogeneous environment and derive the slow system. In section 4, we consider the stabilization caused by the inhomogeneity. Section 5 contains the discussion of the results. Appendix I describes a routine part of the stability analysis. Appendix II contains the details of the homogenization procedure.

1 The governing equations

We consider an inhomogeneous extension of model suggested in [1, 2] for a spatial ‘predator-prey’ community placed into a homogeneous environment. The governing equations are as follows

\[ \partial_T U = \partial_X (k_p Q + k_e F) - k_r s U + D_v \partial_X^2 U; \]  
\[ \partial_T P + \partial_X (P U - D_{pr d} \partial_X P) = 0; \]  
\[ \partial_T Q = k_r p Q \left( 1 - \frac{Q}{k_c} \right) - k_p r P Q + D_{pr y} \partial_X^2 Q. \]  

Here \( X, T \) stand for a spatial coordinate and time; \( P \) stands for the predators distribution density; \( Q \) stands for the prey distribution density; \( U \) stands for the macroscopic velocity of the predators; \( \partial_T \) and \( \partial_X \) denote partial differentiation with respect to \( T \) and \( X \); \( \partial_X^2 \) stands for the double partial differentiation with respect to \( X \); \( D_{pr y}, D_{pr d}, D_v, k_r s, k_r p, k_c, k_p r, \) and \( k_e \) are constant parameters of the model. The model of [1, 2] is a particular case of equations (1.1)–(1.3) corresponding to \( F = \text{const} \) or \( k_e = 0 \).
Equations (1.3) and (1.2) describe balances of the prey and of the predators respectively. We assume that reproduction of the prey and its losses due to predation obey the logistic and Lotka-Volterra laws correspondingly. Parameters $k_c > 0$, $k_{pr} > 0$, $k_{rp} > 0$ denote the the ‘carrying capacity’, the rate of predation and the rate of reproduction of the prey respectively. Parameters $D_{pry}$ and $D_{prd}$ are the diffusion coefficients for the prey and the predators. We neglect the contribution from the reproduction and mortality of the predators, assuming that these processes are much more slow than the other processes considered.

Equation (1.1) describes the evolution of the macroscopic velocity of the predators that depends on the prey density and on the external signal denoted as $F$. The role of the latter can be played by the density distribution of some characteristic of the environment such as salinity or temperature. Coefficient $k_p$ is the intensity of prey-taxis, and $k_e$ is the intensity of the taxis towards the external signal. We assume that $k_p > 0$ as the prey is an attractant for the predators. We also take into account the diffusion of the predators velocity and the resistance to their motion due to the environment and denote the corresponding coefficients as $D_v$ and $k_{rs}$, respectively.

Generically, system (1.1)–(1.3) is not invariant with respect to the spatial or temporal translations except for the special case of homogeneous environment when $F = \text{const}$ or $k_e = 0$. Notice also that Eq. (1.1) is invariant with respect to the transformation $F \mapsto F + F_0(t)$, where $F_0$ can be chosen arbitrarily. In view of this invariance, we shall assume that $\partial_X F \equiv 0$ implies $F \equiv 0$. One can implement such calibration simply by assuming that $F(\cdot; t)$ is zero either on average or at some fixed point for every $t$.

The homogeneous version of system (1.1)–(1.3) had been proposed in [1, 2] as a simple model of inertial prey-taxis. Inertial prey-taxis assumes that, unlike the Patlak-Keller-Segel (PKS) systems, the flux of species has to overcome certain inertia while taking the direction of the stimulus gradient. Tyutyunov, Titova and Senina [6] noticed that integration of Eq. (1.1) with the use of velocity potential reduces the homogeneous version of the system (1.1)-(1.3) to a system with indirect prey-taxis (see e.g. [5]). We shall discuss this issue in more detail in the end of this section.

With a suitable non-dimensionalisation, system (1.1)-(1.3) can be rewritten in the following ‘dimensionless’ form:

$$
\begin{align*}
\partial_t u &= \partial_x (\kappa q + \sigma f) - \nu u + \delta_u \partial_x^2 u; \\
\partial_t p &= \partial_x (\delta_p \partial_x p - pu); \\
\partial_t q &= q(1 - q - p) + \delta_q \partial_x^2 q.
\end{align*}
$$

(1.4) (1.5) (1.6)

Here $u, p, q, x, t$ are the dimensionless counterparts of variables $U, P, Q, X, T$, and $\delta_p, \delta_q, \delta_u, \kappa, \sigma, \nu$ are the dimensionless counterparts of parameters $D_{pry}, D_{prd}, D_v, k_p, k_e, k_{rs}$. All other parameters have been normalized to unity. The units are introduced as follows. We set

$$
T = t \frac{k_{rp}}{k_{pry}}; \quad X = X_0 x; \quad P = \frac{k_{rp} p}{k_{pry}}; \quad Q = k_e q; \quad U = X_0 k_{rp} u; \quad F = F_0 f
$$

(1.7)

where $X_0$ and $F_0$ stand for characteristic scales of length and of the external signal which remain indefinite. The dimensionless parameters take the forms

$$
\delta_q = \frac{D_{pry}}{k_{rp} X_0^2}, \quad \delta_p = \frac{D_{prd}}{k_{rp} X_0^2}, \quad \delta_u = \frac{D_v}{k_{rp} X_0^2}, \quad \nu = \frac{k_{rs}}{k_{rp}}; \quad \kappa = \frac{k_p k_e}{k_{rp}^2 X_0^2}; \quad \sigma = \frac{k_e F_0}{k_{rp}^2 X_0^2}.
$$

(1.8)

Parameters $\sigma$ and $\kappa$ in Eq. (1.4) can be normalized to unity by a suitable choice of the magnitudes of $X_0$ and $F_0$. Nevertheless, we shall not be using this extra normalization until it is necessary.
Let’s return to the above-mentioned analogy between the inertial and indirect prey-taxes. The ansatz $u = \kappa \partial_x \phi$ transforms system (1.4)-(1.6) into the system consisting of equation (1.6) and the following two equations

$$\partial_t \phi = q + \sigma \kappa^{-1} f - \nu \phi + \delta_u \partial_x^2 \phi; \quad \partial_t p = \partial_x (\delta_p \partial_x p - \kappa p \partial_x \phi)$$

System (1.6),(1.9) can be classified as PKS system with indirect prey-taxis in which the velocity potential, $\phi$, plays the role of signal emitted by the prey, and an additional signal, $f$, is produced externally. We recall that $\partial_x f \equiv 0$ implies $f \equiv 0$ in accordance with the calibration of the external signal accepted above. Note that equality $\partial_x f \equiv 0$ takes us back to the homogeneous version of system (1.4)-(1.6); in view of this, the external signal has to be eliminated from (1.9).

2 Homogeneous environment

The homogeneous version of model (1.4)-(1.6) had been investigated in [1, 2]. One of key findings of these studies is that a sufficiently strong prey-taxis makes the system capable of replacing the homogeneous equilibria by wavy motions in response to the increase in the prey deficiency. The waves occurs due to the Poincare-Andronov-Hopf (PAH) bifurcation. For the sake of completeness, we briefly describe these results here.

In general, the PAH bifurcation is the branching of a limit cycle from a smooth family of equilibria of a smooth one-parametric family of dynamical systems. The motions along the limit cycle are periodic self-oscillations. To detect the PAH bifurcation, one should search for the transversal crossing of the imaginary axis at some nonzero point with a smooth branch of eigenvalues of the eigenmodes of small perturbations of the equilibria of this family. An occurrence of such a crossing due to a gradual change of the family parameter is often called an oscillatory instability. Oscillatory instabilities are always accompanied by the PAH bifurcation except for some cases of degeneration. Various systematic expositions of the theory of this bifurcation and its applications can be found in monographs [20, 21, 22, 23].

The homogeneous system (1.4)-(1.6) has a family of homogeneous equilibria in which

$$p \equiv p_e, \quad q \equiv q_e, \quad u = 0, \quad p_e = \text{const} > 0, \quad q_e = \text{const} > 0, \quad p_e + q_e = 1.$$  (2.1)

Here the normalized ‘total mass’ of the predators, $p_e$, plays the role of the family parameter. The oscillatory instability occurs in family (2.1) in response to the increase in $p_e$ provided that parameter $\kappa$ in Eq. (1.4) is greater than a threshold. The eigenmodes of small perturbations of equilibria (2.1) have the following form

$$(\hat{u}, \hat{p}, \hat{q}) \exp(i \alpha x + \lambda t), \quad \lambda = \lambda(\alpha) \in \mathbb{C}, \quad \alpha \in \mathbb{R}.$$  (2.2)

Here $\lambda$ is the eigenvalue of the corresponding spectral problem. To be more specific, we present here the underlying results regarding the eigenmodes of equilibria (2.1). The details are in Appendix I.

We say that eigenmode (2.2) is stable (unstable, neutral) if the real part of $\lambda$ is negative (positive, equal to zero). The results described below are valid provided that the following restrictions hold:

$$\alpha \neq 0, \quad 0 < p_e < 1, \quad \nu (\delta_p + \delta_u + \delta_q) > 0.$$  (2.3)

We have eliminated the endpoints such as $\alpha = 0$ or $p_e = 1$ etc. in order to cut off the excessive degenerations. Note that each equilibrium (2.1) has a neutral homogeneous mode (that corresponds to $\alpha = 0$) but this does not lead to any long-wave instabilities. Note also that the last inequality in (2.3) allows some of the diffusion coefficients (though not all simultaneously) to be zero.
It is convenient to introduce the following notation

$$\beta = \alpha^2, \quad \delta = (\nu, \delta_q, \delta_r, \delta_u).$$

Since the homogeneous system (1.4)-(1.6) is invariant with respect to the reflections \(x \to -x, \ u \to -u\), the spectrum of eigenmodes is invariant with respect to the reflections \(\alpha \to -\alpha\). Therefore we consider the positive wave numbers only.

Let values of parameters \(\kappa, p_e, \beta\), and vector-parameter \(\delta\) be specified. Let’s consider the equilibrium (2.1) in which the total mass of predators is equal to the specified value of \(p_e\). There are three eigenmodes (2.2) of this equilibrium with wave number \(\alpha = \sqrt{\beta}\) for every fixed \(\beta\). There are unstable eigen-modes among them provided that intensity of the prey-taxis, \(\kappa\), is greater than a critical value \(\kappa_c = \kappa_c(p_e, \beta, \delta)\). If \(\kappa < \kappa_c\) then each of those three eigen-modes is stable and if \(\kappa = \kappa_c\) then two of them are neutral with nonzero complex conjugate decrements. The oscillatory instability takes place each time a path in the space of parameters \((p_e, \beta, \delta, \kappa)\) intersects the graph of function \(\kappa = \kappa_c(p_e, \beta, \delta)\) transversally except, perhaps, for some cases of degeneration.

For every \(\delta\) the critical intensity, \(\kappa_c(p_e, \beta, \delta)\), is finite everywhere in the semi-strip which is cut out by inequalities \(0 < p_e < 1, \beta > 0\); the global minimum of \(\kappa_c\) over this semi-strip is positive and attained at some point \(p_0(\delta), \beta_0(\delta)\); that is,

$$\min_{0 < p_e < 1, \beta > 0} \kappa_c(p_e, \beta, \delta) = \kappa_c(p_0(\delta), \beta_0(\delta), \delta) = \kappa_s(\delta) > 0. \quad (2.4)$$

Hence, every mode (2.2) for every equilibrium (2.1) is stable provided that \(\kappa < \kappa_s(\delta)\).

For every \(\kappa > \kappa_s(\delta)\), equation

$$\kappa = \kappa_c(p_e, \beta, \delta) \quad (2.5)$$
determines a closed curve which lies strictly inside the above-mentioned semi-strip and which is approaching boundary of the semi-strip as \(\kappa \to +\infty\). The typical curves determined by Eq. (2.5) are shown in Fig. 1 for various values of \(\kappa\) (the left frame). Figure 1 shows that an increase in \(p_e\) can destabilize only eigenmodes with wave numbers from a finite interval \((\sqrt{\beta_1(\kappa, \delta)}, \sqrt{\beta_2(\kappa, \delta)})\) (see the right frame in Fig. 1). More precisely, let \(\kappa, \delta, \beta\) be constant along a path parameterized by \(p_e\). Generically, such path intersects the graph of \(\kappa_c\) twice or does not intersect it at all (see the right frame in Fig.1). In the latter case, eigenmodes (2.2) with wave numbers \(\alpha = \sqrt{\beta}\) remain stable for every \(p_e \in (0, 1)\). In the former case, a pair of these modes becomes unstable when \(p_e\) exceeds the first critical magnitude \(p_e^{un} = p_e^{st}(\beta, \kappa, \delta)\) and then gets the stability back when \(p_e\) exceeds the second critical magnitude \(p_e^{st} = p_e^{st}(\beta, \kappa, \delta) > p_e^{un}(\beta, \kappa, \delta)\) (see the right frame in Fig.1).

Thus, for an eigenmode with \(\beta \in (\beta_1, \beta_2)\), the oscillatory instability of the homogeneous equilibrium occurs when the density of the predators exceeds \(p_e^{un}(\beta, \kappa, \delta)\) provided that the intensity the prey-taxis, \(\kappa\), is beyond the threshold value defined in (2.4). The threshold value of the density of the predators is determined by minimizing \(p_e^{un}\); that is,

$$p_e(\kappa, \delta) = \min_{\{\kappa, p_e^{un}(\beta, \kappa, \delta) = \kappa\}} p_e^{un} \quad (2.6)$$

The corresponding value of \(\beta, \beta_s(\kappa, \delta)\), is nothing but the squared wave number of the most unstable perturbation (see the right frame in Fig.1).

The nonlinear transitions in homogeneous system (1.4)-(1.6), discovered in articles [1, 2], are consistent with the above results of linear analysis. Before we give more detail, it is worth to note that the spatial domain considered in [1, 2] is finite, so that the the length scale is fixed. As a result, the spectrum is discrete and the eigenvalues and wavenumbers fill certain discrete subsets in the corresponding continuous spectra associated to eigenmodes (2.2). In particular, variational problems (2.4) and (2.6) should be considered on the discrete range
Figure 1: The left frame shows typical curves determined by equation $\kappa_c(p_e, \beta, \delta) = \kappa$ on the $(p_e, \beta)$ plane for $\kappa$ in the range from 15.12 to 50.0 and $\delta = (1, 1, 0, 0)$. The area bounded by a curve increases with $\kappa$. The right frame corresponds to $\delta = (1, 1, 0, 0)$ and $\kappa = 13.56$. The other numerical values are: $p_0 \approx 0.624$; $p_{\text{un}} \approx 0.642$, $p_{\text{st}} \approx 0.707$, $\beta_1 \approx 0.546$, $\beta_2 \approx 0.812$ of $\beta$. An inhomogeneity due to a finite initial perturbation of a homogeneous equilibrium may evolve following three different scenarios. If $\kappa < \kappa_*$, then even rather substantial initial inhomogeneities die out and the system goes back to the homogeneous state irrespective of $p_e \in (0, 1)$. If $\kappa > \kappa_*$ and $p_e < p_{\text{un}}$, then the same happens at least provided that the initial perturbation is sufficiently small. If $\kappa > \kappa_*$ and $p_e > p_{\text{un}}$, then even rather weak initial inhomogeneity survives and gradually develops into a wave. As long as $p_e$ remains close to $p_{\text{un}}$, these waves are periodic in time. For greater $p_e$, they become non-periodic or even chaotic. The system behaves almost in the same way even when $p_e$ exceeds $p_{\text{st}}$. This is, perhaps, because, in spite of the stability of the homogeneous states, their basins of attraction are very narrow.

The transition from the homogeneous equilibria to time-periodic patterns has been studied for more general classes of the chemotaxis systems in [3, 6, 7].

3 Fluctuating environment

Let the external signal in Eq. (1.4) be a short wave, i.e.

$$f = f(x, t, \xi, \tau), \ \xi = \omega x, \ \tau = \omega t, \ \omega \gg 1$$

(3.1)

and let the diffusion rates be of the same order as the wave length, namely:

$$\delta_u = \nu_1 \omega^{-1}, \ \delta_p = \nu_2 \omega^{-1}, \ \nu_1 > 0, \ \nu_2 > 0.$$  

(3.2)

With these assumptions, the response of system (1.4)-(1.6) should be a short wave with smoothly varying amplitude. We have derived a ‘slow system’ governing the evolutions of this amplitude in the limit of $\omega \to +\infty$ using the two-scales expansions (see e.g. [15, 17]). Here we present only the final result. Details of the derivation are in Appendix II.

We define the averaged value of a function $g = g(x, t, \xi, \tau)$ as follows

$$\langle g \rangle = \frac{1}{4\pi} \int_0^{2\pi} \int_0^{2\pi} g(x, t, \xi, \eta) \, d\xi d\eta.$$  

(3.3)
We assume that short-wavelength signal (3.1) is $2\pi$-periodic in both $\xi = \omega x$ and $\tau = \omega t$. The asymptotic of the response of system (1.4)-(1.6) to such signal takes the following form

$$q(x, t) = \bar{q}(x, t) + O(\omega^{-1}), \quad \omega \to +\infty;$$  (3.4)

$$u(x, t) = \bar{u}(x, t) + \bar{u}_0(x, t, \tau, \xi) + O(\omega^{-1}), \quad \omega \to +\infty;$$  (3.5)

$$p(x, t) = \bar{p}(x, t) P(x, t, \tau, \xi) + O(\omega^{-1}), \quad \omega \to +\infty$$  (3.6)

where $\bar{u}_0$ is a $2\pi$-periodic (in both variables $\xi = \omega x$ and $\tau = \omega t$) solution to the problem

$$\partial_{\tau} \bar{u}_0 = \partial_{\xi}(\sigma f + \nu_1 \partial_{\xi} \bar{u}_0); \quad \langle \bar{u}_0 \rangle = 0, \quad (3.7)$$

$P$ is a $2\pi$-periodic (in both $\xi = \omega x$ and $\tau = \omega t$) solution to the problem

$$\partial_{\tau} P = \partial_{\xi}(\nu_2 \partial_{\xi} P - P(\bar{u} + \bar{u}_0)), \quad \langle P \rangle = 1; \quad (3.8)$$

and $\bar{u}, \bar{q}$ and $\bar{p}$ represent a solution to the system

$$\begin{align*}
\partial_t \bar{u} &= \partial_x(\kappa \bar{q} + \sigma \bar{f}) - \nu \bar{u}; \quad \bar{f} = \langle f \rangle \\
\partial_t \bar{p} + \partial_x(\bar{p}(\bar{u} + \langle \bar{u}_0 P \rangle)) &= 0; \quad (3.10) \\
\bar{q}_t &= \bar{q}(1 - \bar{p} - \bar{q}) + \delta_\xi \partial_{\xi}^2 \bar{q}. \quad (3.11)
\end{align*}$$

Note that

$$\bar{u} = \langle u \rangle + O(\omega^{-1}), \quad \bar{p} = \langle p \rangle + O(\omega^{-1}), \quad \bar{q} = \langle q \rangle + O(\omega^{-1}), \quad \omega \to +\infty.$$

Asymptotic formulae (3.4)-(3.6) show that the leading term in the smooth component of the short-wavelength solution is determined by three unknown functions $\bar{p}, \bar{q}, \bar{u}$ which obey Eqs. (3.9), (3.10) and (3.11). We call these equations the slow system.

The slow system differs from the original system (1.4)-(1.6) in two respects. First, there is neither diffusion of the velocity nor diffusion of the predators, and this is a consequence of assumption (3.2). Second, there is additional drift of the predators with velocity equal to $\langle \bar{u}_0 P \rangle$ and it is this drift that is responsible for the effect of the short-wavelength signal on the slow evolution.

Let us consider the drift velocity in more details. Notice that the first equation in (3.8) has only one normalized periodic solution whatever periodic coefficient of the equation is specified (see Appendix II). Hence problem (3.8) implicitly determines a single valued nonlinear mapping

$$\mathcal{P}: (\bar{u}, \bar{u}_0) \mapsto P. \quad (3.12)$$

In the same way, problem (3.7) with $\sigma = 1$ determines a mapping

$$\mathcal{K}: f \mapsto \bar{u}_0. \quad (3.13)$$

Since problem (3.7) is linear, mapping $\mathcal{K}$ is also linear and, therefore, $\mathcal{K}(\sigma f) = \sigma \mathcal{K} f$ for every $\sigma$. Consequently, the evaluation of average $\langle \bar{u}_0 P \rangle$ can be treated as the action of the mapping $\mathcal{V}: (\bar{u}, f) \mapsto \langle \sigma \mathcal{K} f \mathcal{P}(\bar{u}, \sigma \mathcal{K} f) \rangle = \langle \bar{u}_0 P \rangle$ (3.14)

Hence Eq. (3.10) takes the form

$$\partial_t \bar{p} + \partial_x(\bar{p}(\bar{u} + \mathcal{V}(\bar{u}, f))) = 0 \quad (3.15)$$

Since $f$ is given, the slow system consisting of Eq. (3.9), Eq. (3.11) and Eq. (3.10) or, equivalently, Eq. (3.15) represents a closed system for unknown functions $\bar{p}, \bar{q}, \bar{u}$. 

8
4 Stabilization of the relative equilibria

In what follows we assume that
\[ f = f(\xi, \tau). \]  
(4.1)

This assumption imply the invariance of the slow system with respect to the spatial translations. A manifestation of this symmetry is that \( \partial_x V(0, f) = 0 \) and hence the slow system has the family of homogeneous equilibria
\[ \bar{u} = 0, \quad \bar{p} = \bar{p}_e, \quad \bar{q} = \bar{q}_e, \quad \bar{p}_e + \bar{q}_e = 1. \]  
(4.2)

Each equilibrium (4.2) of the slow system determines a short-wavelength pattern of behavior of the original system by virtue of formulae (3.4)–(3.6). This is rather primitive pattern since it is fully imposed by the short-wavelength external signal and steady with respect to slow time. We call these patterns the relative equilibria (of the original system) as they are natural counterparts of the homogeneous equilibria (2.1). Since relative equilibria of the original system and homogeneous equilibria of the slow system are not actually distinguishable in our treatment of the problem, we shall use the same name for both of them.

We note that the relative equilibria (4.2) exist even if \( f = f(t, \xi, \tau) \). Nevertheless, we neglect this opportunity and accept a more restrictive assumption (4.1) for the sake of the invariance with respect to the translations along the time axis. This invariance enables us to examine the stability of the relative equilibria in exactly the same way as it was done in section 2.

Let an external signal, \( f \), be given and has the form of Eq. (4.1). Let \( \eta \) be a constant. Then \( V(\eta, f) \) is another constant and the correspondence
\[ \eta \mapsto V(\eta, f) \]  
(4.3)
determines a mapping of the real axis to itself. We denote the differential of mapping (4.3) evaluated at the origin by \( V'(f) \). The system governing the evolution of a small perturbation of a given relative equilibrium takes the form
\[ \partial_t \bar{u} + \nu \bar{u} - \kappa \partial_x \bar{q} = 0; \]  
(4.4)
\[ \partial_t \bar{p} + \bar{p}_e (1 + V'(f)) \partial_x \bar{u} = 0; \]  
(4.5)
\[ \partial_t \bar{q} + \bar{q}_e (\bar{p} + \bar{q}) - \delta \bar{q} \partial^2_x \bar{q} = 0; \]  
(4.6)

Since \( V'(f) = \text{const} \), factor \( 1 + V'(f) \) can be treated as the effective motility coefficient.

Re-scaling \( \bar{u} \), we transform system (4.4)-(4.6) to the following form
\[ \partial_t \bar{u} + \nu \bar{u} - \bar{k} \partial_x \bar{q} = 0, \quad \bar{k} = (1 + V'(f)) \kappa \]  
(4.7)
\[ \partial_t \bar{p} + \bar{p}_e \partial_x \bar{u} = 0; \]  
(4.8)
\[ \partial_t \bar{q} - q_e (\bar{p} + \bar{q}) - \delta \bar{q} \partial^2_x \bar{q} = 0; \]  
(4.9)
\[ \bar{p}_e + \bar{q}_e = 1. \]

This system almost coincides with that governing the evolution of small perturbations in the homogeneous case provided that \( \delta_p = \delta_u = 0 \) (see Eqs. (6.1)-(6.3) in Appendix I). The only difference is due to the change \( \kappa \mapsto \bar{k} \). Therefore, the effect of the short-wavelength external signal on the stability of relative equilibria manifests itself in altering the prey-taxis intensity or, equivalently, the predators motility as one can see from Eqs. (4.7) and (4.5).

Now we recall that magnitudes of \( \kappa \) and \( \sigma \) can be normalized. As we have mentioned in Sec. 1, this can be done by choosing characteristic scales for length and for the external signal. So, in what follows, we put
\[ \kappa = \sigma = 1. \]
Then all the statements about the stability of equilibria of the homogeneous version of system (1.4)-(1.6), made in Sec. 2, are also true for the stability of the relative equilibria, provided that the prey-taxis intensity, \( \kappa \), is replaced by its effective counterpart \( \bar{\kappa} = (1 + V'(f)) \). In particular, the inequality

\[
1 + V'(f) < \kappa_{\ast}|_{\delta_p=\delta_u=0} \tag{4.10}
\]

implies absolute stabilization of relative equilibria in the sense that there is no instability irrespective of what equilibrium and what the perturbation wave number are considered.

The right hand side of inequality (4.10) is exactly the threshold of the prey-taxis intensity that was introduced in Sec. 2 (see also Appendix I). In view of Eq. (4.5), the left hand side of inequality (4.10) can be interpreted as the effective motility of predators. The threshold of the prey-taxis does not depend on the external signal while the effective motility evidently depends on it and it is interesting to learn to what extent; in particular, whether or not a short-wavelength external signal is capable of the absolute stabilizing the equilibria which are unstable otherwise. More formally, the question is whether or not one can make the left hand side of inequality (4.10) less than 1 by manipulating function \( f \). Let’s show that the answer to this question is affirmative.

Let us denote as \( \langle g \rangle^\xi \) the average value of some function \( g = g(x,t,\xi,\tau) \) with respect to variable \( \xi \); that is,

\[
\langle g \rangle^\xi = \frac{1}{2\pi} \int_0^{2\pi} g(x,t,\xi,\tau) \, d\xi \tag{4.11}
\]

Let the external signal be independent of \( \tau \):

\[
f = f(\xi), \quad \langle f \rangle = 0. \tag{4.12}
\]

Under condition (4.12), evaluation of \( \tilde{u}_0 = \sigma K f \) reduces to the solving of equations

\[
\partial_\xi (\sigma f + \nu_1 \partial_\xi \tilde{u}_0) = 0, \quad \langle u_0 \rangle^\xi = 0. \tag{4.13}
\]

Then evaluation of \( P = \mathcal{P}(\tilde{u}, \tilde{u}_0) \) reduces to the solving of equations

\[
\partial_\xi (\nu_2 \partial_\xi P - P(\tilde{u} + \tilde{u}_0)) = 0, \quad \langle P \rangle^\xi = 1, \tag{4.14}
\]

and \( \mathcal{V}(\tilde{u}, f) = \langle \tilde{u}_0 P \rangle^\xi \). Consequently,

\[
\mathcal{V}'(f) = \langle \tilde{u}_0 P_1 \rangle^\xi \tag{4.15}
\]

where \( P_1 \) is determined by equations

\[
\partial_\xi (\nu_2 \partial_\xi P_1 - P_0 - \tilde{u}_0 P_1) = 0, \quad \langle P_1 \rangle^\xi = 0, \tag{4.16}
\]

\[
\partial_\xi (\nu_2 \partial_\xi P_0 - \tilde{u}_0 P_0) = 0, \quad \langle P_0 \rangle^\xi = 1. \tag{4.17}
\]

Here we are interested only in those solutions to equations (4.13), (4.14), (4.16) and (4.17) that are \( 2\pi \)-periodic in variable \( \xi \).

Straightforward calculations, taking into account the periodicity, yield the following results

\[
P_0 = A_0 e^v, \quad A_0 = \frac{1}{\langle e^v \rangle^\xi}; \tag{4.18}
\]

\[
P_1 = e^v (A_1 + \frac{\partial_\xi^{-1}(A_0 - C_1 e^{-v})}{\nu_2}), \quad A_1 = A_0 (e^v \partial_\xi^{-1}) (C_2 e^{-v} - A_0)^\xi, \quad C_4 = \frac{1}{\langle e^{-v} \rangle^\xi \langle e^v \rangle^\xi}; \tag{4.19}
\]

\[
v = \nu_2 \partial_\xi^{-1} \tilde{u}_0, \quad \langle \partial_\xi^{-1} \rangle^\xi = 0 \tag{4.20}
\]

where transformation \( \partial_\xi^{-1} \) acts on \( 2\pi \)-periodic (in \( \xi \)) functions vanishing on average as the right inverse to \( \partial_\xi \), i.e.

\[
\partial_\xi \partial_\xi^{-1} w = w, \quad \langle \partial_\xi^{-1} \rangle^\xi = 0
\]
for any function \( w \) such that it is \( 2\pi \)-periodic in \( \xi \) and \( \langle w \rangle^\xi = 0 \). Consequently,

\[
\mathcal{V}'(f) = \nu_2 \langle (A_1 + \nu_2^{-1} \partial_\xi^{-1}(A_0 - C_1e^{-v}))e^v \partial_\xi v \rangle^\xi = -\langle e^v(A_0 - C_1e^{-v}) \rangle^\xi = C_1 - 1 = \frac{1}{\langle e^{-v} \rangle^\xi \langle e^v \rangle^\xi} - 1.
\]

Finally, the solving of problem (4.13) yields \( \mathcal{K}f = -(\nu_1 \partial_\xi)^{-1}f \), and then we get

\[
v = (\nu_2 \partial_\xi)^{-1} \mathcal{K}f = -(\nu_2 \partial_\xi)^{-1}(\nu_1 \partial_\xi)^{-1}f.
\]

In what follows we change \( f \) by \(-f\). This does not lead to any mistakes since functional \( \mathcal{V}'(f) \) is even with respect to \( f \). Thus the effective motility \( \bar{\kappa} = 1 + \mathcal{V}'(f) \) takes almost explicit form; namely

\[
\bar{\kappa} = \frac{1}{\langle e^{-v} \rangle^\xi \langle e^v \rangle^\xi}, \quad v = (\nu_1 \nu_2)^{-1} \partial_\xi^{-2}f.
\] (4.21)

Substituting this into inequality (4.10) yields a more explicit form of the criterion for absolute stabilization:

\[
\frac{1}{\langle e^{-v} \rangle^\xi \langle e^v \rangle^\xi} < \kappa_*|_{\delta_p=\delta_u=0},
\] (4.22)

**Example 1** Let \( f = A\sin \xi \), \( A = \text{const} > 0 \). Then \( v = -A(\nu_1 \nu_2)^{-1}\sin \xi \), and

\[
\bar{\kappa}^{-1} = \langle e^{-v} \rangle^\xi \langle e^v \rangle^\xi = I_0^2(a), \quad a = \frac{A}{\nu_1 \nu_2}
\]

where \( I_0 \) is the modified Bessel function of first kind. Consequently, the criterion for absolute stabilization (4.22) takes the following form

\[
I_0^{-2}(a) < \kappa_*|_{\delta_p=\delta_u=0}, \quad a = \frac{A}{\nu_1 \nu_2}
\] (4.23)

The effective motility of the predators that stands on the left hand side of this inequality decreases exponentially when parameter \( a \) grows up. This parameter represents a characteristic amplitude of the external signal. Hence, the increase in the level of the external signal leads to absolute stabilization of the relative equilibria and this effect is rather powerful.

**Remark 1.** In fact, the exponential decrease in effective motility of the predators in response to the increase in the level of the external signal is a generic property of the system. This can be seen by estimating expression (4.21) using the Laplace method for \( f = Af_0, \ A \to \infty \).

Therefore, an increase in the amplitude of a short-wavelength external signal typically stabilizes the relative equilibria as is shown in Example 1.

**Remark 2.** The stabilization described above occurs irrespective of whether the external signal is attractive or repellent for the predators.

## 5 Conclusions

We have studied the effect of small-scale fluctuations of the environment on the two-species community with chemotaxis. It turned out that, on average, the short-wavelength inhomogeneities produce a drift motion of the predators (see Eq. (3.10) or (3.15)) which can radically change the ‘slow’ advection of the predators. In particular, these changes manifest themselves by the loss of the predator motility (see factor \( \bar{\kappa} = 1 + \mathcal{V}'(f) \) in Eq. (4.5)), so that it exponentially decreases in response to an increase in the amplitude of the fluctuations. The exponential loss of the predators motility, in turn, leads to the stabilization of the most primitive spatial pattern.
and prevents the transition to more complex behavior in spite of the fact that an increase in complexity can bring benefits to both species (in the sense that the predators may consume more and, at the same time, keep greater stock of the prey than in the primitive basic state) [1, 2, 12]. Thus, small-scale fluctuations of the environment came making a living community unable to respond to the challenges of overpopulation and the lack of resources. This can be interpreted as a kind of disorientation: the predators, in some sense, get lost and disunited due to the environment fluctuations and that makes them unable to get rid of a primitive pattern of behavior which just mimic the imposed fluctuations.

Note that the characteristic amplitude of the fluctuations, $a$, is proportional to $(\nu_1 \nu_2)^{-1}$ while $\nu_1$ and $\nu_2$ are defined in (3.2) as the relations of the characteristic wave number of the short-wavelength signal to the diffusion rates of the macroscopic velocity of the predators and the predators themselves, respectively (of course, we use the dimensionless quantities, defined by (1.8)). Surprisingly, a decrease in these relative diffusion rates has a powerful stabilizing effect. Perhaps, this is a manifestation of singularity of limits of vanishing $\nu_1$ or $\nu_2$, and this issue is a subject for further investigations.

Another interesting question is to what extent the stabilizing effect depends on the shape of the external signal. This question leads to an optimization problem for the effective motility defined in (4.21) subject to restriction $\langle f^2 \rangle = 1$.

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6 Appendix I. Eigenmodes of the equilibria

Let us choose an equilibrium out of family (2.1) by specifying a value of the family parameter, \( p_e \). The system governing small perturbation of this equilibrium takes the form

\[
\begin{align*}
    u_t + \nu u - \kappa q_x &= \delta_u u_{xx} \quad (6.1) \\
    p_t + p_e u_x &= \delta_p p_{xx} \quad (6.2) \\
    q_t + q_e (p + q) &= \delta_q q_{xx} \quad (6.3) \\
    p_e + q_e &= 1.
\end{align*}
\]

Eigenvalues for the eigenmodes (2.2) having a specific wavenumber \( \alpha \) are solutions to the following algebraic equation

\[
\lambda^3 + (D_1 + D_2 + D_3)\lambda^2 + (D_2 D_3 + D_1 D_3 + D_1 D_2)\lambda + D_1 D_2 D_3 + \beta \kappa p_e q_e = 0, \quad (6.4)
\]

\[
D_1 = \nu + \beta \delta_u; \quad D_2 = \beta \delta_p; \quad D_3 = q_e + \beta \delta_q; \quad \beta = \alpha^2.
\]

In view of restrictions (2.3), all the coefficients of the polynomial on the left hand side of Eq. (6.4) are strictly positive. Consequently, this polynomial has neither positive nor zero roots. Hence, no unstable or neutral eigenmode corresponds to a real eigenvalue.

It follows from the Routh-Hurwitz theorem that the necessary and sufficient condition for all roots of polynomial (6.4) to be in the open left half-plane of the complex plane is

\[
(D_1 + D_2)(D_1 + D_3)(D_2 + D_3) > \beta \kappa p_e q_e.
\]

This inequality admits a more compact form, namely:

\[
(D_1 + D_2)(D_1 + D_3)(D_2 + D_3) > \beta \kappa p_e q_e.
\]

Hence the results of linear analysis described in Sec. 2 are valid provided that one defines the critical magnitude of the prey-taxis as

\[
\kappa_c = \frac{(D_1 + D_2)(D_1 + D_3)(D_2 + D_3)}{\beta p_e q_e}. \quad (6.5)
\]

Indeed, the degree of polynomial (6.4) is 3. Consequently, \( \kappa = \kappa_c \) is the necessary and sufficient condition for a root of polynomial (6.4) to lie on the imaginary axis (this root cannot be zero).

Let us consider the threshold value \( \kappa_* \) that has been defined in (2.4). Although we do not have an explicit expression for \( \kappa_* \), its positiveness as well as the other properties mentioned in Sec. 2 are almost obvious or, in any case, can be verified directly using expression (6.5). A useful auxiliary result is the explicit minimization of \( \kappa_c \) relative to \( q_e \):

\[
\min_{0 < q_e < 1} \kappa_c = \frac{2}{\beta} \left( \frac{\sqrt{a(1+a)} + \sqrt{b(1+b)}}{\sqrt{(1+a)(1+b) - ab}} \right)^2 \text{ where } \quad a = (\delta_p + \delta_q)\beta, \quad b = \nu + \beta (\delta_u + \delta_q), \quad c = \nu + \beta (\delta_p + \delta_u).
\]

As was discussed in Sec. 4, small perturbations of the relative equilibria are governed by system (6.1)-(6.3) with \( \delta_u = \delta_p = 0 \). Therefore, all the above expressions become much simpler. In particular, the critical magnitude of the prey-taxis takes the form

\[
\kappa_c|_{\delta_p=\delta_u=0} = \frac{\nu (\delta_q \beta + \nu q_e) (\delta_q \beta + q_e)}{q_e \rho e \beta}.
\]
Appendix II. Derivation of the slow system

Let the external signal be specified as $f = f(x, t, \xi, \tau)$ where $\xi = \omega x$ and $\tau = \omega t$ in accordance with assumption (3.1). Let the diffusion rates satisfy condition (3.2). For such a short-wavelength signal, we seek a short-wavelength response depending on variables $(x, t, \xi, \tau)$. In what follows, we assume that both the external signal and the system response are $2\pi$-periodic in $\xi = \omega x$, $\tau = \omega t$.

On introducing the fast variables into the governing equations (1.4)-(1.6), they take the following form

\begin{align}
\omega((\partial_t + \omega \partial_\tau)u - (\partial_x + \omega \partial_\xi)(\kappa q + \sigma f) + \nu u) &= \nu_1(\partial_x + \omega \partial_\xi)^2 u; \\
\omega((\partial_t + \omega \partial_\tau)p + (\partial_x + \omega \partial_\xi)(up)) &= \nu_2(\partial_x + \omega \partial_\xi)^2 p; \\
(\partial_t + \omega \partial_\tau)q - q(1 - p - q) &= \delta_q(\partial_x + \omega \partial_\xi)^2 q.
\end{align}

We look for an asymptotic expansion of the solution to system (7.1)-(7.3) in the form

\[ (u, p, q) = \sum_{k \geq 0} \omega^{-k}(u_k, p_k, q_k)(x, t, \xi, \tau), \omega \to \infty. \]

where all coefficients are required to be $2\pi$-periodic in $\xi$ and $\tau$. Substitution of (7.4) into system (7.1)-(7.3) and collecting terms of equal order in $\omega$ yields a sequence of equations which will be solved step by step.

Terms of order $\omega^2$ in Eq. (7.3) lead to the equation

\[ \partial_{\xi\xi}q_0 = 0 \]

that obviously has no periodic solutions except for solutions independent of $\xi$. Thus

\[ q_0 = q_0(x, t, \tau). \]

where function $q_0$ is to be determined at subsequent steps. In view of (7.6), the collecting of terms of order $\omega^2$ in Eqs. (7.1-7.2) leads to the equations

\begin{align}
(\partial_x - \nu_1 \partial_\xi)u_0 &= \sigma \partial_\xi f; \\
(\partial_x - \nu_2 \partial_\xi)p_0 + \partial_\xi(u_0 p_0) &= 0; \\
(u_0, p_0) &= (u_0, p_0)(x, t, \xi, \tau), \quad (\xi, \tau) \in T^2.
\end{align}

Note that equation (7.7) is exactly the first equation in problem (3.7). Equation (7.7) has only one periodic solution vanishing on average in the sense of definition (3.3). We denote this solution as $\bar{u}_0$. Thus $u_0 = \bar{u} + \bar{u}_0$, $\bar{u} = \langle u_0 \rangle$, and we have justified the leading term in the asymptotic approximation for $u$, given by (3.5), (3.7).

We also need the following result.

**Lemma.** Let $w = w(\xi, \tau)$ be a smooth $2\pi$-periodic (in both $\xi$ and $\tau$) function. Consider equation

\[ \partial_x Q + \partial_\xi(wQ - \epsilon \partial_\xi Q) = 0, \quad \epsilon = \text{const} > 0. \]

Then there exists a unique $2\pi$-periodic (in $\xi$ and $\tau$) solution to Eq. (7.9) satisfying the additional condition

\[ \langle Q \rangle = 1. \]

A proof of this statement will be given in the end of this Appendix.

We continue constructing the asymptotic expansion. Equation (7.8) coincides with (7.9) up to the replacing $\epsilon$ by $\nu_2$ and $w$ by $\bar{u} + \bar{u}_0$, so that we can apply the above lemma, which yields

\[ p_0 = \bar{p}(x, t)P(x, t, \xi, \tau). \]
where $P$ is uniquely determined by (3.8). Hence we have justified the leading term in the asymptotic approximation determined by (3.6) for unknown $p$.

Now let us consider the terms of order $\omega$. From Eq. (7.3), with the help of (7.6), we get

$$\delta q \partial_{\xi}q_1 = \partial_{\tau}q_0, \quad (7.12)$$

where $q_0$ does not depend on $\xi$. Hence, this equation has a periodic solution if and only if $q_0$ does not depend on $\tau$. Thus $q_0 = \bar{q}(x,t)$ and we arrive at the leading term in the asymptotic approximation (3.4). Further, every solution to Eq. (7.12) has to have a form

$$q_1 = q_1(x,t,\tau). \quad (7.13)$$

Functions $q_1$ and $\bar{q}$ are to be determined at subsequent steps of the procedure. Note that existence of a periodic solution to Eq. (7.12) justifies the error estimate (i.e. $O-$ term) in the asymptotic approximation (3.4).

Terms of order $\omega$ in Eq. (7.1)-(7.2), together Eq. (7.13), lead to equations

$$\begin{align*}
(\partial_{\tau}u_1 - \nu_1 \partial_{\xi}u_1)u_1 &= 2\nu_2 \partial_{xx}u_0 + \partial_{\xi}(\kappa q_0 + \sigma f) - \nu u_0 - \partial_{\xi}u_0, \quad (\xi, \tau) \in T^2; \quad (7.14) \\
\partial_{\tau}p_1 + \partial_{\xi}(u_0p_1) - \nu_2 \partial_{xx}p_1 &= 2\nu_2 \partial_{xx}p_0 - \partial_{\xi}p_0 - \partial_{\xi}(u_0p_0) - \partial_{\xi}(u_1p_0), \quad (\xi, \tau) \in T^2. \quad (7.15)
\end{align*}$$

On averaging Eqs. (7.14) and (7.15) and using (7.11), we obtain the slow system (3.9)-(3.11). Note that the averaging procedure not only leads to the slow system, but simultaneously implies that Eqs. (7.14) and (7.15) have periodic solutions $u_1$ and $p_1$ (which, in turn, justifies the error estimates in the approximations (3.5) and (3.6)).

Thus, the asymptotic expansion presented in Sec. 3 is fully justified, except for the lemma. Before we start proving it in full generality, let us consider the particular case of $w = w(\xi)$.

Then the periodic solution to Eq. (7.9) has to depend on a single variable $\xi$ and equation (7.9) reduces to equation

$$\partial_{\xi}(\epsilon \partial_{\xi}Q - wQ) = 0.$$

Its general solution takes the form

$$Q = \exp \left( \epsilon^{-1} \int w(\xi)d\xi \right) \int \exp \left( -\epsilon^{-1} \int w(\xi)d\xi \right) d\xi$$

There is only one periodic solution among those given by this integral. To write it down explicitly, consider a decomposition $w(\xi) = \mu + \tilde{w}(\xi)$, where $\mu = \langle w(\xi) \rangle$, and set

$$E(\xi) = \exp((\epsilon \partial_{\xi})^{-1}\tilde{w}(\xi)).$$

Then

$$Q = AE(\xi) \int_0^\infty \frac{e^{-sds}}{E(\xi + \frac{s}{\mu})}, \mu \neq 0, A = \text{const}$$

and

$$Q = AE(\xi), \mu = 0, A = \text{const}. \quad (7.16)$$

Obviously, we can normalize the solution as required in (7.10) by suitable choice of $A$ in both cases but, for our purposes, we need to write down the periodic solution in a form that covers both cases. To do this, we consider the Fourier series

$$E(\xi) = \sum_k \psi_k e^{ik\xi}, \quad E^{-1}(\xi) = \sum_k \phi_k e^{ik\xi}.$$
Then
\[ P = AE(\xi) \left( \phi_0 + \mu \sum_{k=0}^{\infty} \frac{\phi_k e^{ik\xi}}{\mu - ik} \right), \quad A^{-1} = \phi_0 \psi_0 + \mu \sum_{k=0}^{\infty} \frac{\phi_k \psi_k^*}{\mu - ik} \]
where \( \psi_k^* \) are the complex-conjugate Fourier coefficients.

Let us pass to the general case. Let \( H \) be space of the Fourier series in \( \xi, \tau \) with square-summable coefficients and let \( \mathcal{L}_v : H \to H \) be operator defined by the left hand side of Eq. (7.9). We have to prove that

\[ \dim \text{Ker} \mathcal{L}_v = 1, \quad \langle w \rangle \neq 0 \quad \forall \quad w \in \text{Ker} \mathcal{L}_v \setminus \{0\}. \quad (7.16) \]

Let \( \mathcal{L}_v^* \) denote the operator adjoint to \( \mathcal{L}_v \). Define

\[ \tilde{\mathcal{L}}_v^* = J \mathcal{L}_v^* J \]

where \( J : H \to H \) is the action of inversion \((\xi, \tau) \mapsto (-\xi, -\tau)\). Then

\[ \tilde{\mathcal{L}}_v^* : \varphi \mapsto (\partial_\tau - \epsilon \partial_\xi)\varphi + u_0 \partial_\xi \varphi. \]

Notice that PDE

\[ (\partial_\tau - \epsilon \partial_\xi)\varphi + u_0 \partial_\xi \varphi = 0 \]

obeys the strong maximum and minimum principles (see e.g. [24] or [25]). Hence,

\[ \text{Ker} \tilde{\mathcal{L}}_v^* = \{ \varphi \equiv \text{const} \} = \text{Ker} \mathcal{L}_v^*. \]

Applying unilateral strong maximum/minimum principles to PDE

\[ (\partial_\tau - \epsilon \partial_\xi)\varphi + u_0 \partial_\xi \varphi = 1 \]

shows that neither equation \( \tilde{\mathcal{L}}_v^* \tilde{\psi} = 1 \) nor equation \( \mathcal{L}_v^* \psi = 1 \) has a solution in \( H \). Consequently, the resolvent operator \( (\mathcal{L}_v^* - \lambda \mathcal{J})^{-1} \), \( \lambda \in \mathbb{C} \) has a simple pole at the origin. Moreover, since this resolvent is compact, the pair of operators \( \mathcal{L}_v^* \) and \( \mathcal{L}_v \) obeys the Fredholm theorems. Hence \( \dim \text{Ker} \mathcal{L}_v = 1 \). Furthermore, if \( \langle w \rangle = 0 \) for some \( w \in \text{Ker} \mathcal{L}_v \setminus \{0\} \), this would imply the existence of solution to equation \( \mathcal{L}_v^* \psi = \text{const} \neq 0 \) but this contradicts to what has been proved above. This completes the proof.