Transport Equations and Chemosensitive Movement

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Preface

The mathematical modeling of biological phenomena provides new insights into biological processes. On the one hand mathematics and statistics help to understand and describe experiments. In some cases they allow for predictions which can be tested afterwards. On the other hand mathematical modeling allows a more global view to identify basic principles and general mechanisms, which qualitatively explain the outcome of many known experiments. Using different abstraction levels, fundamental truth can be revealed for a whole class of phenomena, independently of the concrete data at hand. Moreover the abstract results translate back to the experiments and they allow for explanations and predictions.

This monograph deals with the analysis of mathematical models for spatial spread and interactions of populations of (almost) identical individuals. Examples include swarms of bacteria or slime molds. The models are used to study the phenomena of *chemotaxis* and *aggregation*. Chemotaxis describes the active orientation of individuals or populations on chemical signals, which are produced by the population itself. In some situations this mechanism leads to aggregation and spatial pattern formation. Emphasis is given on the discussion of the relevance of transport models and advection-diffusion models.

The four main chapters (Chapters 2-5) reflect four key ideas which focus on different aspects of the modeling of spatial spread. In Chapter 2 I discuss the *Cattaneo system*. The Cattaneo system has been introduced by C. Cattaneo in 1948 and it modifies Fourier's law such that heat propagation with finite speed can be modeled. However, at present there is no stochastic process known which (in an appropriate limit) leads to the Cattaneo system in more than one dimension. In Chapter 2 I derive the Cattaneo system via a variational method from a transport equation. Then the Cattaneo system appears as an approximation to a stochastic process and the error can be controlled. The Cattaneo system is an appropriate model for spatial spread especially for short time ranges. In Chapter 3 I generalize the approach from Chapter 2 to generate moment closures for the moment equations of general transport models. Here the theory of *Extended Thermodynamics* acts as a guideline. The approach in Chapter 3 differs from the theory of Extended Thermodynamics in the use of entropies and analytical properties of the turning operator. Especially the proof of the existence of an entropy-maximizer has to be modified. In Chapter 4 I discuss transport in connection to birth-death processes. I

assume that birth events take place at rest only. Using singular perturbation methods and matched asymptotic expansions I identify conditions such that reaction-diffusion models are appropriate. In Chapter 5 I present a modification of the classical Patlak-Keller-Segel model for chemosensitive movement which allows for global existence of solutions. The local cell density regulates the chemotactic sensitivity. Above a certain maximal cell density the chemical signal can no longer be detected. Global existence in time is proved. This proof will appear in a joint paper with K. Painter [53], where we added numerical simulations which show a variety of spot or labyrinthian spatial patterns. Also merging of local maxima and coarsening has been observed in [53].

These four main parts are completed by an ample introduction (Chapter 1), where biological motivation is given, the classical models are discussed and the relevant literature is presented.

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1 Introduction

1.1 Overview

It is a great challenge to the live sciences to understand the response of individuals and communities to external stimuli. All species recognize signals from their surrounding environment and they adapt their behavior according to it. Examples are orientation towards light sources, the avoidance of harmful substances, foraging strategies, aggregational tendencies in amoeba and strategies to find a sexual partner. Many of the responses to different stimuli have been measured experimentally, which leads to a good understanding of the biological phenomenon. The experiments can roughly be classified into two classes: (i) measurements of individual behavior and (ii) measurements of population behavior. Of course the behavior of a population is determined by the individual behavior of its members. It is far from obvious how the individual behavior affects the collective behavior. Indeed these question is one of the leading questions for mathematical biology today.

The mathematical modeling provides an excellent tool to connect the individual behavior to the collective behavior. We will demonstrate this relation for birth death processes and random walks in Chapter 4 and for the chemotaxis problem in the last section of this introduction (Chemotaxis describes the active orientation of individuals along chemical signals and we give the biological background in Section 1.2).

One advantage of mathematical modeling is that basic models can be derived from specific experiments (e.g. the response of *E.coli* to fucose) and they are often applicable to many similar problems (e.g. response of *Dictyostelium discoideum* to cAMP). Another advantage of modeling is that a good model covers the phenomena where one is interested in. The model can be reduced without destroying the qualitative properties and a simpler model follows. It becomes a mathematical object on its own and powerful analytical and numerical methods can be applied to gain non trivial results. One gets insight into the phenomenon itself (e.g. aggregation) independently of its biological realization. The mathematical results translate back to the original biological problem and predictions can be given and can be tested.

In cases, where an external chemical signal guides the individual movement behavior the response is called *chemotaxis* and *chemokinesis*. We discuss the differences of chemotaxis and chemokinesis in Section 1.2. For chemotaxis and chemokinesis a mathematical

discipline on its own has evolved. Starting with the *Patlak-Keller-Segel* model (PKS), which bases on Brownian motion, results on aggregation and finite time blow-up have been achieved. We summarize known results for the PKS model and for alternative models in this Introduction. In the last chapter (Chapter 5) we present a version of the PKS model which allows for pattern formation, pattern interaction and for global existence.

Whereas the PKS model bases on diffusion, another class of models bases on correlated random walk assumptions, which lead to nonlinear transport equations. The main part of this text focuses on transport models for chemotaxis and for birth-death processes. Two methods will be presented which allow to reduce the transport equations to simpler models. From a multi scale analysis we obtain diffusion based models. We will explain, that transport models base on the individual movement behavior whereas diffusion models are population models. The question of individual versus collective translates into the connection of transport models to diffusion based models. For chemotaxis this connection has been studied in detail in [52, 87]. In Chapter 4 we consider birth-death processes. The parabolic limit method leads to a reaction-diffusion equation which describes the outer solution in terms of singular perturbation theory. We consider inner solutions and matching as well.

Another technique to reduce a full kinetic transport model is the moment closure method. The moment closure leads to hyperbolic sub-models. In the two-moment case the reduced models depend on Cattaneos law of heat conduction. We will illustrate the moment closure method in Chapters 2 and 3 and we discuss applications to birth-death processes and to chemosensitive movement.

1.1.1 Velocity Jump Processes and Transport Equations

As observed in experiments with bacteria (see e.g. Adler [2], Dahlquist, Lovely, Koshland [24], or Berg and Brown [12]), bacteria have a characteristic movement behavior. They move in a certain direction with an almost constant speed (run). Suddenly they stop and choose a new direction (tumble) to continue movement. The tumbling intervals are short compared to the mean run times. This type of individual movement pattern can be modeled by a stochastic process which is called *velocity jump process* (see Stroock [111]). The characteristic parameters are mean runtime, turning distribution and mean speed. Stroock showed how a transport equation (see (1.1) below) for the spatial distribution of one particle can be derived from such a velocity jump process.

In Hillen and Othmer [52, 87] the transport model (1.1) has been studied systematically with respect to different forms of biases; possible limit equations (of PKS-type) and relations between the relevant parameters have been considered. Let $p(t,x,v)$ denote the population density at time $t \geq 0$ at spatial position $x \in \mathbb{R}^n$ with velocity $v \in \mathbb{R}^n$. Most important are space dimensions of $n = 1, 2, 3$, the theory however works for all $n \in \mathbb{N}$. We assume that individuals choose any direction with bounded velocity. We

denote the set of possible velocities as V, where we assume $V \subset \mathbb{R}^n$ is bounded and symmetric (i.e. $v \in V \Rightarrow -v \in V$). Then the linear transport model, which bases on a velocity jump process (see e.g. Stroock [111] or Othmer *et al.* [86]) reads

$$\frac{\partial}{\partial t}p(t,x,v) + v \cdot \nabla p(t,x,v) = -\mu p(t,x,v) + \mu \int T(v,v')p(t,x,v')dv', \qquad (1.1)$$

where μ is the turning rate or turning frequency, hence $\tau = \frac{1}{\mu}$ is the mean run time and $T(v,v')$ is the probability kernel for the new velocity v given the previous velocity was v'. Of course

$$\int T(v,v')dv = 1$$

to ensure particle conservation.

From a mathematical point of view the use of transport models for populations is not rigorously justified. The transport model has been derived for a one-particle distribution function (Stroock [111]). If individuals move independently transport models are still suitable. If, however, there are correlations between individuals, which might come from birth-death interactions or from alignment or chemosensitive movement, then the verification of transport models from stochastic processes, even in 1-D, is an active field of mathematical research. The same holds for diffusion based models. Here we assume that transport equations are at least as good for populations as diffusion models.

If motion is modeled by a diffusion process and birth and death should be included then reaction-diffusion models result (see e.g. Murray [79]). Similarly for transport models we obtain *reaction-transport models*. Depending on concrete experiments the reactions may depend on the actual velocity of the particle, hence a nonlinear reaction-transport equation reads ([46])

$$p_t + v \cdot \nabla p = -\mu p + \mu \int T(v,v')p(t,x,v')dv' + f(v,p,m^0), \qquad (1.2)$$

where the total population density is denoted as

$$m^0(t,x) = \int_V p(t,x,v)\,dv.$$

In the isotropic case the nonlinearity f depends on the total population density m^0 only. Reaction-transport models of this form have been studied by Hadeler [47, 48] and by Schwetlick [101, 102]. In Chapter 4 we will assume that individuals give birth at rest only. In the parabolic limit a reaction-diffusion model follows with effective birth and death rates.

Transport equations appear in physics as models for dilute gases, i.e. Boltzmann equations (see e.g. Cercignani, Illner and Pulvirenti [18], Bellomo [10] or Babovsky [7]), in neutron transport theory (see e.g. Jörgens [60]), as models for radiation transport (see

e.g. Mihalas and Weibel-Mihalas [76])) or in semiconductor theory (see e.g. Markowich *et al.* [74]). In the cases of gases and neutrons reorientation results from collisions of two particles (collisions of more than two particles at exactly one instant are negligible), hence the right hand side of the transport equation (1.2) has a specific quadratic dependence on p ([18]). In case of radiation transport the right hand side of (1.2) consists of a linear absorbing term and the Planck function, which describes emission of radiation. In physical applications some quantities are conserved, among these are energy, momentum and mass. In biological applications the only conserved quantity is the total particle number (in case of no birth or death reactions). Nevertheless the rich theory on Boltzmann equations and the variety of available methods serves as a tool book for the study of (1.2).

1.1.2 The Moment Closure Method

One common feature in understanding the dynamic properties of reaction-transport equations and of Boltzmann equations are *moment methods*. By multiplication of (1.1) with powers of v and integration one can derive an infinite sequence of equations for the v-moments of p. As a matter of fact in the equation for the n–th moment the $(n+1)$–st moment appears. To close the equations for the first n moments one needs an approximation of the $(n+1)$–moment. This "closure problem" is well known and widely discussed in transport theory. Most authors use *ad hoc* arguments or regular expansions to close the moment system (see e.g. [3] or [92]). Here we present a theory for closing the moment equations, which bases on a minimization principle.

For Boltzmann equations the closure problem has been treated in the theory of Extended Thermodynamics (see e.g. Müller and Ruggeri [77]). An entropy functional is maximized under the constraint of fixed first n moments. One assumes that the $(n+1)$–st moment of the minimizer approximates the $(n+1)$–st moment of the true solution. This gives the desired closure. It appears that theories for a large number of moments are capable to approximate steep gradients and shocks [116].

In a biological context the negative $L^2(V)$-norm can be seen as an entropy as defined in thermodynamics. We close the moment system by minimizing the L^2-norm under the constraint of fixed first n-moments. This minimization flattens oscillations, details and high oscillations: high frequencies in space and time will be smoothed out and the global structure of the solution is emphasized. We introduce this procedure in Chapter 2 to close the system for the first two moments (total population density and population flux). The closed system is a Cattaneo system, which is well known in heat transport theory (see the next section). Later we generalize this approach to close the moment system at any order and we discuss the 3-moment closure in more detail. Finally we apply this method to the transport equation for chemosensitive movement and to reaction-transport equations.

1.1.3 Cattaneo's Law

The Cattaneo system has the following form

$$\begin{aligned} u_t + \nabla v &= 0 \\ \tau v_t + d\nabla u + v &= 0, \end{aligned} \tag{1.3}$$

where $u(t,x) \in \mathbb{R}$ and $v(t,x) \in \mathbb{R}^n$ are functions of space $x \in \Omega \subset \mathbb{R}^n$ and time $t \geq 0$. The diffusion constant d and the time constant τ are positive. There are two interpretations of this system. First it appears to describe heat transport with finite speed, or heat transport in media with memory ([61, 44]). Then u is the temperature and v is the heat flux. Second it can be seen as a generalization of a correlated random walk ([46]). Then u is the population density and v the population flux. The Cattaneo law (second equation in (1.3)) has been used by Cattaneo [17] to describe heat transport with finite speed. It has been known to Maxwell [75] who cast out the time derivative, because it "*... may be neglected, as the rate of conduction will rapidly establish itself.*" For $\tau = 0$ Cattaneo's law becomes Fourier's law. For $\tau \neq 0$ the flux is not directly proportional to the temperature gradient, it adapts with a time constant of τ. The Cattaneo system directly leads to a damped wave equation

$$\tau u_{tt} + u = D\Delta u,$$

which for $\tau \to 0$ formally converges to the heat equation (see the review article of Joseph and Preziosi [61] on heat transport or Hillen [51] on the Cattaneo system). It can also be motivated in terms of heat propagation in media with memory (Gurtin and Pipkin [44]), where the influence of the past decays exponentially. This property is important for biological species, since memory and adaptation effects play a role in many sensory processes. In Section 2.6.2 we show that the Cattaneo law appears as gradient flux of an exponentially weighted Dirichlet integral. The connections of the Cattaneo system to biological applications has first been considered by Hadeler [46]. The derivation presented here (Chapter 2) gives a new understanding of the role of the Cattaneo system in biological applications. Moreover, the relevant parameters are now related to the individual movement behavior of the underlying species.

1.2 Chemosensitive Movement

In this section we give a summary of mathematical models for chemotaxis, chemokinesis and related responses. At the beginning we briefly recall the phenomena of chemotaxis and chemokinesis and we give several examples. We introduce the notion of *chemosensitive movement* and we discuss definitions which have been used throughout the literature, starting with the book of Fraenkel and Gunn [37] from 1940's. The best known and

widely used model for chemotaxis is the Patlak-Keller-Segel (PKS) model (also called Keller-Segel model), which has been introduced by Patlak in 1953 [92] and by Keller and Segel in 1970 [64]. The parameters of the Patlak-Keller-Segel equations are the motility d and the chemotactic sensitivity χ which can be derived from the measuring of mean squared displacement and mean drift velocity. It turns out that in some situations these parameters are too abstract and hard to estimate from experiments. It seems to be better to work with individual speed, directions of movement, distribution of directional changes and turning frequencies. Hence transport-models for chemosensitive movement appear naturally.

1.2.1 Taxis and Kinesis

The movement behavior of most species is guided by external signals: amoeba move upwards chemical gradients, insects orient towards light sources, the smell of a sexual partner makes it favorable to choose a certain direction. Some species are able to extract directed information from its surrounding (e.g. gradient of chemical) others are too small to sense chemical gradients and they turn more often, when they move in an unfavorable direction. Both behaviors lead to orientation towards the source of a chemical, but the mechanisms have been distinguished into chemotaxis (for directed movement) and chemokinesis (for undirected movement). If the movement is towards or away from the source of stimulus we call it positive or negative bias, respectively.

The distinction of chemotaxis versus chemokinesis is by far not straightforward and we denote responses to chemical stimuli in general by *chemosensitive movement*. This includes chemokinesis, chemotaxis and responses to non-local information as well. Some of the most studied species for chemosensitive movement are bacteria (e.g. *E. coli*), slime molds (e.g. *Dictyostelium discoideum*), or leukocytes.

Observations in several experiments where kinesis and taxis are not strictly separated have caused an elaborate discussion among scientists on what kinesis and taxis are.

Fraenkel and Gunn [37] were the first who gave definitions of these phenomena. For kinesis they state: *"Undirected locomotory reactions in which the speed of movement or the frequency of turning depend on the intensity of the stimulus"* ([37] p.10), whereas *"the term taxis is used today for directed orientation reactions. (...) We use the word only for reactions in which the movement is straight towards or away from the source of stimulation"* ([37], p.10). These definitions do not include directed movement with a net angle with respect to the straight line towards the source. For such behavior Fraenkel and Gunn use *transverse orientations* (p.10). In later definitions this behavior falls into the notion of *taxis*.

Especially for chemical stimuli Keller *et al.* define as follows: *"Chemokinesis. A reaction by which the speed or frequency of locomotion of cells and/or the frequency and magnitude of turning (change of direction) of cells or organisms moving at random is determined by substances in the environment. "* ([66]), whereas *"Chemotaxis: A reaction*

by which the direction of locomotion of cells or organisms is determined by substances in their environment." ([66]).

From these definitions it becomes clear that an undirected information causes kinesis and a directed information causes taxis. However, there are undecided cases. As pointed out by Dunn [31], the same stimulus and the same receptor kinetics can lead to directed or undirected changes in the individual movement patterns. On the other hand a directed information can be obtained if an individual cell moves through a spatial gradient to obtain a time varying signal distribution. Here the distinction of taxis and kinesis is not straightforward. A special section in Lecture Notes in Biomathematics 98 [5] is devoted to that discussion. Especially the articles of Dunn and Doucet and of Alt and Tranquillo try to solve this controversy. It was not the aim of these authors to define a unique way of how to use the words taxis or kinesis, it is a collection of common-use nomenclature. Their intention was to inspire further discussions. Surprisingly, Vicker writes in his introduction to that chapter of [5] that *"one way out of this biological and clinical monotony appears to have come, somewhat surprisingly, from mathematical analysis."* ([5], p. 472). Up to date kinesis and taxis and also undecided cases have been observed for many species in many experiments. We think that a unifying definition, which does not rely on special species, specific receptor kinetics etc. can be obtained only in a theoretical or mathematical way.

Dunn and Doucet for example define kinesis and taxis from a more global view: *"... the distinction between taxis and kinesis depends on whether positional or directional information respectively is transfered from the stimulus field to the response field."* ([31], p.12). A similar definition is given by Tranquillo and Alt ([5], p.516).

The definitions of Dunn, Doucet and of Alt and Tranquillo are very useful and cover most known examples. Here, however, we prefer to formalize further. Of course in a single experiment it is important to know how the signal is transduced through the chemical network and how this causes movement changes. On a more global and abstract level however, the distinction of taxis and kinesis is no longer needed. We prefer to summarize these effects into the notion of *chemosensitive movement*. This includes responses to undirected, directed or even non-local external information from one or more chemical cues. This point of view allows to systematically study different forms of biases and responses within a common theoretical framework.

1.2.2 The Classical Patlak-Keller-Segel Model

The earliest model for chemosensitive movement has been developed by Patlak [92] and Keller and Segel [64]. Here we give a brief derivation of the PKS model. We assume that in absence of any external signal the spread of a population density $u(t,x)$ is described by the diffusion equation

$$u_t = d\Delta u, \tag{1.4}$$

where $d > 0$ is the diffusion constant. We define the net flux as $j = -d\nabla u$. If there is some external signal S we just assume that it results in a *chemotactic velocity* β. Then the flux is

$$j = -d\nabla u + \beta u.$$

To be more specific, we assume that the chemotactic velocity β has the direction of the gradient ∇S and that the *sensitivity* χ to the gradient depends on the signal concentration $S(t, x)$. Then

$$\beta = \chi(S)\nabla S.$$

We use this modified flux in (1.4) to obtain the *parabolic chemotaxis equation*

$$u_t = \nabla(d\nabla u - \chi(S)\nabla S u). \tag{1.5}$$

If $\chi(S)$ is positive, which means that the chemotactic velocity is in direction of the gradient, we call it *positive bias*, whereas $\chi < 0$ is called *negative bias*. In earlier papers it is also called positive or negative taxis. We mentioned that we also include chemokinesis and other mechanisms. Hence we avoid "taxis" here.

Depending on the species at hand, the external signal is produced by the individuals and decays, which is described by a nonlinear function $f(S, u)$. We assume that the spatial spread of the external signal is driven by diffusion. Then the full system for u and S reads

$$\begin{aligned} u_t &= \nabla(d\nabla u - u\chi(S)\nabla S), \\ \tau S_t &= \alpha\Delta S + f(S, u). \end{aligned} \tag{1.6}$$

The time constant $0 \leq \tau \leq 1$ indicates that the spatial spread of the organisms u and the signal S are on different time scales. The case of $\tau = 0$ corresponds to a quasi-steady state assumption for the signal distribution.

This system has first been derived by Patlak [92] from a position jump process. Since the early work of Patlak is difficult to read, model (1.6) has become well known as the Keller-Segel model for chemotaxis. Here we presented the derivation of Keller and Segel [64] for (1.6).

The PKS model has been used in many applications to study aggregation or pattern formation (see e.g. Murray [79], Okubo [85], Keller and Segel [65]). The model has been criticized, though. First, the movement process of the population is modeled by diffusion. However for bacteria it is known that they move along straight lines, suddenly stop to choose a new direction and then continue moving in the new direction. This is not a Brownian motion, it is a velocity jump process, which we will describe later in detail. Second the diffusion terms in (1.6) allow for infinite fast propagation of information, which is an undesired property. Finally, the relevant parameters like diffusion constants d, α and chemotactic sensitivity χ are not directly related to the individual movement pattern of the species. They can be measured only indirectly (see e.g. Tranquillo [5],

Segel [103] or Ford [36]). In this context it is useful to study alternative models, like hyperbolic equations and transport models (see the following sections).

As we have shown in [52] the parabolic system (1.6) describes the long time asymptotics of solutions of transport models ([78], [52]). Which means that if we wait long enough the description of an experiment with (1.6) is as good as with a transport equation. This explains the success of parabolic models so far.

The first rigorous derivation of the Keller-Segel system from an interacting stochastic many particle system has been given by Stevens [109]. The position of each particle fulfills a stochastic differential equation, where e.g. the chemotactic sensitivity of each particle depends on the other particles in a certain neighborhood around it. In the limit, when population size tends to infinity, this range of interaction is rescaled in a moderate way.
A related approach to formally derive the Keller-Segel model starts with a simplified version of a cellular automaton model for the gliding and aggregation of myxobacteria, presented in Stevens [108], [110]. Like the slime mold amoebae, these bacteria aggregate under starvation conditions. With the automaton, especially the slime trail following of the myxobacteria is simulated. The basic mechanism behind the automaton model for the slime trail following is related to a self-attracting reinforced random walk described by Davis [26]. He proved that a single particle, which moves on an integer grid, localizes on one point if an attractive reinforced non-diffusing substance is produced super linearly and does not localize, if the substance is produced only linearly (compare [26] for the exact conditions). The approximating parabolic chemotaxis-system translates this localization behavior into a finite time blowup.

1.2.3 Theoretical Results on the PKS Model

Since the PKS model is designed to describe the behavior of bacteria and bacteria aggregates, the question arises whether or not these model is able to show aggregation. Intensive theoretical research uncovered exact conditions for aggregations and for blow up (see e.g. Childress and Percus [22, 21], Jäger and Luckhaus [59], Nagai [80], Gajewski and Zacharias [38], Senba [104], Rascle and Ziti [96], Herrero and Velazquez [50, 49], Othmer and Stevens [89] or Levine and Sleeman [71]). Following the definitions given in Othmer and Stevens, *aggregation* denotes a global existing solution which has a unique global maximum, whereas *blow up* denotes a solution with a maximum that grows to infinity in finite time. After blow up has occured the model is no longer appropriate. That is the reason that several authors denote the blow up scenario with *chemotactic collapse.*

The possibility of blow-up has been shown to depend strongly on space dimension. For $\chi = const.$ and linear reproduction, $f(u, S) = \gamma u - \delta S$, finite time blow-up never occurs in 1-D (unless there is no diffusion of the attractant, S), but can always occur in n-D for $n \geq 3$. The 2-D case is ambiguous and thresholds θ_{rad} for radially symmetric

solutions and $\theta_{\text{dom}} = \theta_{\text{rad}}/2$ for solutions in smooth domains have been found. If the initial distribution exceeds its threshold, then the solution blows up in finite time. When the initial mass is below its threshold, the solution exists globally. An interior blow up point is supported by a mass of exactly θ_{rad}, a boundary blow up has half of this mass. Horstmann considers the case, where the total mass is inbetween these thresholds. He shows that in these cases blow up occurs only at the boundary [58, 57]. Senba and Suzuki [105] consider stationary solutions and they use the above thresholds to estimate the number of blow-up points. The number of possible blow-up points is limited by the total mass divided by θ_{dom}.

Global existence below these thresholds has been proven using a Lyapunov functional in Gajewski, Zacharias [38], Nagai, Senba and Yoshida [83] and Biler [13]. The Lyapunov technique has been generalized to obtain similar thresholds for chemotactic sensitivities $\chi(S)$ given by a primitive $\phi(S) = \int \chi(S)$ which is *strictly sub-linear* (see [14]). This includes functional forms of $\phi(S) = \log S, \phi(S) = S^p$, for $0 < p < 1$ or equally bounded functions $\phi(S)$ (see Nagai *et al.* [84, 81, 82], Biler [14]). Post [95] considers chemotactic velocities with saturation in S and linear in u. Using a modification of the Lyapunov function from [38], global existence of solutions was shown. Horstmann [56] gave sufficient conditions for reaction-diffusion systems in general, such that a Lyapunov function of the above form exists.

A version of the PKS model, that allows for global existence in any space dimension, will be discussed in Chapter 5. There we assume that the individuals sense the local cell density (e.g. E.coli releases a *quorum sensing molecule*), and the chemotactic sensitivity is reduced or vanishes at high population densities.

1.3 Hyperbolic Models in 1-D

It is fairly useful to study models for chemosensitive movement in one space dimension first. This provides good insights into basic phenomena, which also become important in 2 or 3 dimensions. Furthermore some experimental situations can be formally reduced to a one dimensional problem, e.g. experiments in a cylindrical test chamber where the medium is homogeneous in each cross section (see Chen, Ford, Cummings [19]).

1.3.1 The Goldstein-Kac Model

Before we state the full hyperbolic model for chemotaxis in one space dimension (1.10) we illustrate some basic modeling ideas with a simpler model, the Goldstein-Kac model for a correlated random walk ([40], [62]). It is assumed that the total population density $u(t, x)$ can be split into densities for right/left moving part of the population, $u^{\pm}$, respectively. Of course $u = u^+ + u^-$. We assume that the individuals move with constant speed $\gamma > 0$ and that they stop according to a Poisson process with rate $\mu > 0$, independently of

each other. The resting period is short and they reverse direction with probability 1/2. The Goldstein-Kac model for this correlated random walk reads:

$$\begin{aligned} u_t^+ + \gamma u_x^+ &= \tfrac{\mu}{2}(u^- - u^+) \\ u_t^- - \gamma u_x^- &= \tfrac{\mu}{2}(u^+ - u^-), \end{aligned} \tag{1.7}$$

where lower case indices denote partial derivatives with respect to that variable. This model is a special case of (1.1) for two velocities $v \in \{\pm\gamma\}$ in one space dimension and with $T(v, v') \equiv \frac{1}{2}$.

In terms of the total population density u and the population flow $v = u^+ - u^-$ system (1.7) is equivalent to

$$\begin{aligned} u_t + \gamma v_x &= 0 \\ v_t + \gamma u_x &= -\mu v. \end{aligned} \tag{1.8}$$

Using Kac's trick we obtain an equation for u alone: Differentiate the first equation with respect to time and the second equation with respect to space and eliminate the v-variable. Then u satisfies a *telegraph equation*

$$\frac{1}{\mu} u_{tt} + u_t = \frac{\gamma^2}{\mu} u_{xx}. \tag{1.9}$$

A diffusion equation $u_t = D u_{xx}$ follows formally by considering a limit of high turning rates $\mu \to \infty$ and large speed $\gamma \to \infty$ in such a way that

$$D = \lim \frac{\gamma^2}{\mu} < \infty.$$

This special scaling is called *parabolic limit*. It can be shown that a time and space scaling of $\tau = \varepsilon^2 t$ and $\xi = \varepsilon x$ with fixed γ, μ leads to the same limit for $\varepsilon \to 0$ ([52]).

1.3.2 Chemosensitive Movement in 1-D

Now we come back to chemosensitive movement. Due to recent experiments by e.g. Soll and Wessels [107] or Fisher *et al.* [33] and others [68, 11] it turned out that in general the speed and the turning rates of individuals depend not only on the magnitude of an external signal $S(t, x)$ but on temporal and spatial variations $S_t(t, x)$ and $S_x(t, x)$ as well. Depending on the situation at hand, the signal can be produced and decay in time. This will be described by a function $f(S, u^+ + u^-)$. Then a modification of the Goldstein-Kac model (1.7) gives the following hyperbolic model for chemosensitive movement in one space dimension:

$$\begin{aligned} u_t^+ + (\gamma(S, S_t, S_x)u^+)_x &= -\mu^+(S, S_t, S_x)u^+ + \mu^-(S, S_t, S_x)u^-, \\ u_t^- - (\gamma(S, S_t, S_x)u^-)_x &= \mu^+(S, S_t, S_x)u^+ - \mu^-(S, S_t, S_x)u^-, \\ \tau S_t &= \alpha S_{xx} + f(S, u^+ + u^-)\ ,\ \tau \geq 0, \\ u^\pm(0, .) = u_0^\pm, &\qquad S(0, .) = S_0. \end{aligned} \tag{1.10}$$

Here the rates $\mu^{\pm}$ are turning rates, whereas in (1.7) μ is a stopping rate and each direction will be chosen with probability of 0.5.

Segel [103] has considered a hyperbolic model of type (1.10) without the equation for S. He studied a given increasing attractant concentration and constant particle speed γ, constant turning rate μ^-, and μ^+ depending on the gradient of S in characteristic direction. The external stimulus S is assumed to decay with a constant rate. His model has been used by Rivero *et al.* [97] to describe experiments with flagellated bacteria and with *leukocytes*.
Greenberg and Alt [41] consider the special case of (1.10), where the speed is constant, with special choice of the turning rates, and f is linear. They pose the problem of existence of solutions for their hyperbolic model and use it to motivate a non local PKS model.
The hyperbolic model proposed in (1.10) allows more general dependencies in the turning rates and the velocity, and it compares with the experiments of Soll ([106]).
Chen *et al.* [20, 19] considered a model of the above type to describe experimental data for the movement of *E. coli* bacteria. In their model the bacterial speed is close to constant and the turning frequency depends on the temporal gradient of the external signal. Consequently the bacteria "feel" spatial gradients by moving through them. The model is put into relation with a one dimensional projection of a 3-D model by Alt [4], which we discuss later.
The connection of the hyperbolic model (1.10) to the PKS model ([64]) opens a wide field of interesting questions concerning scaling and modeling of crucial parameters. Some of them have been answered in [52, 87]. For the special case of constant speed and for turning rates depending on S and S_x we have proven local and global existence of solutions in L^∞ in [55]. To achieve an abstract existence result for dependence on S_t a more detailed analysis is required. Without S_t dependence the preservation of total population size suffices to show existence of weak solutions in L^∞. To control S_t stronger pre-assumptions are required. If the speed depends on S or its gradients we expect the formation of steep gradients. This case has been considered in [54]. There we showed global in time existence for $\gamma = \gamma(S)$, where we assumed that the signal distribution is in quasi-equilibrium ($\tau = 0$). Then, with a vanishing-viscosity method we obtain local and global existence.

1.3.3 The Parabolic Limit in 1-D

In this section we consider the parabolic limit for the full hyperbolic model for chemosensitive movement (1.10). The mathematical details are presented in [55]. One first derives an equivalent system for $u = u^+ + u^-$ and $v = u^+ - u^-$. From this a general telegraph equation (1.9) can be derived. The resulting telegraph equation is independent of v only

if we assume that the auxiliary function

$$h(t) := \mu^+(S, S_t, S_x) + \mu^-(S, S_t, S_x) - \frac{\gamma_t(S, S_t, S_x)}{\gamma(S, S_t, S_x)} \tag{1.11}$$

does not depend on the spatial position x. Of course this is a restriction to the parameters $\mu^\pm, \gamma$ which, however, is satisfied for many examples. We give examples in the next subsection.

Since here γ and $\mu^\pm$ are functions of $S(t,x)$ we can not just pass to the limit of $\gamma, \mu^\pm \to \infty$. We introduce an additional dimensionless small parameter $\varepsilon > 0$ and set

$$\gamma = \frac{\gamma_0}{\varepsilon}, \quad \text{and} \quad \mu^\pm = \frac{\mu_0^\pm}{\varepsilon^2}, \tag{1.12}$$

where γ_0 and $\mu_0^\pm$ are of order 1 with respect to ε. Then the auxiliarry function h scales as

$$h(t) = \frac{h_0(t)}{\varepsilon^2}, \quad \text{with} \quad h_0 = \mu_0^+ + \mu_0^- - \varepsilon^2 \frac{\gamma_{0,t}}{\gamma_0}. \tag{1.13}$$

and for $\varepsilon \to 0$ we obtain

$$D = \lim_{\varepsilon \to 0} \frac{\gamma^2}{h(t)} = \frac{\gamma_0^2}{\mu_0^+ + \mu_0^-}. \tag{1.14}$$

We introduce this scaling in the corresponding telegraph equation (see [55] for deatils) and for $\varepsilon \to 0$ we formally obtain the following limit equation of PKS type:

$$u_t = \left(Du_x - \chi u S_x\right),$$

with diffusion parameter given by (1.14) and chemotactic sensitivity χ given by

$$\chi S_x = -\frac{\gamma_0}{\mu_0^+ + \mu_0^-} \left(\gamma_{0,x} + \lim_{\varepsilon \to 0} \frac{1}{\varepsilon}(\mu_0^+ - \mu_0^-)\right). \tag{1.15}$$

A similar relation has also been found by Rivero *et al.* [97].

Since the chemotactic sensitivity consists of two terms we can identify two effects which lead to positive or negative biases.

1. We consider $\gamma = \gamma(S) \geq 0$ and we assume, that the difference $\mu_0^+ - \mu_0^-$ is of order ε^κ, for $\varepsilon \to 0$, with some $\kappa > 1$, then $\mu^+ - \mu^- = O(\varepsilon^{\kappa-2})$ and

   $$\chi S_x = -\frac{\gamma_0}{\mu_0^+ + \mu_0^-} \gamma_0' S_x \tag{1.16}$$

   and the limiting equation for chemosensitive movement reads

   $$u_t = \left(\frac{\gamma_0}{\mu_0^+ + \mu_0^-} \left(\gamma_0 u_x + \gamma_0' S_x u\right)\right)_x. \tag{1.17}$$

If $\gamma'(S) < 0$, which means that the population slows down at high concentrations of S, then a net flow of the population in direction of higher concentrations of S follows, which is a positive bias.

If $\gamma'(S) > 0$, which means that higher concentrations of S enhance the speed, then the population has a stronger tendency to spread out than compared to simple diffusion. This causes a negative bias. Hence the population glides in direction of decreasing concentrations S.

2. Now we assume that $\gamma = const.$ and that the difference in turning has an expansion as

$$\mu^+ - \mu^- = \varepsilon^{-1}\varphi_1 + \varphi_2,$$

with appropriate functions $\varphi_1(S, S_t, S_x), \varphi_2(S, S_t, S_x)$. This means $\mu_0^+ - \mu_0^- = \varepsilon\varphi_1 + \varepsilon^2\varphi_2$. Then the chemotactic sensitivity is given by

$$\chi S_x = -\frac{\gamma_0}{\mu_0^+ + \mu_0^-}\varphi_1.$$

Moreover, if we assume linearity in S_x, e.g. $\varphi_1 = \varphi_0(S)S_x$ then a PKS model follows

$$u_t = \left(\frac{\gamma_0^2}{\mu_0^+ + \mu_0^-}u_x + \frac{\gamma_0}{\mu_0^+ + \mu_0^-}\varphi_0(S)S_x u\right)_x. \tag{1.18}$$

Here the swarming or aggregation behavior depends exactly on the sign of the difference between the turning frequencies.

If $S_x > 0$ and $\varphi_0 < 0$, then the right moving population, which is moving up the gradient, turns less often than the left moving one, which is moving down the gradient. This is the basic behavior also observed in experiments with bacteria.

If $S_x > 0$ and $\varphi_0 > 0$, then the right moving population, which is moving up the gradient again, turns more often than the left moving one. This behavior enhances the spreading out of the total population.

Hence two effects lead to positive bias: When moving upwards a signal gradient individuals slow down, they lower their turning rate, or both. These effects have also been found by Schnitzer [99] in a similar one-dimensional hyperbolic model for bacterial movement, where memory effects have been included.

1.4 Transport Models for Chemosensitive Movement

In Stroock [111] and in Keller [63] a transport equation has first been proposed for bacterial chemotaxis. Soll and Voss (in [107]) showed how the movement rules of "run"

and "tumble" can also be applied to movement behavior of slime mold amoeba like *Dictyostelium discoideum*. W. Alt studied a transport equation for amoeba-chemotaxis in two papers [3, 4]. He assumed specific movement and signal detection rules and he used the run length as another state variable. In case of constant run length the model of Stroock or Keller follows from Alt's transport equation. Alt uses singular perturbation methods to derive a diffusion equation of PKS-type. In Othmer, Dunbar and Alt [86] different forms of random movement for biological species are compared; position jump processes, velocity jump processes and diffusion models. Chen *et al.* [20] study perturbation expansions and projections of Alt's equation, which reduce to a special case of the one dimensional hyperbolic model for chemosensitive movement discussed above (1.10). Grünbaum [43] generalized Stroock's model to incorporate internal dynamics. Then the chemical network of signal recognition, transduction pathway and adaptation processes can be incorporated into the model. His analysis bases on specific scaling assumptions, but the mathematical methods need further justifications. An overview of results and known facts related to internal dynamics and chemical pathways is presented in a survey article of Othmer and Schaap [88]. Dickinson and Tranquillo [28] and Dickinson [27] study perturbation expansions of a stochastic velocity jump process with external bias due to chemotaxis. We will compare their results to the results of [52, 87] later in a discussion section (Section 1.4.5).

The diffusion approximation of transport models is a well known technique in many physical applications. We will summerize known results from neutron transport, kinetic theory of gases, radiation transport and stochastic processes in Section 1.4.5. For a detailed comparison it is better to first present the methods we used in [52, 87].

In the case of chemosensitive movement in (1.1) the turning rate μ and the velocity distribution kernel $T(v, v')$ may depend on the signal distribution $S(t, x)$, its gradient $\nabla S(t, x)$ or on other properties of S (e.g. non-local dependence can be included).

$$\mu = \mu(S, \nabla S, \ldots), \quad T(v, v') = T(v, v', S, \nabla S, \ldots) \tag{1.19}$$

There are many experimental data available, where the dependence of turning rates μ and velocity distribution T on concentrations or spatial or temporal gradients have been measured (e.g. Berg and Brown [11], Soll and Wessels [106, 107], Fisher, Merkl, Gerisch [33], Tani and Naitoh [112], Vicker [115], Macnab [72] to name but a few). See also the Dicty-home-page: `http://dicty.cmb.nwu.edu/dicty/dicty.html`.

In [52, 87] we consider general transport models for chemosensitive movement based on (1.1) and (1.19). A theory has been derived to generate a diffusion limit from a multi-scale analysis, which generalized the work of Alt [3, 4]. The long time asymptotics of solutions of the transport model for chemosensitive movement are given in certain situations by a PKS-model. With this analysis a very natural connection of the parameters of the transport model (turning rate μ, velocity distribution T) to the parameters of the PKS-model (motility d, chemotactic sensitivity χ) has been found. We briefly recall the main results of [52, 87]:

1.4.1 Basic Assumptions (T1)-(T4)

In [52] the linear transport equation (1.1) is considered in $\Omega = \mathbb{R}^n$. It is assumed that the set of velocities $V \subset \mathbb{R}^n$ is compact and symmetric such that $v \in V$ implies $-v \in V$. Let $\mathcal{K}$ denote the cone of non-negative functions in $L^2(V)$. Define the following operators on $L^2(V)$:

$$\begin{aligned} \mathcal{T}p(v) &= \int_V T(v,v')p(x,v',t)dv', \qquad \mathcal{T}^* p(v) = \int_V T(v',v)p(x,v',t)dv', \\ \mathcal{L} &= -\mu(I-\mathcal{T}), \end{aligned}$$

where I denotes the identity. We state the following assumptions on the kernel T.

(T1) $T(v,v') \geq 0, \quad \int T(v,v')dv = 1, \quad$ and $\quad \int\int T^2(v,v')dv'dv < \infty.$

(T2) There exist some $u_0 \in \mathcal{K}$ with $u_0 \not\equiv 0$, some integer N and a constant $\rho > 0$ such that for all $(v,v') \in V \times V$

$$u_0(v) \leq T^N(v',v) \leq \rho u_0(v),$$

where the N-th iterate of T is

$$T^N(v,v') := \int \dots \int T(v,w_1)T(w_1,w_2)\cdots T(w_{N-1},v')dw_1 \dots dw_{N-1}.$$

(T3) $\|\mathcal{T}\|_{\langle 1\rangle^\perp} < 1$, where $\langle 1\rangle^\perp$ denotes the orthogonal complement of the subspace $\langle 1\rangle \subset L^2(V)$ of functions constant in v.

(T4) $\int_V T(v,v')dv' = 1.$

The turning operator has the following properties:

Proposition 1.1 *Assume* (T1)-(T4). *Then*

1. 0 *is a simple eigenvalue of* $\mathcal{L}$ *with eigenfunction* $\phi(v) \equiv 1$.
2. *There exist an orthogonal decomposition* $L^2(V) = \langle 1\rangle \oplus \langle 1\rangle^\perp$ *and for all* $\psi \in \langle 1\rangle^\perp$ *we have*
$$\int \psi \mathcal{L}\psi dv \leq -\nu_2 \|\psi\|^2_{L^2(V)}, \quad \textit{with} \quad \nu_2 \equiv \mu(1 - \|\mathcal{T}\|_{\langle 1\rangle^\perp}).$$
3. *Each eigenvalue* $\lambda \neq 0$ *satisfies* $-2\mu < Re\ \lambda \leq -\nu_2 < 0$, *and there is no other positive eigenfunction.*
4. $\|\mathcal{L}\|_{\mathcal{L}(L^2(V),L^2(V))} \leq 2\mu.$

5. $\mathcal{L}$ restricted to $\langle 1\rangle^{\perp} \subset L^2(V)$ has a linear inverse $\mathcal{F}$ with norm

$$\|\mathcal{F}\|_{\mathcal{L}(\langle 1\rangle^{\perp},\langle 1\rangle^{\perp})} \leq \frac{1}{\nu_2}.$$

The proof for is given in [52]. In (T1) we state that $\mathcal{T}$ and $\mathcal{T}^*$ are compact Hilbert-Schmidt operators. Assumption (T2) ensures that $\mathcal{T}$ is u_0-positive in the sense of Krasnoselskii [69]. There exists a unique positive eigenfunction $\phi(v) = 1$. The assumption (T2) generalizes the corresponding assumption (T2) in [52] and it allows to include turn-angle distributions, which are zero for larger turn-angles. If, for example, individuals choose new velocities in an arc of 45° compared to the previous velocity, then the iterate $\mathcal{T}^4$ would be u_0 positive. With assumption (T4) we obtain the orthogonal decomposition of $L^2(V)$. Property (T3) represents the dissipative character of the transport model and this condition becomes important to show that the limit equation, which we will derive, indeed is parabolic.

1.4.2 The Parabolic Scaling

It is well known that transport equations and more general transport processes lead in some appropriate limit to diffusion models (see Section 1.4.5). Two interpretations lead to the diffusion limit. Either the turning rate and the velocity are large or time and space scale are chosen so that in the limit the quotient x^2/t stays bounded.

For some species (e.g. for *E.coli*) it appears that per unit of time there are many directional changes with a small net displacement. This behavior can be classified into three time scales: the *mean run time* $1/\mu$, the *drift-time scale* of about 100 individual turns and a *diffusion-time scale* of about 10000 individual turns. These scales can be modeled using the *parabolic scaling*

$$\tau = \varepsilon^2 t \quad \text{and} \quad \xi = \varepsilon x \tag{1.20}$$

for a small parameter ε ($\sim 10^{-2}$). We transform equation (1.1) accordingly and for $k > 2$ we consider an expansion of p:

$$p(\tau,\xi,v) = \sum_{i=0}^{k} p_i(\tau,\xi,v)\varepsilon^i + p_{k+1}(\tau,\xi,v)\varepsilon^{k+1}.$$

When we collect terms of equal order in ε, we arrive at a sequence of systems for the unknown functions $p_0, p_1, p_2, \ldots$.

Theorem 1.2 *Let* (T1)-(T4) *be true and let $\mathcal{F}$ denote the pseudo inverse from Proposition 1.1. For $k > 2$ we define a sequence of functions $p_0(\xi,\tau)$, $p_1(\xi,v,\tau)$, ..., $p_k(\xi,v,\tau)$*

as follows:

$(a1)$ p_0 *solves the* **parabolic limit equation**

$$p_{0,\tau} - \nabla \cdot (D \nabla p_0) = 0, \qquad p_0(\xi, 0) = \int_V p(\xi, v, 0) dv.$$

with diffusion tensor $$D \equiv -\frac{1}{\omega} \int_V v \mathcal{F} v^T \, dv.$$

$(a2)$ *for each* $1 \leq j \leq k$ *let* $\int_V p_j(\xi, v, \tau) dv = 0.$

$(a3)$ *for each* $2 \leq j \leq k$ *let* $\int_V v \, p_j(\xi, v, \tau) dv = 0,$

$(a4)$ $p_1(\xi, v, \tau) := \mathcal{F}(v \cdot \nabla p_0(\xi, \tau)).$

$(a5)$ $p_j(\xi, v, \tau) := \mathcal{F}(p_{j-2,\tau} + v \cdot \nabla p_{j-1}),$ *für* $2 \leq j \leq k.$

Then for each $\vartheta > 0$ *there is a constant* $C_0 > 0$ *with the property that the sum*

$$q_k := \sum_{j=0}^{k} \varepsilon^j p_j$$

satisfies

$$\| p(x, ., t) - q_k(x, ., t) \|_{L^2(V)} \leq C \, \varepsilon^{k+1}.$$

for all $\vartheta/\varepsilon^2 < t < \infty$ *and each* $x \in \Omega$.

Hence the asymptotic behavior of solutions of (1.1) is described by the diffusion equation in (a1). The proof of this result uses an induction argument. Especially property (T3) is important to show that the limit equation in (a1) is parabolic.

In Chapter 4 we will generalize this result to transport models with birth-death terms for approximations of order ε^2. A complete proof is given in that chapter.

1.4.3 The Diffusion Tensor D

It appears that in the limit the diffusion is described by a diffusion tensor D. We will show under which conditions this tensor is isotropic, i.e. it is a scalar multiple of the identity. We define the *expected velocity*

$$\bar{v}(v) \equiv \int T(v, v') v' dv'. \tag{1.21}$$

With assumption (T1) it follows that $\int_V \bar{v}(v) dv = 0$. Moreover we assume that V is symmetric with respect to $SO(n)$. Then there exists a constant K_V such that

$$\int_V v v^T dv = K_V I$$

(which can be seen by applying the left hand side onto two test-vectors and using the divergence theorem). In case of $V = sS^{n-1}$ we have $K_V = \omega_0 s^2/n$.

We compare three statements:

(S1): *There is an orthonormal basis* $\{e_1, \dots, e_n\}$ *of* $\mathbb{R}^n$ *such that for each* $i = 1, \dots, n$ *the coordinate mappings* $\pi_i : V \to \mathbb{R}, \quad \pi_i(v) = v_i$ *are eigenfunctions of* $\mathcal{L}$ *with common eigenvalue* $\nu \in (-2\mu, 0)$.

(S2): *There is a constant* $\gamma \in (-1, 1)$ *such that for each* $v \in V$ *the expected velocity* $\bar{v}(v)$ *satisfies*

$$\bar{v}(v) \parallel v \quad \text{and} \quad \frac{\bar{v}(v) \cdot v}{|\bar{v}(v)||v|} = \gamma.$$

(S3): *There is a constant* $d > 0$ *such that the diffusion matrix is given by* $D = d\, I_n$.

Theorem 1.3 *Let* (T1)-(T4) *hold and assume that* V *is symmetric with respect to* $SO(n)$. *Then we have*

$$\text{(S1)} \quad \Longleftrightarrow \quad \text{(S2)} \quad \Longrightarrow \quad \text{(S3)}.$$

The constants ν, γ *and* d *are related as follows.*

$$\gamma = \frac{\nu + \mu}{\mu}, \qquad d = -\frac{K_V}{\omega\nu} = \frac{K_V}{\omega\mu(1-\gamma)}.$$

If T *also satisfies* **(T5):** *There is a matrix* M *such that* $\bar{v}(v) = Mv$ *for all* $v \in V$, *then all three statements are equivalent.*

This Theorem is proven in [52].

If T has the symmetric form of $T(v, v') = t(|v - v'|)$ then the diffusion limit is isotropic (see also Alt [3]).

1.4.4 Application to Chemosensitive Movement

Let T_0 and μ_0 denote turning kernel and turning rate in absence of any chemical substance. In [87] we systematically study perturbations which come form chemical cues of the form

$$T(v, v', \hat{S}) = T_0(v, v') + \varepsilon^k T_1(v, v', \hat{S}), \quad \mu(v, \hat{S}) = \mu_0 + \varepsilon^l \mu_1(v, v', \hat{S}),$$

for $k = 0, 1$ and $l = 1$, where $\hat{S}$ denotes dependence on the function S and not only on the local value $S(t, x)$, e.g. dependence on $S(t, x), \nabla S(t, x), \int S(t, x)dx$ etc are included. Perturbations of higher order $k, l \geq 2$ will not affect the parabolic limit equation. Perturbations of the turning rate μ_0 of order one ($l = 0$) do not fit into the framework

developed here. But that case can be handled in the theory of moment closure as illustrated in Chapter 2 in Section 2.5.1. There it is shown that also order one perturbations in the turning rate lead to PKS-type models.

We omit the most general formulations as stated in [87] and we prefer to give some illustrative examples, where the parabolic scaling applies. For all examples we restrict to fixed speed $|v| = s, V = sS^{n-1}$ and $\omega = |V|$.

Example 1: To get used to the method and the notations we start with a simple biased random walk without chemical signal. We assume that the probability of a change of velocity v' to v depends on the angle between these two velocities.

$$T_1(v, v') = \frac{1}{\omega}\left(1 + \frac{a}{s^2}(v \cdot v')\right) \quad \text{with} \quad a < n. \tag{1.22}$$

It is easy to check that the *expected velocity* is

$$\bar{v}(v) := \int v' T_1(v, v') dv' = \frac{a}{n} v \tag{1.23}$$

The factor $\frac{a}{n} = \psi_d$ is denoted as persistence index (see Othmer *et al.* [86]).
Theorem 1.3 applies and the first order approximation $p_0(\tau, \xi)$ fulfills the isotropic diffusion equation

$$\frac{\partial}{\partial \tau} p_0 = d \Delta p_0 \tag{1.24}$$

with

$$d = \frac{s^2}{\mu(n-a)}. \tag{1.25}$$

The case of $a = 0$ corresponds to random walk without persistence and the corresponding diffusion constant is

$$d = \frac{s^2}{\mu n}. \tag{1.26}$$

We have checked that a perturbation of lower order $T(v, v') = \frac{1}{\omega}(1 + \varepsilon \frac{a}{s^2}(v \cdot v'))$ does not effect the limit equation at all and (1.24) results with (1.26).

Example 2: Here we consider chemosensitive movement and we assume that an individual actively chooses directions upward chemical gradients (positive taxis). Then the angle of new velocity v and signal gradient ∇S is an important variable and we assume

$$T_2(v, v', S) = \frac{1}{\omega}(1 + \varepsilon a(S)(v \cdot \nabla S)). \tag{1.27}$$

Passing to the limit of small ε leads to a PKS-type model

$$\frac{\partial}{\partial \tau} p_0 = \nabla\Big(d \nabla p_0 - p_0 \chi(S) \nabla S\Big) \tag{1.28}$$

with $d = \frac{s^2}{\mu n}$ and $\chi(S) = \frac{s^2}{n} a(S)$.

Example 3 (Bacteria): For bacterial chemotaxis the velocity distribution appears to be independent of signal gradients. But the turning rate increases if individuals move down the gradient and it decreases if they move upwards. Hence we assume $T(v, v') = \frac{1}{\omega}$ and

$$\mu_2(S) = \mu_0(1 - \varepsilon b(S)(v \cdot \nabla S)) \tag{1.29}$$

Then a PKS-model follows

$$\frac{\partial}{\partial \tau} p_0 = \nabla \Big(d \nabla p_0 - \chi(S) p_0 \nabla S \Big) \tag{1.30}$$

with $d = \frac{s^2}{\mu n}$ and $\chi(S) = \frac{s^2}{n} b(S)$ This example directly applies to the experiments of Ford *et al.* with *E. coli* bacteria ([36, 35, 34, 16]). We illustrated the details in [87].

Example 4 (Amoeba): If we consider amoebae-chemotaxis we obtain both, change of turning rate as in Example 3 and the active choice of preferred directions as modeled in Example 2. A combination of both

$$T_4(v, v') = T_2(v, v'), \qquad \mu_4(S) = \mu_2(S)$$

just leads to additional effects in the chemotaxis term

$$\chi(S) = \frac{s^2}{n}(a(S) + b(S)). \tag{1.31}$$

This case is also covered by the results of Patlak [92] and of Alt [3].

For general situations it turned out in [52],[87] that the diffusion limit is non isotropic. We give one example.

Example 5 (non-isotropic diffusion): We assume that a stream of elongated bacteria such as myxobacteria is oriented in the direction $\eta \in \mathbb{R}^n$. To describe alignment towards this stream we choose the turning kernel

$$T_5 = \kappa(v \cdot \eta)(v' \cdot \eta), \qquad |\eta| = 1.$$

If the actual direction v' is in the direction η or $-\eta$, then there is an increased probability to choose a new velocity v in the direction η or $-\eta$, respectively. If κ is small enough then the diffusion limit is

$$\frac{\partial}{\partial \tau} p_0 = \nabla D \nabla p_0$$

with non-isotropic diffusion

$$D(\xi,\tau) = \frac{s^2}{\lambda_0 n}\left(I + \frac{\omega s^2}{n}\kappa\eta\eta\left(I - \frac{\omega s^2}{n}\kappa\eta\eta\right)^{-1}\right),$$

The diffusivity in the direction η or $-\eta$ is enhanced, whereas it has the standard value $s^2/(\lambda_0 n)$ in the orthogonal direction.

Example 6 (non-local gradient): A non local gradient, which might be measured by amoeba along their surface, can be modeled by

$$\overset{\circ}{S}(x,t) = \frac{n}{\omega_0 R}\int_{S^{n-1}} \sigma\, S(x + R\sigma, t)\, d\sigma, \tag{1.32}$$

where $R > 0$ is the *effective sampling radius*. If $R \to 0$ then this expression approximates the local gradient ∇S. For chemosensitive movement we treat the non-local gradient $\overset{\circ}{S}$ in exactly the same way as we used ∇S in the previous Examples 2,3 and 4.

Example 7 (directional derivative): Bacteria, for example, are too small to measure chemical gradients along their body axis. They move through a signal field and they measure the signal variation along their path. Hence the turning rate should depend on the directional derivative:

$$\partial_v S := S_t + v \cdot \nabla S.$$

In the parabolic scaling this leads to $\delta_v S = \varepsilon^2 S_\tau + \varepsilon v \cdot \nabla_\xi S$. The time derivative is of lower order compared to the gradient term. Hence to first order we obtain the same limit as in Example 3.

1.4.5 Diffusion Limits of Transport Equations

The approximation of a transport equation with its diffusion limit is a classical method in many physical applications. This ranges from the kinetic theory of gases and thermodynamics over neutron transport theory to radiation transport models. We will summarize the relevant literature later in this section. First we will discuss the literature concerned with biological applications. The results of Alt [3, 4] , Schnitzer [99], Chen *et al.* [20], Othmer, Dunbar, Alt [86] and Grünbaum [43] have been mentioned in the introduction of this Section 1.4.

Dickinson and Tranquillo [28] and Dickinson [27] divide the movement process of the population into three subprocesses, each characterized by its own time scale. *Locomotion*, the fastest time scale, describes inter-cellular pathways; *translocation* is the scale of individual movement and the slowest time scale, *migration* characterizes the movement of the whole population. The authors consider a stochastic process which includes linear

transport, reorientations, diffusion in velocity and rotations. They use the method of *adiabatic elimination of fast variables* (see Gardiner [39]) to derive the corresponding Smoluchovski equation. The Smoluchovski equation is a drift-diffusion model, which depends on the scaling parameter. The method of Dickinson *et al.* differs from our approach presented here in many ways. The adiabatic scaling corresponds in our notation to a choice of $\tilde{\tau} = \varepsilon t, \xi = \varepsilon x$, which leads to a diffusion limit depending on ε. If one scales the time variable of the drift-diffusion limit accordingly ($\tau = \varepsilon\tilde{\tau}$) then the diffusion limit follows. On the other hand a perturbation expansion in $(\tilde{\tau}, \xi)$ would lead to an elliptic limit equation (see [52]). The connection of the adiabatic scaling to the parabolic scaling has to be checked in more detail. For now we denote the adiabatic scaling $(\varepsilon t, \varepsilon x)$ by (i) and the parabolic scaling $(\varepsilon^2 t, \varepsilon x)$ by (ii).

It turns out that both methods are present in different areas of physical applications. In neutron transport theory the diffusion limit is used to describe reactor kinetics. In Habetler and Matkowsky [45] the diffusion limit has been related to singular perturbation theory. It is assumed that the mean free path is small compared to a typical length of the experiment at hand. This identifies a small parameter for singular perturbation analysis and it leads to method (i). Some more recent articles of Banasiak and Mika [9] or Banasiak [8] use the parabolic scaling (ii) for neutron transport.

For radiation transport a comprehensive source is given by Mihalas and Weibel-Mihalas [76]. A most recent publication is a preprint of Klar and Schmeiser [67], who use the parabolic scaling (ii). They study the diffusion limit as an outer expansion in a singular perturbation analysis.

For the Boltzmann equation in kinetic theory of gases the diffusion limit is known in connection with hydrodynamical limits (see Cercignani *et al.* [18]). In Babovsky [7] the two methods, (i) and (ii), for deriving a diffusion limit from a linearized Boltzmann equation are illustrated. It turns out that the first (i) is better suited for stochastic differential equations, whereas the second method (ii) is better for singular perturbation theory and partial differential equations. Bellomo considers Boltzmann equations for applications in biology, such as tumor growth and epidemiology [10].

From a mathematical point of view there are estimates for the accuracy of the diffusion approximation. First of all in a paper of Papanicolaou [91] the diffusion approximation of the backward transport equation has been studied and estimates have been derived. Similar results have been derived by many authors for different applications and we found a good summary in Dautray and Lions [25]. In Dautray and Lions a singular perturbation method has been used, which bases on the parabolic scaling (ii). Estimates of the accuracy of the diffusion approximation include the initial layer as well. The standard procedure is to show that solutions of transport equations can be approximated by solutions of appropriate diffusion models. We will demonstrate this method in Chapter 4 for a transport model with birth-death processes and resting phases.

The discussion of diffusion limits is also well known in the field of stochastic processes. The central limit theorem and Donsker's theorem for martingales refer to the property

that under certain conditions a stochastic process approximates Brownian motion (see Durrett [32] for details).

In all of the above studies it turned out that they are not directly applicable to problems which come from biology. In case of Boltzmann equations there is conservation of mass, momentum and energy, whereas for populations we have at most conservation of the total particle number. This translates into different functional analytic properties of the turning operator. The kernel of the turning operator for the Boltzmann equation is five dimensional, which corresponds to the Maxwellian distributions. The kernel for biological applications is one dimensional, which corresponds to particle conservation. In neutron transport theory, or in radiation transport most authors consider symmetric kernel. In case of chemosensitive movement however, we find an anisotropy in direction of the signal gradient. Other authors assume strictly positive turning kernel, which we relaxed into condition (T2).

Overall we think that the set of conditions given above, (T1)-(T4), represents a quite general sufficient set of conditions such that the diffusion limit for biological applications can be obtained in a clear and transparent way.

2 The Cattaneo Approximation

We consider the moment closure approach to transport equations. We present a method which allows to close the first two moment equations. The closure leads to semilinear Cattaneo systems, which are closely related to damped wave equations. We derive estimates for the residuum. The method is used to study a transport model for chemosensitive movement. We show that the 2-moment approximation is a Cattaneo model for chemosensitive movement, which in a parabolic limit converges (formally) to the classical PKS equation. In a discussion section we show how to derive boundary conditions for the Cattaneo approximation, we illustrate that the Cattaneo system is the gradient flow of a weighted Dirichlet integral and we show simulations.

2.1 Introduction

Here we consider the equations of the first two moments (m^0, m^i), $i \in \{1, \dots, n\}$ of p, where m^0 is defined by (3.8) and the higher moments of p are denoted by

$$m^i(t,x) = \int_V v^i p(t,x,v)\, dv, \qquad i = 1, \dots, n \tag{2.1}$$

$$m^{ij}(t,x) = \int_V v^i v^j\, p(t,x,v)\, dv, \qquad i,j = 1, \dots, n. \tag{2.2}$$

Note that m^0 is scalar, m^i is a vector and m^{ij} is a 2-tensor. Here we use upper case indices for the components of velocity $v = (v^1, \dots, v^n)^T$. Since in Chapter 3 we will generalize this approach to higher moments we use the tensor notation of m^i, m^{ij} and all other tensors. All indices run from 1 to n and we use the summation convention for repeated upper and lower case indices.

For constant turn angle distribution $T(v, v')$ we will show that the negative of the $L^2(V)$-norm is an entropy for (1.1). We minimize the $L^2(V)$-norm under the constraint of fixed moments m^0 and m^i. Then we assume that the second moment $m^{ij}(u_{\min})$ of the minimizer $u_{\min}$ approximates the second moment $m^{ij}(p)$. This leads to a closed hyperbolic system (2.13) for an approximate density M^0 and an approximate flow M^i. Since the resulting system is known from heat transport theory as the Cattaneo system

we call it *Cattaneo approximation* to (m^0, m^i). We derive an error estimate for $(m^0, m^i) - (M^0, M^i)$ in $L^2(\mathbb{R}^n)$ in Theorem 2.7. This estimate motivates the use of Cattaneo systems as models for the movement of microorganisms like bacteria or amoeba (see Remark 2.4).

The approximation method presented here can also be interpreted in the sense that minimizing of the $L^2(V)$-norm minimizes oscillations (see Remark 2.1). Qualitatively the approximate solution is smoother than the true solution. High frequencies are damped and envelopes of the particle distribution are formed. It turns out that the minimizer is the orthogonal projection of p onto the $n+1$-dimensional subspace of $L^2(V)$ spanned by the functions $1, v^1, \ldots, v^n$. Schnitzer [99] derived a Cattaneo model for chemosensitive movement ((5.12) in [99]) with the *ad hoc* assumption that the density can be expanded as $p = p_0(t,x) + v^i p_i(t,x)$. The minimizing procedure developed here gives a justification of his ansatz.

Since our estimates are valid for all times (in the linear case) the Cattaneo approximation can be used to approximate the transport model for all times whereas the parabolic approximations are valid for large times only (see the discussion in Section 6).

In context of the moment closure method presented here the Cattaneo approximation is the first nontrivial approximation to the transport process. If we fix the zero's moment m^0 only and minimize the $L^2(V)$-norm then the minimizer is simply the mean density with respect to velocity v. It does not depend on v and t and the equilibrium distributions result (see Remark 2.2). Generalizations to higher closure levels, general sets of velocities V and general kernel T are given in the next chapter (Chapter 3).

In case of one spatial dimension with only two velocities $\pm s$ the even moments are proportional to the zero–moment and the odd moments are proportional to the first moment. Hence the first two moment equations are closed by itself and the 1-D Cattaneo system is equivalent to the 1-D transport equation ([86, 46]).

For Boltzmann equations the moment closure problem has been studied intensively in the theory of *Extended Thermodynamics* [77]. In that context there is a physical entropy and it is maximized to close the moment system. Up to now there is no rigorous criterion for the accuracy of the closed moment system as an approximation to the Boltzmann equation. Error estimates of the type shown here (Theorem 2.7) have not been derived for the Boltzmann equation. Our estimates base on the boundedness of the space of velocities, V. In case of Boltzmann equation this space is not *a priori* bounded. The most important first moment approximations to the Boltzmann equation are the Euler equations and the Navier-Stokes equations ([77]). Here the Cattaneo system (2.13) ranges at the same level as the Euler equations.

The Cattaneo system of heat transport also appears in the theory of extended thermodynamics. There it ranges inbetween the Navier-Stokes-Fourier model and the 13 moment model. In this context the Cattaneo law is not appropriate since one would have to neglect some terms in the 13 moment system, which might have the same order in magnitude than other remaining terms (see Müller and Ruggeri [77] for details).

Application to chemosensitive movement and to reaction transport equations are given at the end of this Chapter. In case of chemosensitive movement we use our method to close the first moment equations and obtain a *Cattaneo system for chemosensitive movement*. Then we consider appropriate scaling of speed and turning rate (parabolic limit) to arrive at the well known and well studied PKS equation [64]. In this framework we are able to handle order one perturbations of the turning rate due to chemical cues. This was not possible with the parabolic scaling, as illustrated in the previous Section 1.4.

In Section 2.2 we present the minimizing principle for the linear transport equation (1.1) for equally distributed turn angle distribution $T(v,v')$ =const. We calculate the minimizer $u_{\min}$ which motivates the Cattaneo approximation (2.13) for (M^0, M^i). In Section 2.3 we consider the $L^2(V)$-norm of the true solution p and compare it to the norm of the minimizer $u_{\min}$ (Theorem 2.4). An $L^2(\mathbb{R}^n)$–estimate is derived for $(m^0, m^i) - (M^0, M^i)$ in Theorem 2.7. In Section 2.4 we generalize the moment closure method to nonlinear reaction transport equations (1.2), again with equally distributed kernel T. A nonlinear Cattaneo system (2.33) follows, which has been studied in detail in [51]. In Section 2.5 we introduce a prototype model for chemosensitive movement based on a transport equation (1.1). We show that under natural assumptions the 2-moment approximation is a Cattaneo model for chemosensitive movement (2.41) which in a parabolic limit converges (formally) to the classical PKS equations ([64]). In the discussion section (Section 2.6) we show that the moment closure method presented here can be used to find appropriate boundary conditions for the Cattaneo system on bounded domains. Moreover we show that the Cattaneo system is the minimizing flux of a weighted Dirichlet integral. Finally we show simulations of the Cattaneo model for chemosensitive movement, which have been developed in collaboration with Y. Dolak [30].

2.2 A Minimization Principle and L^2-Projections

We consider a transport equation which corresponds to a velocity jump process with fixed speed, but variable direction (*Pearson walk* [94]). In this case $V = sS^{n-1}$ with $s > 0$ and we denote $\omega = |V| = s^{n-1}\omega_0$, where $\omega_0 = |S^{n-1}|$. The turn angle distribution is assumed to be constant $T(v,v') = \frac{1}{\omega}$. The method developed here will be generalized to more general kernel T and more general velocity sets V in Chapter 3.

The initial value problem for the linear transport equation reads

$$p_t + v \cdot \nabla p = \mu \left(\frac{m^0}{\omega} - p \right), \tag{2.3}$$

$$p(0,x,v) = \varphi_0(x,v). \tag{2.4}$$

The shift operator $\Phi := -v \cdot \nabla$ on $L^2(\mathbb{R}^n \times V)$ with domain

$$\mathcal{D}(\Phi) = \{\phi \in L^2(\mathbb{R}^n \times V) : \phi(.,v) \in H^1(\mathbb{R}^n)\}$$

is skew-adjoint. Hence it generates a strongly continuous unitary group on $L^2(\mathbb{R}^n \times V)$ (see Dautray, Lions [25] and Pazy [93]: Stones Theorem). The right hand side of (2.3) is bounded, therefore the linear transport equation (2.3) defines a strongly continuous solution group on $L^2(\mathbb{R}^n \times V)$. For $\varphi_0 \in \mathcal{D}(\Phi)$ solutions $p(t,x,v)$ exist in

$$\mathcal{X} = C^1([0,\infty), L^2(\mathbb{R}^n \times V)) \cap C([0,\infty), \mathcal{D}(\Phi)). \tag{2.5}$$

A detailed existence theory on transport and reaction-transport equations on bounded domains is given in Schwetlick [100].

Later we will use the L^2-norm to carry out the moment closure. Hence in this context it is natural to work in L^2 spaces. For other applications the L^1-theory is preferred, since the total particle number is preserved by the linear transport equation (see e.g. [8] for neutron transport).

To derive the equations for the first two moments m^0 and m^i we integrate (2.3) over V to obtain the conservation law

$$m^0_t + \partial_j m^j = 0. \tag{2.6}$$

Multiplication of (2.3) with v^i and integration gives

$$\int v^i p_t \, dv = -\int v^i v^j \partial_j p \, dv + \mu \frac{m^0}{\omega} \int v^i \, dv - \mu \int v^i p \, dv.$$

From the symmetry of $V = sS^{n-1}$ it follows that $\int v^i dv = 0$. Hence

$$m^i_t + \partial_j m^{ij} = -\mu m^i. \tag{2.7}$$

To close this system of two moment equations (2.6) and (2.7) we want to replace $m^{ij}(p)$. We derive a function $u_{\min}(t,x,v)$ which minimizes the $L^2(V)$ norm $\|u(t,x,.)\|_2^2$ under the constraint that $u_{\min}$ has the same first moments m^0 and m^i as p has. We will show in (2.17) that this norm is an entropy in the sense of thermodynamics. Once we have such a function $u_{\min}$ we replace $m^{ij}(p)$ by $m^{ij}(u_{\min})$.

We introduce Lagrangian multipliers $\Lambda_0 \in \mathbb{R}$ and $\Lambda_i \in \mathbb{R}$ for $i = 1, \ldots, n$ and define

$$H(u) := \frac{1}{2} \int_V u^2 dv - \Lambda_0 \left(\int_V u dv - m^0 \right) - \Lambda_i \left(\int_V v^i u dv - m^i \right).$$

The Euler-Lagrange equation (first variation) of $H(u)$ reads $u - \Lambda_0 - \Lambda_i v^i = 0$, which gives

$$u = \Lambda_0 + \Lambda_i v^i. \tag{2.8}$$

We use the constraints to determine Λ_0 and Λ_i:

1.
$$m^0 = \int_V u\,dv = \int_V \Lambda_0\,dv + \int_V v^i \Lambda_i\,dv.$$
We have $\int_V v^i\,dv\Lambda_i = 0$ hence
$$\Lambda_0 = \frac{m^0}{\omega}. \tag{2.9}$$

2.
$$m^i = \int_V v^i u\,dv = \int_V v^i \Lambda_0 dv + \int_V v^i(\Lambda_j v^j)dv$$
The first integral vanishes. To evaluate the second integral note that
$$\int_{S^{n-1}} \sigma\sigma^T\,d\sigma = \frac{\omega_0}{n} I_n,$$
where I_n denotes the $n \times n$ identity matrix. Hence
$$\int_V vv^T\,dv = \int_{S^{n-1}} (s\sigma)(s\sigma)^T s^{n-1} d\sigma = \omega\frac{s^2}{n} I_n. \tag{2.10}$$
It follows that Λ_i is given by
$$\Lambda_i = \frac{n}{\omega s^2} m^i.$$

Then from (2.8) we get an explicit representation of the minimizer
$$u_{\min}(t,x,v) = \frac{1}{\omega}\left(m^0(t,x) + \frac{n}{s^2}(v_i m^i(t,x))\right). \tag{2.11}$$

Remark 2.1 *1. Let $\langle 1, v^1, \ldots, v^n\rangle \subset L^2(V)$ denote the subspace generated by the constant functions and linear functions. Let Π denote the orthogonal projection to this subspace*
$$\Pi\phi(v) = \frac{1}{\omega}\int \phi(v')dv' + \frac{n}{\omega s^2}\int v_i'\phi(v')dv' \cdot v^i.$$
It turns out that the minimizer u_{min} in (2.11) satisfies $u_{min} = \Pi p$ for each $(t,x) \in \mathbb{R}^+ \times \mathbb{R}^n$.

2. If we minimize the functional
$$H_a(u) := \frac{1}{2}\int_V (u-a)^2 dv - \Lambda_0\left(\int_V u dv - m^0\right) - \Lambda_i\left(\int_V v^i u dv - m^i\right),$$
for some arbitrary $a \in \mathbb{R}$ with the same constraints as above we arrive at the same minimizer (2.11). For fixed $a \in \mathbb{R}$ the norm $\|u(t,x,.) - a\|_2$ is a measure of the oscillation around the level a. Hence u_{min} minimizes oscillations with respect to every given level.

3. *The extremum u_{min} is indeed a minimum, since the second variation of H is $\delta^2 H(u) = 1 > 0$.*

To finally derive the moment closure we consider the second moment of the minimizer $u_{\min}$:

$$\begin{aligned} m^{ij}(u_{\min}) &= \int_V v^i v^j \, u_{\min}(t,x,v) dv \\ &= \frac{1}{\omega} \int_V v^i v^j \, m^0 \, dv + \frac{n}{\omega s^2} \int_V v^i v^j v_k \, dv \, m^k \\ &= \frac{s^2}{n} m^0 \, I, \end{aligned} \tag{2.12}$$

where (2.10) has been used, and because the tensor $\int_V v^i v^j v_k \, dv$ vanishes (see the following Lemma).

Lemma 2.1 *For all vectors $a, b, c \in \mathbb{R}^n$ we have*

$$\int_V (v^i a_i)(v^j b_j)(v^k c_k) dv = 0.$$

Proof: Using the divergence theorem on the ball $B_s(0) \in \mathbb{R}^n$ gives

$$\begin{aligned} \int_V (v^i a_i)(v^j b_j)(v^k c_k) dv &= \int_V v^i (a_i (v^j b_j)(v^k c_k)) dv \\ &= s \int_{B_s(0)} \frac{\partial}{\partial v^i} (a_i (v^j b_j)(v^k c_k)) dW \\ &= s \left((a_i b^i) c_k \int_{B_s(0)} v^k dW + (a_i c^i) b_j \int_{B_s(0)} v^j dW \right) \\ &= 0, \end{aligned}$$

where here dv describes the surface element on V and dW the volume element on $B_s(0)$. □

We have chosen $u_{\min}$ such that $m^0(u) = m^0(p)$ and $m^i(u) = m^i(p)$. Now we close the system of the first two moments (2.6), (2.7) by assuming that $m^{ij}(u) \approx m^{ij}(p)$. Then, replacing m^{ij} in (2.7) together with (2.6) gives a linear Cattaneo system

$$\begin{aligned} M^0_t + \partial_j M^j &= 0, \\ M^i_t + \tfrac{s^2}{n} \partial_i M^0 &= -\mu M^i, \end{aligned} \tag{2.13}$$

with initial conditions

$$M^0(0,.) = m^0(0,.), \quad M^i(0,.) = m^i(0,.). \tag{2.14}$$

We introduce capital letters to distinguish between the moments (m^0, m^i) of p and the solutions (M^0, M^i) of the Cattaneo system (2.13). Of course, if $m^{ij}(u) \neq m^{ij}(p)$ then $(M^0, M^i) \neq (m^0, m^i)$. In the next Section we consider errors between $u_{\min}$ and p and between (M^0, M^i) and (m^0, m^i).

We will study solutions of the Cattaneo approximation (2.13) also in L^2-spaces. In [51] the Cattaneo system has been studied in $L^2(\Omega)$ with homogeneous Dirichlet or Neumann boundary conditions. Existence was shown using Stones theorem for skew adjoint generators (see Pazy [93]). The same argument applies on an unbounded domain. Using a simple scaling of the space coordinates the generator of the Cattaneo system (2.13) has the form

$$G := \begin{pmatrix} 0 & -\partial_1 & \cdots & -\partial_n \\ -\partial_1, & 0 & & \\ \vdots & & \ddots & \\ -\partial_n & & & 0 \end{pmatrix}$$

with domain

$$\mathcal{D}(G) := \{(\varphi^0, \ldots, \varphi^n) \in L^2(\mathbb{R}^n)^{n+1} : \ \partial_i \varphi^0, \partial_i \varphi^i \in L^2(\mathbb{R}^n), \ i = 1, \ldots, n\}$$

The operator G is skew adjoint. Therefore it is dissipative, the spectrum belongs to the imaginary axis and it generates an unitary group on $(L^2(\mathbb{R}^n))^{n+1}$. Since the Cattaneo approximation (2.13) is linear we have global existence:

Lemma 2.2 *For each $(\varphi^0, \varphi^i) \in \mathcal{D}(G)$ there exists a unique global solution (M^0, M^i) of (2.13) with*

$$(M^0, M^i) \in C^1((-\infty, \infty), L^2(\mathbb{R}^n)^{n+1}) \cap C^0((-\infty, \infty), \mathcal{D}(G)),$$

with $M^0(0) = \varphi^0$ and $M^i(0) = \varphi^i$.

Remark 2.2 *The minimizer $u_{min}(t, x, v)$ given by (2.11) is the first nontrivial approximation to $p(t, x, v)$ in the following sense: If we only fix the first moment m^0 then minimizing the $L^2(V)$-norm leads to*

$$\tilde{u}_{min}(t, x, v) = \frac{1}{\omega} m^0(t, x).$$

Then $\tilde{u}_{min}$ is the projection of p onto the space of functions constant in v. The first moment of this minimizer $\tilde{u}_{min}$ vanishes and it follows from the conservation law (2.6) that the corresponding moment closure is simply

$$M_t^0 = 0.$$

To develop a sequence of approximating functions $(\tilde{u}_{\min}, u_{\min}, \ldots)$ one can derive equations for higher moments and fix more and more moments in the minimizing procedure. We will do this in the following Chapter 3.

2.3 Error Estimates

2.3.1 Estimate of $u_{\min}$ Versus p

The $L^2(V)$-norm of the minimizer (2.11) is

$$\begin{aligned}
\|u_{\min}(t,x,.)\|_2^2 &= \frac{1}{\omega^2}\int_V \left(m^0 + \frac{n}{s^2}(v_i m^i)\right)^2 dv \\
&= \frac{1}{\omega^2}\int_V \left((m^0)^2 + 2m^0\frac{n}{s^2}(v_i m^i) + \frac{n^2}{s^4}(v_i m^i)^2\right) dv \\
&= \frac{1}{\omega^2}\left(\omega(m^0)^2 + \frac{n^2\omega s^2}{s^4 n} m^i m_i\right), \\
&= \frac{1}{\omega}\left((m^0)^2 + \frac{n}{s^2} m^i m_i\right), \qquad (2.15)
\end{aligned}$$

which of course is the L^2 norm of p restricted to the subspace $\langle 1, v^1, \ldots, v^n\rangle$ (see Remark 2.1).

For the L^2-norm of p we have

$$\begin{aligned}
\frac{d}{dt}\|p(t,x,.)\|_2^2 &= 2\int_V p p_t\, dv \\
&= -2\int_V p v^i \partial_i p\, dv - 2\mu\int_V p^2 dv + 2\mu\int_V p\frac{m^0}{\omega} dv,
\end{aligned}$$

which leads to the balance equation

$$\frac{d}{dt}\|p(t,x,.)\|_2^2 + \partial_j F^j(p) = -2\mu\|p(t,x,.)\|_2^2 + \frac{2\mu}{\omega}(m^0)^2(t,x) \qquad (2.16)$$

with energy flow

$$F^j(p) = \int_V v^j p^2 dv.$$

Moreover, the negative $L^2(V)$-norm satisfies an H-Theorem, i.e., it is an entropy for equation (2.3):

Proposition 2.3

$$\frac{d}{dt}\|p(t,x,.)\|_2^2 + \partial_j F^j(p) \le 0. \qquad (2.17)$$

Proof: The right hand side of (2.16) can be written as

$$\begin{aligned}
-2\mu\|p(t,x,.)\|_2^2 + \frac{2\mu}{\omega}(m^0)^2 &= 2\mu\left(-\int_V p^2 dv + \frac{1}{\omega}\left(\int_V p\, dv\right)^2\right) \\
&= -2\mu\int_V \left(p - \frac{m^0}{\omega}\right)^2 dv \\
&\le 0.
\end{aligned}$$

□

We denote the square of the L^2-norm on $\mathbb{R}^n \times V$ by

$$\mathcal{E}(p) := \int_{\mathbb{R}^n} \|p(t,x,.)\|_2^2 dx$$

and we abbreviate

$$\mathcal{E}^0 = \int_{\mathbb{R}^n} \int_V p(0,x,v)^2 dv\, dx.$$

Theorem 2.4 *Let $p(t,x,v) \in \mathcal{X}$ denote the solution of (2.3), (2.4) and let $u_{min}(t,x,v)$ denote the minimizer constructed in (2.11). Then for all $t \geq 0$*

$$0 \leq \mathcal{E}(p(t)) - \mathcal{E}(u(t)) \leq e^{-2\mu t}\mathcal{E}^0 + \frac{1}{\omega}\left(\sup_{0\leq\vartheta\leq t} \|m^0(\vartheta,.)\|_2^2 \left(1 - e^{-2\mu t}\right) - \|m^0(t,.)\|_2^2\right). \tag{2.18}$$

Proof: We integrate the balance equation (2.16) over $\mathbb{R}^n$ and observe that

$$\frac{d}{dt}\mathcal{E}(p) = -2\mu\mathcal{E}(p) + \frac{2\mu}{\omega}\|m^0(t,.)\|_2^2. \tag{2.19}$$

Hence

$$\mathcal{E}(p)(t) = e^{-2\mu t}\mathcal{E}^0 + \frac{2\mu}{\omega}\int_0^t e^{-2\mu(t-\vartheta)}\|m^0(\vartheta,.)\|_2^2 d\vartheta. \tag{2.20}$$

Since $u_{\min}$ is a minimizer we have $\|u_{\min}(t,x,.)\|_2 \leq \|p(t,x,.)\|_2$. From (2.15) we obtain

$$\mathcal{E}(u_{\min}) = \frac{1}{\omega}\left(\|m^0(t,.)\|_2^2 + \frac{n}{s^2}\|(m^1(t,.),\ldots,m^n(t,.))\|_2^2\right).$$

Then with (2.20) it follows that

$$0 \leq \mathcal{E}(p) - \mathcal{E}(u) = (I) + (II) + (III)$$

with

$$\begin{aligned}
(I) &:= e^{-2\mu t}\mathcal{E}^0 \\
(II) &:= \frac{1}{\omega}\left(2\mu\int_0^t e^{-2\mu(t-\vartheta)}\|m^0(\vartheta,.)\|_2^2 d\vartheta - \|m^0(t,.)\|_2^2\right) \\
(III) &:= -\frac{n}{\omega s^2}\|(m^1(t,.),\ldots,m^n(t,.))\|_2^2.
\end{aligned}$$

The first term (I) tends to zero exponentially for $t \to \infty$. The third term (III) is non-positive. We consider the second term (II) in more detail. For this let $y(t) := \|m^0(t,.)\|_2^2$.

$$\begin{aligned}
2\mu\int_0^t e^{-2\mu(t-s)}y(s)ds &\leq \left(\sup_{0\leq\vartheta\leq t} y(\vartheta)\right)2\mu\int_0^t e^{-2\mu(t-s)}ds \\
&= \left(\sup_{0\leq\vartheta\leq t} y(\vartheta)\right)\left(1 - e^{-2\mu t}\right)
\end{aligned}$$

Putting all this together we arrive at (2.18). □

Remark 2.3 *1. The right hand side of (2.18) is bounded by* $\mathcal{E}^0 + \frac{1}{\omega}\sup_{0\le\vartheta\le t}\|m^0(\vartheta,.)\|_2^2$. *If in addition we know that* $\|m^0(t,.)\|_2$ *is not decreasing in time, then the right hand side converges to zero for* $t\to\infty$.

2. It follows from (2.17) and from (2.19) that $\mathcal{E}(p)$ *tends to zero in* $L^2(\mathbb{R}^n\times V)$ *for* $t\to\infty$. *Hence solutions converge to zero, which was to be expected by a dissipative system on the whole of* $\mathbb{R}^n$.

2.3.2 Estimates of the True Moments (m^0, m^i) Versus the Solution of the Cattaneo System (M^0, M^i)

We define

$$r := m^0 - M^0 \quad \text{and} \quad q^i := m^i - M^i.$$

From the moment equations (2.6), (2.7) and from the Cattaneo system (2.13) it follows that

$$r_t + \partial_j q^j = 0, \tag{2.21}$$

$$q^i_t + \mu q^i + \frac{s^2}{n}\partial_i m = \partial_j(m^{ij}(u) - m^{ij}(p)), \tag{2.22}$$

$$r(0,.) = 0, \qquad q^i(0,.) = 0. \tag{2.23}$$

Integration of the first equation (2.21) gives $\frac{d}{dt}\int r dx = 0$, hence due to the initial conditions (2.23) it follows that

$$\int_{\mathbb{R}^n}(m^0 - M^0)(t,x)dx = 0. \tag{2.24}$$

Integration of the second equation (2.22) gives $\frac{d}{dt}\int q^i dx = -\mu\int q^i dx$, for $i = 1,\dots,n$, then from the initial conditions (2.23) it follows that

$$\int_{\mathbb{R}^n}(m^i - M^i)(t,x)dx = 0, \qquad \text{for } i = 1,\dots,n. \tag{2.25}$$

We aim to estimate r and q^i, $i = 1,\dots,n$ in terms of $m^{ij}(u) - m^{ij}(p)$. For this we define an energy

$$\mathsf{e}_s(r,q) := \frac{1}{2}\int_{\mathbb{R}^n} r^2 + \frac{n}{s^2}\, q^i q_i\, dx, \tag{2.26}$$

which is the L^2- norm in space, where the speed s appears as a parameter.

Lemma 2.5 *Solutions (r,q) of (2.21)-(2.23) satisfy the energy estimate*

$$\mathsf{e}_s(r(t,.),q(t,.)) \le \frac{n}{2\mu s^2}\int_0^t\int_{\mathbb{R}^n} e^{-\mu(t-\vartheta)}\Big(\partial_j(m^{ij}(u)-m^{ij}(p))\Big)^2 dx d\vartheta.$$

Proof: We differentiate the energy with respect to time. With Young's inequality we get

$$\begin{aligned}
\frac{d}{dt}\mathsf{e}_s(r,q) &= \int r r_t + \frac{n}{s^2}q_j q_t^j\,dx\\
&= \int -\partial_j q^j + \frac{n}{s^2}q_j\left(-\mu q^j - \frac{s^2}{n}\partial_j r + \partial_i(m^{ji}(u)-m^{ji}(p))\right)dx\\
&= -\mu\int \frac{n}{s^2}q^j q_j\,dx + \int \frac{n}{s^2}\,q^j\,\partial_i(m^{ji}(u)-m^{ji}(p))dx\\
&\le -\mu\int \frac{n}{s^2}q^i q_i\,dx + \frac{\mu}{2}\int\frac{n}{s^2}q^i q_i\,dx + \frac{1}{2\mu}\int\frac{n}{s^2}\Big(\partial_i(m^{ji}(u)-m^{ji}(p))\Big)^2 dx\\
&\le -\mu\,\mathsf{e}_s(r,q) + \frac{n}{2\mu s^2}\int\Big(\partial_i(m^{ji}(u)-m^{ji}(p))\Big)^2 dx.
\end{aligned}$$

With Gronwall's Lemma the assertion follows. □

Lemma 2.6 *For all $(t,x)\in[0,\infty)\times\mathbb{R}^n$ we have*

$$\begin{aligned}
|(m^{ij}(u)-m^{ij}(p))(t,x)|_2 &\le b_n s^2 |m^0(t,x)|,\\
|D_\alpha\,(m^{ij}(u)-m^{ij}(p))(t,x)|_2 &\le b_n s^2 |D_\alpha\, m^0(t,x)|,
\end{aligned}$$

where D_α denotes partial derivative with respect to $\alpha\in\{t,x_1,\dots,x_n\}$ and the constant b_n is given in (2.29).

Proof: Remember that $m^{ij}(u)=\frac{s^2}{n}\delta^{ij}\,m^0=\frac{s^2}{n}\delta^{ij}\int_V p(t,x,v)dv$, hence we can write

$$m^{ij}(u)-m^{ij}(p)=\int B^{ij}_{n,v}p(t,x,v)dv,$$

with the $n\times n$ matrix

$$B_{n,v}:=\frac{s^2}{n}I_n - vv,$$

with entries

$$b^{ij}:=B^{ij}_{n,v}=\frac{s^2}{n}\delta^{ij}-v^iv^j.$$

If $i=j$ then $b_{ii}=\frac{s^2}{n}-(v^i)^2$. Since $s=|v|\ge(v^i)^2$ we have $\frac{s^2}{n}-s^2\le b^{ii}\le\frac{s^2}{n}$. Hence

$$|b^{ii}|\le s^2,\ \text{for}\ \ n=1,\quad\text{and}\quad |b^{ii}|\le s^2\frac{n-1}{n},\ \text{for}\ n\ge 2. \tag{2.27}$$

If $i \neq j$ then $b^{ij} = -v^i v^j$. Since $-\frac{1}{2}((v^i)^2 + (v^j)^2) \leq v^i v^j \leq \frac{1}{2}((v^i)^2 + (v^j)^2)$ it follows that

$$|b^{ij}| \leq \frac{s^2}{2}. \tag{2.28}$$

For now we denote the vector-norms in $\mathbb{R}^n$ by $|.|_2$ and $|.|_\infty$. Then we have for $n \geq 2$ that

$$|B_{n,v}|_2 \leq \sqrt{n}|B_{n,v}|_\infty \leq \sqrt{n}(n-1)\frac{n+2}{2n}\, s^2 =: b_n s^2 \tag{2.29}$$

and the same estimate $|B_{n,v}| \leq b_n s^2$ with $b_n = 1$ for $n = 1$. Then for each vector $\zeta \in \mathbb{R}^n$ we have

$$\begin{aligned} |(m^{ij}(u) - m^{ij}(p))(t,x)\zeta_j|_2 &= \left| \int B^{ij}_{n,v}(\zeta_j p)dv \right|_2 \\ &\leq b_n s^2 \left| \zeta^i \int_V p(t,x,v)dv \right|_2 \\ &= b_n s^2 |m^0(t,x)|\, |\zeta^i|_2. \end{aligned}$$

The same lines apply for $D_\alpha(m^{ij}(u) - m^{ij}(p))$. □

Together with Lemma 2.5 we arrive at the following result:

Theorem 2.7 *The solution (r,q) of (2.21)-(2.23) satisfies for each $t \geq 0$*

$$\mathsf{e}_s(r(t,.),q(t,.)) \leq n b_n^2 \frac{s^2}{2\mu} \|\nabla_x m^0\|^2_{L^2([0,t]\times\mathbb{R}^n)}. \tag{2.30}$$

Remark 2.4 *1. Here the L^2 norm of the differences in the first two moments is estimated by the norm of ∇m^0. If the gradient of m^0 is small, we obtain a good approximation. Some experimental setups for bacteria are designed for shallow gradients (see e.g. Chen* et al. *[20]). Patlak [92] derived the classical PKS-model for chemosensitive movement under the assumption, that on an average distance traveled by particles between turns, the change in particle distribution – hence $\|\nabla m^0\|$ – is small.*

2. In contrast to parabolic approximations the estimate (2.30) is valid for all times $t \geq 0$. This motivates to use the Cattaneo model for small times and parabolic models for longer times and asymptotics.

2.4 The Nonlinear Case: Reaction Transport Equations

Here we consider the nonlinear reaction transport equation:

$$p_t + v \cdot \nabla p = \mu\Big(\frac{m^0}{\omega} - p\Big) + f(v,p,m^0), \tag{2.31}$$

where f describes birth, death and interaction of particles. Reaction transport equations as models for biological populations have been derived by Othmer, Dunbar, Alt [86] and Hadeler [46]. In Chapter 4 we introduce and discuss a more detailed model, which accounts for the fact, that birth occurs while the mother is at rest. If the resting period is short compared to periods of movement then the above model is appropriate.

We choose f such that the reaction transport equation (2.31) admits a solution semigroup in $L^2(\mathbb{R}^n \times V)$. This surely is the case if f is continuous and linearly bounded in p. Again we formulate the equations for the first moments m^0, m^i and m^{ij}.

$$\begin{aligned} m^0_t + \partial_j m^j &= g \\ m^i_t + \partial_j m^{ij} &= -\mu m^i + h^i \end{aligned}$$

with the v-moments of f

$$g(t,x) = \int_V f(v,p,m^0)\,dv, \qquad h^i(t,x) = \int_V v^i\, f(v,p,m^0)\,dv.$$

To find an appropriate expression for m^{ij}, we again minimize the $L^2(V)$-norm with the same constraints as in the previous sections. Hence we continue with the minimum (2.11). Again the second moment of the minimizer $u_{\min}$ is given by (2.12) and a semilinear Cattaneo system follows

$$\begin{aligned} M^0_t + \partial_j M^j &= G \\ M^i_t + \tfrac{s^2}{n}\partial_i M^0 &= -\mu M^i + H^i, \end{aligned} \tag{2.32}$$

where now

$$G(t,x) = \int_V f(v,U,M^0)\,dv, \qquad H^i(t,x) = \int_V v^i\, f(v,U,M^0)\,dv,$$

with

$$U = \frac{1}{\omega}\Big(M^0 + \frac{n}{s^2}(v_i M^i)\Big).$$

In case of reactions, which are independent of the actual velocity, $f = f(m^0)$, we have

$$H^i = \int v^i f(M^0)dv = 0 \quad \text{and} \quad G = \int f(M^0)dv = \omega\, f(M^0).$$

Then a semilinear Cattaneo system follows which has been studied qualitatively in [51]:

$$\begin{aligned} M^0_t + \partial_j M^j &= \omega f(M^0) \\ M^i_t + \tfrac{s^2}{n}\partial_i M^0 &= -\mu M^i. \end{aligned} \tag{2.33}$$

2.5 Transport Equations for Chemosensitive Movement

The two independent parameters in the general velocity jump process (1.1) are the turning rate μ and the kernel T, which describes the probability of changing from velocity v' into velocity v. As mentioned earlier, in case of bacterial chemotaxis it has been observed in experiments, that bacteria significantly change their turning rate in response to external stimuli, but they do not change their turn angle distribution ([11]). Hence we modify the turning rate to derive a model for chemosensitive movement. As in the 1-D model considered in Hillen, Stevens [55] and Hillen, Rohde, Lutscher [54], the turning rate should depend on the velocity v, on the concentration of the external signal S and on its gradient ∇S

$$\mu = \mu(v, S, \nabla S)$$

It is, however, clear that bacteria are too small to measure concentration gradients along their body axis. They measure gradients while moving through them. Then the turning rate depends not directly on ∇S but on the directional derivative

$$\delta_v S := S_t + v \cdot \nabla S.$$

An assumption which has also been used by Alt [4] and by Grünbaum [42] (To see that $\delta_v S$ is the correct term consider a Taylor series expansion of the difference in the signal concentrations at (x,t) and at $(x + v\Delta t, t + \Delta t)$ for a small time increment Δt). If the chemical concentration equilibrates fast compared to the movement of the species then $S(t,x)$ would be close to equilibrium in each time step and we can assume $\delta_v S = v \cdot \nabla S$. This quasi-steady state assumption for the signal has been used e.g. by Jäger and Luckhaus [59] or by Nagai, Senba, Yoshida [83] for the PKS-model. Here we continue to consider the full characteristic derivative $\delta_v S$. It will turn out that in the parabolic scaling the S_t-term is of lower order and it vanishes for the parabolic limit equation. We assume

$$\mu = \mu(S, \delta_v S). \tag{2.34}$$

We choose a kernel $K(v, v')$ in such a way that the total particle number is preserved. This can be achieved with $K(v, v') = \mu(S, \delta_{v'} S) T(v, v')$ with $\int_V T(v, v') dv = 1$. Then the transport equation for chemosensitive movement reads

$$p_t + v \cdot \nabla p = -\mu(S, \delta_v S)\, p(v) + \int_V \mu(S, \delta_{v'} S)\, T(v, v')\, p(v') dv'. \tag{2.35}$$

Restricted to 1-D with two speeds $\pm s$ the model considered by Hillen and Stevens follows ([55]).

To become more specific and to have an explicit prototype we consider

$$\mu(S, \delta_v S) = \mu_0 (1 - \alpha(S) \delta_v S) \tag{2.36}$$

with some constant $\mu_0 > 0$ and an appropriate function $\alpha(S)$. We will write α instead of $\alpha(S)$ throughout the following calculations. We assume moreover that $T(v, v') = 1/\omega$, then a prototype model for chemosensitive movement reads

$$p_t + v \cdot \nabla p = -\mu_0(1 - \alpha\delta_v S)\, p(v) + \frac{\mu_0}{\omega} \int_V (1 - \alpha\delta_{v'} S)\, p(v')\, dv'. \tag{2.37}$$

2.5.1 A Cattaneo Model for Chemosensitive Movement

Using the notation of the moments m^0 and m^i we can write (2.37) equivalently as

$$p_t + v \cdot \nabla p = -\mu_0 \left(1 - \alpha(S_t + v \cdot \nabla S)\right) p(v) + \frac{\mu_0}{\omega} \left(m^0 - \alpha m^0 S_t - \alpha m^i \partial_i S\right). \tag{2.38}$$

To derive the equations for the first two moments we integrate (2.38) and obtain

$$m_t^0 + \partial_j m^j = 0. \tag{2.39}$$

Multiplication of (2.38) with v^i and integration gives

$$m_t^i + \partial_j m^{ij} = -\mu_0(1 - \alpha S_t) m^i + \mu_0 \alpha\, \partial_j S\, m^{ij}. \tag{2.40}$$

Again with (2.12) the corresponding Cattaneo system for chemosensitive movement reads

$$\begin{aligned} M_t^0 + \partial_j M^j &= 0 \\ M_t^i + \tfrac{s^2}{n} \partial_i M^0 &= -\mu_0(1 - \alpha S_t) M^i + \tfrac{s^2}{n} \mu_0 \alpha\, \partial_i S\, M^0. \end{aligned} \tag{2.41}$$

To obtain a parabolic limit we divide the second equation of (2.41) by μ_0 and consider the limit of

$$\mu_0, s \to \infty, \quad \alpha \to 0, \quad \frac{s^2}{\mu_0 n} \to D < \infty, \quad \mu_0 \alpha \to \chi < \infty.$$

Note that χ depends on S via $\alpha(S)$. We divide the second equation of (2.41) by μ_0 and in the above limit the S_t-term vanishes. Formally the second equation of (2.41) becomes

$$M^i = -D\partial_i M^0 + D\chi(S) M^0 \nabla S. \tag{2.42}$$

Hence the limiting equation is the PKS model (1.5):

$$M_t^0 = D\nabla(\nabla M^0 - \chi(S) M^0 \nabla S).$$

Remark 2.5 *1. The prototype chemotaxis model* (2.37) *leads to the well-known Keller-Segel model in two steps: First closure of the first two moment equations to get the Cattaneo approximation* (2.41) *and then passing to the parabolic limit for large speeds and large turning rates.*

2. *As shown by Patlak [92] or Alt [4] and also in [52] one can directly scale the transport equation to derive the parabolic limit (1.5) (see Chapter 1). If we use the expression for M^i in (2.42) to calculate the minimizer u given in (2.11) we arrive at an ad hoc assumption which was made by Patlak or Alt. In the framework of moment closure the assumption of Patlak and Alt can be justified* a posteriori.

2.5.2 A Chemotaxis Model with Density Control

In the last Chapter 5 a parabolic chemotaxis model with density control is introduced. The density control leads to the effect that at high population densities the chemotaxis is turned off and pure diffusion dominates. Solutions exist globally and now blow-up occurs. The model in Chapter 5 can be constructed from a transport equation via a corresponding Cattaneo approximation. We consider a turning rate of the form

$$\mu(S, \delta_v S) := \mu_0 \left(1 - \frac{n}{s^2}\beta(m^0)\chi(S)\delta_v S\right),$$

where $\beta(m^0)$ is a density dependent sensitivity. The function β is assumed to have a zero at some $\bar{m}^0 > 0$ and $\beta(m) > 0$ for $0 < m < m^0$ (see the details in Chapter 5). With turning kernel $T(v, v') := \omega^{-1}\mu(S, \delta_{v'} S)$ the moment closure procedure leads to a *Cattaneo model for chemosensitive movement with density control*

$$\begin{aligned} M^0_t + \partial_j M^j &= 0 \\ M^i_t + \tfrac{s^2}{n}\partial_i M^0 &= -\mu_0 \left(1 - \tfrac{n}{s^2}\beta(M^0)\chi(S)S_t\right) M^i + \beta(M^0)\chi(S)\, M^0\, \partial_i S. \end{aligned} \tag{2.43}$$

The parabolic limit of this equation is the model which will be studied in Chapter 5 in detail.

2.6 Discussion

Since the closure problem is well known in transport theory there are a large number of heuristic arguments based on logical insight or scaling properties to close the first two moment equations for m^0 and m^i. Here minimizing of an appropriate energy motivates the choice of the approximation to the second moment $m^{ij}(p)$. This method is directly generalizable to equations for arbitrarily high moments $(m^0, m^i, \ldots, m^{i_1 \ldots i_k})$. We will present this in the following chapter.

The Cattaneo approximation developed here gives a new model for applications which can be used to understand the behavior of biological systems for short times without using the full transport equation. It is well known that at large times the transport equation and the Cattaneo system behave as their parabolic limit. This explains the

success of reaction diffusion equations in mathematical biology. However, there is no doubt that for small or intermediate values of time the diffusion model is inaccurate. For those time ranges the Cattaneo approximation helps to understand the dynamic behavior of the biological system. The relevant parameters of the Cattaneo approximation can be estimated directly from experiments.

2.6.1 Boundary Conditions

The use of this method for bounded domains with boundary conditions has to be considered carefully. It is not obvious, how boundary conditions for transport models translate into boundary conditions of the Cattaneo approximation. We will give two examples for a bounded domain $\Omega \in \mathbb{R}^n$ with smooth boundary $\partial\Omega$. For $x \in \partial\Omega$ we denote the outer normal by $\eta(x)$. We assume V is symmetric with respect to $SO(n)$ and at each $x \in \partial\Omega$ we split V into inward and outward pointing velocities:

$$V^-(x) := \{v \in V : \ v_i \eta^i(x) < 0\}, \quad V^+(x) := \{v \in V : \ v_i \eta^i(x) \geq 0\}.$$

a) Dirichlet boundary conditions: The homogeneous Dirichlet boundary condition for the transport equation (2.3) reads

$$p(t, x, v) = 0, \quad \forall\, x \in \partial\Omega,\, v \in V^-(x).$$

We stipulate that the energy minimizer $u_{\min}$ constructed in (2.11) satisfies the same boundary condition, then

$$m^0(t, x) + \frac{n}{s^2} v_i m^i(t, x) = 0, \quad \forall\, x \in \partial\Omega,\, v \in V^-(x).$$

We integrate this boundary condition along V^- and obtain

$$m^0 = \frac{n}{s^2} \frac{2\kappa_V}{\omega} \eta_i m^i, \quad \text{with} \quad \kappa_V := \int_{\{v \in V : v^1 \geq 0\}} v\, dv \cdot e_1, \tag{2.44}$$

where e_1 denotes the first unit vector in an orthonormal basis of $\mathbb{R}^n$ and $\omega = |V|$ as usual. Hence the Dirichlet boundary conditions of the Cattaneo approximation are given by

$$M^0 = \frac{n}{s^2} \frac{2\kappa_V}{\omega} \eta_i M^i. \tag{2.45}$$

This condition has been suggested by Hadeler [46] and it has been used in [51] for a nonlinear Cattaneo system. It is remarkable that the Dirichlet condition appears in form of a Robin condition for the Cattaneo system. Note that in the parabolic scaling of $s \to \infty, \mu \to \infty$ with $s^2/\mu < \infty$ the homogeneous Dirichlet boundary condition $M^0 = 0$ follows.

b) Neumann boundary conditions: General reflection boundary conditions for the transport model (2.3) have the following form:

$$p(t,x,v) = \int_{V^+} B(v,v')p(t,x,v')dv', \quad \forall\, v \in V^-,$$

with a nonnegative symmetric kernel B with $\int_{V^-} B(v,v')dv = \int_{V^+} B(v,v')dv' = 1$. We assume the same boundary condition to hold for the minimizer $u_{\min}$, which leads to

$$\frac{1}{\omega}\left(m^0 + \frac{n}{s^2}v_i m^i\right) = \int_{V^+} B(v,v')\frac{1}{\omega}\left(m^0 + \frac{n}{s^2}v_i' m^i\right)dv', \quad \forall\, v \in V^-,$$

hence

$$v_i m^i = \int_{V^+} B(v,v')v_i'\, dv'\, m^i, \quad \forall\, v \in V^-. \tag{2.46}$$

In case of pure physical reflection an outgoing velocity $v' \in V^+$ is reflected into the inward going velocity $v = r(v') := v' - 2(\eta_i v'^i)\eta$. In this case the kernel B is given by

$$B(v,v') = \delta_0(v - r(v')),\ v' \in V^+, v \in V^-.$$

Condition (2.46) reduces to

$$v_i m^i = \left(v_i - 2(\eta_i v^i)\eta_i\right) m^i, \quad \forall\, v \in V^-$$

Since on V^- we have $\eta_i v^i \neq 0$ it follows that

$$\eta_i m^i = 0, \quad \text{on} \quad \partial\Omega.$$

Hence the corresponding Neumann boundary condition for the Cattaneo approximation reads

$$\eta_i M^i = 0. \tag{2.47}$$

Also this boundary condition has been suggested in Hadelers article [46].

2.6.2 Memory Effects

Gurtin and Pipkin ([44]) show that the Cattaneo system appears if the medium under consideration remembers its history with exponentially decay backwards in time. This interpretation can be extended to the following fact:

Lemma 2.8 *The Cattaneo system* (2.13) *is the minimizing flux of the exponentially weighted Dirichlet integral*

$$J(u) := \frac{D}{2\tau}\int_0^t \int_\Omega e^{-\frac{1}{\tau}(t-s)}\,|\nabla u|^2 dx ds.$$

Proof: The minimizing flux of J is given by the solution of

$$u_t = -\nabla j$$

with

$$j = \frac{D}{\tau} \int_0^t e^{-\frac{1}{\tau}(t-s)} \nabla u \, ds.$$

Hence j satisfies the Cattaneo law:

$$\tau j_t = -j + D\nabla u.$$

□

2.6.3 Numerical Simulations

For illustration purposes we show some numerical simulations of the Cattaneo model for chemosensitive movement with density control (2.43), which are part of ongoing research. The simulations in $1 - D$ are related to the model (1.10) which has been studied in [55] and [54].

In Figures 1 and 2 we consider an interval of length $l = 1$ and we assume that the species move with constant speed $\gamma = 0.2$. The turning rates $\mu^{\pm}$ are density dependent as discussed in Section 2.5.2:

$$\mu^{\pm}(S, \nabla S, u^+ + u^-) = \left(\frac{\gamma^2}{2D} \mp \beta(u^+ + u^-)\chi(S)\nabla S \right)^+,$$

with effective diffusion coefficient $D = 0.036$. The super-index $+$ indicates to take the positive part. The density-sensitivity function β and the chemotactic sensitivity χ are given as $\beta(u) = 1 - u$ and $\chi(S) = 1/(1 + S)$. The parameters for the signal equation in (1.10) are $\tau = 1, \alpha = 4{\cdot}10^{-6}$ and the reproduction term is $f(S, u^+ + u^-) = -aS + u^+ + u^-$. For simulations we use a Godunov-scheme (see [55] and [54]). In Fig.1 we show the long time behavior in the case of not degrading signal ($a = 0$), whereas in Fig.2 we assume that there is a small decay rate of $a = 0.001$. The initial conditions in both runs are random perturbations of 0.3% of the constant level $u^{\pm} = 0.3$ and S is assumed to be initially constant at a low level of $S_0 = 0.5$.

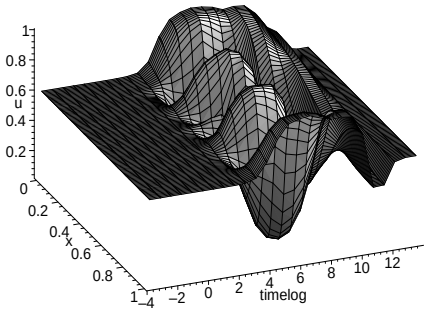

Fig.1: Long-time evolution of the total particle density $u = u^+ + u^-$ in a time-logarithmic plot without degradation of S.

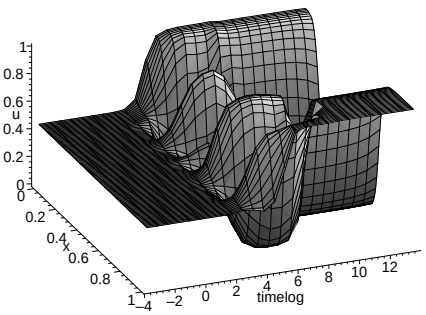

Fig.2: Long-time evolution of u with degradation of S.

The simulation in Fig.1 shows a transient development of patterns, which eventually decays to the homogeneous steady state. This is in good agreement with observations on bacteria as shown by Tyson *et al.* [114]. The second simulation (with decay of S) shows the same initial patterns, which eventually coarsen, and a global pattern remains. The transient behavior in Fig.1 can be explained by a linear stability analysis of homogeneous solutions. We carry this out for $a \neq 0$ (otherwise we would not have a non-zero stationary equilibrium for S). The calculations are straightforward and it turns out that a stationary homogeneous solution $(\bar{u}^+, \bar{u}^-, \bar{S})$ with $\bar{u}^+ = \bar{u}^-$ is linearly unstable, if

$$\gamma(\pi^2\alpha + a) < 2\bar{u}^+\beta(2\bar{u}^+)\chi(\bar{S}). \tag{2.48}$$

This condition can be used to understand the transient behavior for $a = 0$. The chemotactic sensitivity $\chi(S)$ has been chosen to converge to 0 as $S \to \infty$. Hence in the beginning of the simulation of Fig.1 the homogeneous solution is linearly unstable, whereas later, when S increases drastically, the chemotaxis term fades out, the diffusion dominates and the homogeneous steady state becomes linearly stable.

In two space dimensions we developed a numerical scheme for the Cattaneo model for chemosensitive movement (2.43) in collaboration with Y. Dolak. The algorithm bases on a Lax-Wendroff scheme (the details can be found in [30]). Here we show a typical time evolution for randomly chosen initial data with constant χ and $\beta = 1 - u$ (for exact parameter values see [30]):

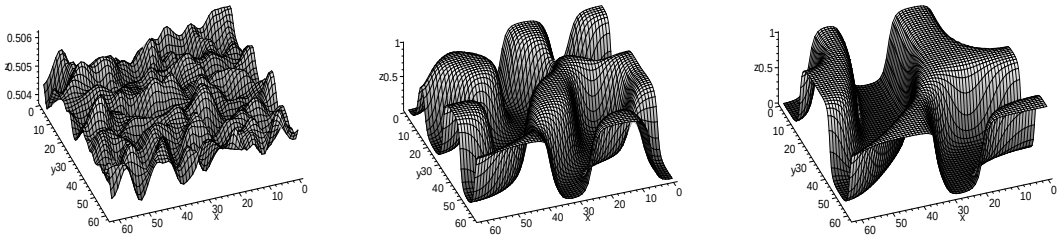

Fig.3: Typical time evolution. Particle density shown for $t = 1, 150$ and 500.

One clearly observes merging local maxima and coarsening of the pattern. The dynamics of these patterns and the underlying bifurcations have to be studied further.

3 Moment Closure

In this chapter we carry out the moment closure for an arbitrary finite number of moments. We generalize the H-Theorem of the previous section for kernel T which satisfy the basic assumptions (T1)-(T4) given earlier (Theorem 3.6). With use of a variational principle we show that the closure can be obtained by minimizing the $L^2(V)$-norm with constraints. The Cattaneo closure is a special case for two moments and we explicitly calculate the three moment closure for two space dimensions. It turns out that the steady states of the two and three moment systems are determined by the steady states of a corresponding diffusion problem.

3.1 Notations and Basic Assumptions

We consider a compact set of velocities $V \subset \mathbb{R}^n$. In some cases we assume symmetry of V but then we will state it explicitely. On $V \times V$ we consider distribution kernels $T(v, v')$ with the properties **(T1)-(T4)** defined in Section 1.4.1. Moreover we assume that

(T5) For each $v' \in V$ there exists a moment generating function for $T(., v')$.

Assumption (T5) ensures that the v-moments of the kernel T are bounded and that the distribution $T(., v')$ can be generated from its moments (see Billingsley [15]).

We define the velocity moments of a distribution function $p(t, x, v)$ as

$$\begin{aligned} m^0(t,x) &= \int p(t,x,v)dv \\ m^i(t,x) &= \int v^i p(t,x,v)dv, \quad i \in \{1,\dots,n\} \\ &\vdots \\ m^{i_1\dots i_k}(t,x) &= \int v^{i_1}\cdots v^{i_k} p(t,x,v)dv, \quad k \in \mathbb{N}, \quad (i_1,\dots,i_k) \in \{1,\dots,n\}^k. \end{aligned}$$

We use tensor notation, which means that $m^{i_1\dots i_k}$ denotes the $(i_1, \dots, i_k)$-component of a k-tensor. Since we are working in Euclidean spaces $\mathbb{R}^n$, we use both sub and super

indices and we stress the summation convention, which means that we always consider a sum on repeated indices, e.g.

$$\Lambda_{i_1\dots i_k} m^{i_1\dots i_k} = \sum_{(i_1,\dots,i_k)\in\{1,\dots,n\}^k} \Lambda_{i_1\dots i_k} m^{i_1\dots i_k}.$$

For fixed $k \in \mathbb{N}$ we denote the tuple of all tensor indices for tensors of lower or equal order than k by

$$\begin{aligned} \alpha_k \;:=\; & (0,1,2,\dots,n,(1,1),(1,2),\dots,(n,n),\dots, \\ & \dots,(\underbrace{1,\dots,1}_{k\text{ times}}),\dots,(\underbrace{n,\dots,n}_{k\text{ times}})). \end{aligned} \tag{3.1}$$

The index-vector α_k has the length

$$|\alpha_k| = \sum_{l=0}^{k} n^k =: N_k.$$

Then m^{α_k} denotes a vector of length N_k of all moments of order $\le k$:

$$\begin{aligned} m^{\alpha_k} \;:=\; & (m^0, m^1, m^2, \dots, m^n, m^{11}, m^{12}, \dots, m^{nn}, \dots, \\ & \dots, m^{1\dots1}, \dots, m^{n\dots n}) \,. \end{aligned} \tag{3.2}$$

We use this notation for products of velocity components as well. If we define $v^{i_1\dots i_l} = v^{i_1}\cdots v^{i_l}$ then it makes sense to write v^{α_k}.

3.1.1 The Velocity Tensors

For later use we define

$$\bar{v}^{i_1\dots i_k} := \int v^{i_1}\cdots v^{i_k} dv$$

and now we consider $V = sS^{n-1}$. It is clear that $\bar{v}^0 = \int dv = \omega = \omega_0 s^{n-1}$, with $\omega_0 = |S^{n-1}|$, and that $\bar{v}^i = \int v^i dv = 0$. Moreover we give explicit formulas for the velocity tensors $\bar{v}^{i_1\dots i_k}$ for odd and even order.

Lemma 3.1 *1. If $k \in \mathbb{N}$ is odd, then*

$$\bar{v}^{i_1\dots i_k} = 0, \quad \textit{for all} \quad i_1,\dots,i_k \in \{1,\dots,n\}.$$

2. If $k \in \mathbb{N}$ is even, then there is a constant $c_k > 0$ such that

$$\bar{v}^{i_1\dots i_k} = s^{k+n-1} c_k \left(\sum_{\mathcal{P}(i_1,\dots,i_k)} \delta^{i_{j_1} i_{j_2}} \dots \delta^{i_{j_{k-1}} i_{j_k}} \right), \tag{3.3}$$

where the set of all pairs of indices out of $(i_1, \ldots, i_k)$ *is defined as*

$$\begin{aligned}\mathcal{P}(i_1, \ldots, i_k) \;:=\; \Big\{ \Big((i_{j_1}, i_{j_2}), \ldots, (i_{j_{k-1}}, i_{j_k})\Big) :\\ \{j_1, j_2\}, \ldots, \{j_{k-1}, j_k\} \in \{1, \ldots, k\}^2,\\ \textit{with } \{j_1, \ldots, j_k\} = \{1, \ldots, k\} \Big\}.\end{aligned}$$

The constants c_k *are given by*

$$c_0 = \omega_0, \quad c_2 = \frac{\omega_0}{n}, \quad c_k = \frac{c_{k-2}}{k-2+n}, \quad \textit{for } \; k \geq 4.$$

Proof: 1.: Let $(i_1, \ldots, i_k) \in \{1, \ldots, n\}^k$. In case of k odd we split V into V^+ and V^- defined by

$$V^+ := \{v \in V : v^{i_1} > 0\}, \qquad V^- := \{v \in V : v^{i_1} < 0\}.$$

Then for each $v \in V^+$ we have $-v \in V^-$. Since the set of $\{v^{i_1} = 0\} \subset V$ is a set of measure zero we get

$$\begin{aligned}\bar{v}^{i_1 \ldots i_k} &= \int_{V^+} v^{i_1} \cdots v^{i_k} dv + \int_{V^-} v^{i_1} \cdots v^{i_k} dv\\ &= \int_{V^-} (-1)^k v^{i_1} \cdots v^{i_k} dv + \int_{V^-} v^{i_1} \cdots v^{i_k} dv\\ &= 0,\end{aligned}$$

since k is assumed odd.

2.: In the case of k even we use an induction argument and the divergence theorem on the ball $B_s(0)$ in $\mathbb{R}^n$.
$k = 0$: $\bar{v}^0 = \omega_0 s^{n-1}$.
$k = 2$: For any two vectors $a^1, a^2 \in \mathbb{R}^n$ we obtain

$$\begin{aligned}a^1_{i_1} a^2_{i_2} \bar{v}^{i_1 i_2} &= \int_V (a^1_{i_1} v^{i_1} a^2_{i_2} v^{i_2}) dv\\ &= s \int_V \frac{v_{i_1}}{|v|} (a^{1,i_1} a^2_{i_2} v^{i_2}) dv\\ &= s \int_{B_s(0)} \partial_{v_{i_1}} (a^{1,i_1} a^2_{i_2} v^{i_2}) dv\\ &= s \int_{B_s(0)} dv \; a^{1,i_1} a^2_{i_2} \delta^{i_2}_{i_1}\end{aligned}$$

Now we have

$$\begin{aligned}|B_s(0)| &= s^n |B_1(0)| = \frac{s^n}{n} \int_{B_1(0)} \partial_{v_i} v^i dv = \frac{s^n}{n} \int_{S^{n-1}} \sigma_i \sigma^i d\sigma\\ &= \frac{s^n}{n} \omega_0.\end{aligned}$$

Then we get

$$a^1_{i_1} a^2_{i_2} \bar{v}^{i_1 i_2} = s^{n+1} \frac{\omega_0}{n} a^1_{i_1} a^2_{i_2} \delta^{i_1 i_2},$$

which shows that

$$\bar{v}^{i_1 i_2} = s^{n+1} \frac{\omega_0}{n} \delta^{i_1 i_2}. \tag{3.4}$$

Since in the case $k = 2$ the set of pairs $\mathcal{P}(i_1, i_2)$ for $i_1, i_2 \in \{1, \ldots, n\}$ reduces to

$$\begin{aligned} \mathcal{P}(i_1, i_2) &= \left\{ (i_{j_1}, i_{j_2}) : \{j_1, j_2\} \in \{1, 2\}^2 \text{ with } \{j_1, j_2\} = \{1, 2\} \right\} \\ &= \{(i_1, i_2)\}, \end{aligned}$$

we obtain

$$\sum_{\mathcal{P}(i_1, i_2)} \delta^{i_{j_1} i_{j_2}} = \delta^{i_1, i_2}.$$

and (3.4) is (3.3) for $k = 2$.

$k - 2 \to k$: Assume (3.3) holds for $k - 2$. For any vectors $a^1, \ldots, a^k \in \mathbb{R}^n$ we have

$$\begin{aligned} a^1_{i_1} \ldots a^k_{i_k} \bar{v}^{i_1 \ldots i_k} &= \int_V (a^1_{i_1} v^{i_1} \ldots a^k_{i_k} v^{i_k}) dv \\ &= s \int_V \frac{v_{i_1}}{|v|} a^{1, i_1} \left(a^2_{i_2} v^{i_2} \ldots a^k_{i_k} v^{i_k} \right) dv \\ &= s \int_{B_s(0)} \partial_{v_{i_1}} a^{1, i_1} \left(\prod_{l=2}^{k} a^l_{i_l} v^{i_l} \right) dv \\ &= s \int_{B_s(0)} dv \; a^{1, i_1} \sum_{r=2}^{k} a^r_{i_r} \delta^{i_r}_{i_1} \left(\prod_{l=2, l \neq r}^{k} a^l_{i_l} v^{i_l} \right) dv \\ &= s a^{1, i_1} \sum_{r=2}^{k} a^r_{i_r} \delta^{i_r}_{i_1} \int_{B_s(0)} \prod_{l=2, l \neq r}^{k} a^l_{i_l} v^{i_l} \; dv. \end{aligned} \tag{3.5}$$

To exclude one entry from a tuple we will now use the notation for $l \leq r \leq k, l < k$

$$(i_l, \ldots, i_k)_{\setminus \{r\}} := \begin{cases} (i_{l+1}, \ldots, i_k), & \text{if } r = l, \\ (i_l, \ldots, i_{r-1}, i_{r+1}, \ldots i_k) & \text{if } l < r < k, \\ (i_l, \ldots, i_{k-1}), & \text{if } r = k. \end{cases}$$

With use of this notation we study the integral term in (3.5) separately. We will use the assumption that (3.3) holds for $k - 2$.

$$\int_{B_s(0)} \prod_{l=2, l \neq r}^{k} a^l_{i_l} v^{i_l} \; dv$$

$$
\begin{aligned}
&= \int_0^s \int_{\sigma S^{n-1}} \left(\prod_{l=2, l\neq r}^{k} a_{i_l}^l v^{i_l} \right) dv d\sigma \\
&= \int_0^s \sigma^{k-2+n-1} c_{k-2} \left(a_{i_2}^2 \dots a_{i_k}^k \right)_{\setminus\{r\}} \sum_{\mathcal{P}((i_1,\dots,i_k)_{\setminus\{r\}})} \delta^{i_{j_1} i_{j_2}} \dots \delta^{i_{j_{k-3}} i_{j_{k-2}}} \, d\sigma \\
&= \frac{s^{k-2+n}}{k-2+n} c_{k-2} \left(a_{i_2}^2 \dots a_{i_k}^k \right)_{\setminus\{r\}} \sum_{\mathcal{P}((i_1,\dots,i_k)_{\setminus\{r\}})} \delta^{i_{j_1} i_{j_2}} \dots \delta^{i_{j_{k-3}} i_{j_{k-2}}}.
\end{aligned}
$$

Using this equality in (3.5) we finally get

$$
\begin{aligned}
& a_{i_1}^1 \dots a_{i_k}^k \, \bar{v}^{i_1 \dots i_k} \\
= \; & s^{k+n-1} \frac{c_{k-2}}{k-2+n} a^{1,i_1} \sum_{r=2}^{k} a_{i_r}^r \delta_{i_1}^{i_r} \left(\left(a_{i_2}^2 \dots a_{i_k}^k \right)_{\setminus\{r\}} \sum_{\mathcal{P}((i_1,\dots,i_k)_{\setminus\{r\}})} \delta^{i_{j_1} i_{j_2}} \dots \delta^{i_{j_{k-3}} i_{j_{k-2}}} \right) \\
= \; & s^{k+n-1} c_k \left(\sum_{\mathcal{P}(i_1,\dots,i_k)} \delta^{i_{j_1} i_{j_2}} \dots \delta^{i_{j_{k-1}} i_{j_k}} \right).
\end{aligned}
$$

□

Example for $\mathcal{P}(i_1, \dots, i_4)$:

$$
\begin{aligned}
\mathcal{P}(i_1, \dots, i_4) &= \Big\{ \Big((i_{j_1}, i_{j_2}), (i_{j_3}, i_{j_4}) \Big) : \\
&\qquad \{j_1, j_2\}, \{j_3, j_4\} \in \{1,2,3,4\}^2, \text{ with } \{j_1, j_2, j_3, j_4\} = \{1,2,3,4\} \Big\} \\
&= \Big\{ \Big((i_1, i_2), (i_3, i_4) \Big), \Big((i_1, i_3), (i_2, i_4) \Big), \Big((i_1, i_4), (i_2, i_3) \Big) \Big\}. \qquad (3.6)
\end{aligned}
$$

In case of $n = 2$ with polar representation $v = s(\cos\theta, \sin\theta)$ we explicitly calculate, e.g.

$$
\bar{v}^{1111} = \int_0^{2\pi} cos^4\theta d\theta = 3\frac{\pi}{4}, \quad \bar{v}^{1122} = \int_0^{2\pi} cos^2\theta \sin^2\theta d\theta = \frac{\pi}{4},
$$

$$
\bar{v}^{1222} = \int_0^{2\pi} cos\theta \sin^3\theta d\theta = 0.
$$

3.1.2 Symmetry of the Moments and the Velocity Tensors

Lemma 3.2 *The tensors $m^{i_1 \dots i_k}$, and $\bar{v}^{i_1 \dots i_k}$ are invariant with respect to exchange of two indices.*

This follows directly from the definitions of $m^{i_1 \dots i_k}$, and $\bar{v}^{i_1 \dots i_k}$. For later use we will introduce an operator for change of two indices. For $1 \leq r \leq l \leq k$, $1 < k$ we define

$$
\eta_{r,l}(i_1, \dots, i_r, \dots, i_l, \dots, i_k) := (i_1, \dots, i_l, \dots, i_r, \dots, i_k).
$$

And we allow $\eta_{r,l}$ to act on tensors and vectors as well, i.e.

$$
\eta_{r,l} a^{i_1 \dots i_k} := a^{\eta_{r,l}(i_1 \dots i_k)}, \qquad \text{etc..}
$$

3.2 Moment Closure for the General Linear Model

The general linear transport equation for a particle density $p(t,x,v)$ at time $t \geq 0$ at spatial position $x \in \mathbb{R}^n$ and with velocity $v \in V$ reads

$$\begin{aligned} p_t(t,x,v) + v_j \partial^j p(t,x,v) &= -\mu p(t,x,v) + \mu \int_V T(v,v') p(t,x,v') dv' \\ &= -\mu(I - \mathcal{T})p \\ &= \mathcal{L}_0 p. \end{aligned} \tag{3.7}$$

Since we assume (T1)-(T5) for the kernel T, the turning operator $\mathcal{L}_0$ has the properties as summarized in Proposition 1.1.

3.2.1 Moment Equations

We derive the system of moment equations by multiplying with combinations of $v^{i_1} \cdots v^{i_k}$ and integrate along V: Integration of (3.7) leads, with $\int T(v,v')dv = 1$, to a conservation law for the particle number:

$$m_t^0 + \partial_j m^j = 0. \tag{3.8}$$

For higher order moment equations we use the following abbreviation. Let the *T-modulated moments of $p(t,x,v)$* be denoted by

$$w^{i_1 \ldots i_k} := \int \int v^{i_1} \cdots v^{i_k} T(v,v') p(t,x,v') dv' dv. \tag{3.9}$$

Using this definition, multiplication of equation (3.7) by v^i and integration leads to

$$\begin{aligned} m_t^i + \partial_j m^{ij} &= -\mu m^i + \mu \int \int v^i T(v,v') dv \; p(t,x,v') dv' \\ &= \mu(w^i - m^i). \end{aligned} \tag{3.10}$$

and analogously we get for the l-moment, $l \leq k$:

$$m^{i_1 \ldots i_l} + \partial_j m^{i_1 \ldots i_l j} = \mu(w^{i_1 \ldots i_l} - m^{i_1 \ldots i_l}). \tag{3.11}$$

Finally, for all $k \in \mathbb{N}$ we have the system of moments which consists of equations (3.8), (3.10) and (3.11) for all $l \leq k$. In the highest order equation for $m^{i_1 \ldots i_k}$ the divergence of the next higher moment $m^{i_1 \ldots i_k j}$ appears, hence the system is not closed. If, moreover, the T-modulated moments depend on moments of p of order $> k$, then these higher moments appear as well. We will show that in some important cases the T-modulated moments of order k are linear functions of p-moments of order less or equal k (Lemma 3.5). We give two examples first:

Example 3.3 *1. Assume $T(v,v') = 1/\omega$ describes uniform choice of any direction. Then*

$$w^{i_1\dots i_k} = \frac{\bar{v}^{i_1\dots i_k}}{\omega}\, m^0.$$

2. Assume, for example, that $T(v,v') = \delta(v-v')$ (which is not included in our general hypotheses, but illustrates possible dependencies). Then

$$w^{i_1\dots i_k} = m^{i_1\dots i_k}.$$

Since we aim to close the moment system (3.8), (3.10) and (3.11) with respect to the k-th order moment we distinguish two cases:

Definition 3.4 *The system of moments (3.8), (3.10) and (3.11) is called l-quasi closed for some $l \in \mathbb{N}, 1 \le l \le k$, if all T-modulated moments of order less or equal l depend on p only via the moments of p of order less or equal l, but not higher, i.e.*

$$w^{\alpha_l} = w^{\alpha_l}(m^{\alpha_l}).$$

The moment systems in both examples in Example 3.3 are l-quasi closed for each $l \in \mathbb{N}, l \ge 1$.

If the moment system is not k-quasi closed then we have to use the minimization procedure below to find good approximations for w^{α_k} as well.

Lemma 3.5 *1. If $w^{i_1\dots i_k}$ depends on some moments of p it is a linear function of these.*

2. System (3.8), (3.10) and (3.11) is l-quasi closed if and only if the moments of $T(v,v')$ are linear in v'^{α_l}, i.e. for each $v \in V$ there exists a linear mapping $R(v) : \mathbb{R}^{N_l} \to \mathbb{R}^{N_l}$ such that

$$\int v^{\alpha_k} T(v,v')dv = \left(R(v)v'^{\alpha_k}\right)_{\alpha_k}. \tag{3.12}$$

Proof:

1. We write

$$w^{i_1\dots i_l} = \int Q^{i_1\dots i_l}(v')p(v')dv', \quad \text{with} \quad Q^{i_1\dots i_l}(v') = \int v^{i_1}\cdots v^{i_l}T(v,v')dv'.$$

Now assume $w^{\alpha_l} = w^{\alpha_l}(m^{\alpha_j})$ for some $j \in \mathbb{N}$. Then for two functions $p, q \in L^2(V)$ and $c_1 \in \mathbb{R}$ we have

$$\begin{aligned} w^{\alpha_k}\left(c_1 m_p^{\alpha_j} + m_q^{\alpha_j}\right) &= \int Q^{\alpha_l}(v')\left(c_1 p(v') + q(v')\right)dv' \\ &= c_1 w^{\alpha_l}\left(m_p^{\alpha_j}\right) + w^{\alpha_l}\left(m_q^{\alpha_j}\right). \end{aligned}$$

2. We assume that the moment system is l quasi closed. Since w^{α_l} is a linear function in m^{α_l}, we can find a linear map $R(v) : \mathbb{R}^{N_l} \to \mathbb{R}^{N_l}$ with

$$w^{\alpha_l} = (R(v)m^{\alpha_l})_{\alpha_l} = \int (Rv'^{\alpha_l} p(v'))_{\alpha_l} dv'. \tag{3.13}$$

On the other hand

$$w^{\alpha_l} = \int\int v^{\alpha_l} T(v, v') p(v') dv',$$

which equals (3.13) if and only if

$$\int \left[(Rv'^{\alpha_l})_{\alpha_l} - \int v^{\alpha_l} T(v, v') dv \right] p(v') dv' = 0, \quad \text{for all} \quad p \in L^2(V).$$

This is true only if

$$(Rv'^{\alpha_l})_{\alpha_l} = \int v^{\alpha_l} T(v, v') dv.$$

□

Besides the examples shown above we get a k-quasi closed moment system if T has the form

$$T(v, v') = a_0(v) + a_i(v)v'^i + \ldots + a_{i_1 \ldots i_l} v'^{i_1} \ldots v'^{i_l} \tag{3.14}$$

for some $l \leq k$ and bounded integrable coefficients $a_{\alpha_k}(v)$.

Note. If a system of moments is l-quasi closed it needs not to be k-quasi closed for $k > l$.

3.2.2 Minimizing the L^2-Norm

First we show that the negative L^2-norm is an entropy for the general transport model (3.7). We denote the $L^2(V)$-norm by

$$E(u) := \int \frac{u^2}{2} dv$$

and the corresponding flux by

$$F(u) := \int v \frac{u^2}{2} dv.$$

Theorem 3.6 (H-Theorem) *Assume* (T1)-(T4). *Solutions* $p(t, x, v) \in \mathcal{X}$ *(* $\mathcal{X}$ *defined in (2.5)) of the linear transport equation* (1.1) *satisfy*

$$\frac{d}{dt} E(p) + \partial_j F^j(p) \leq 0.$$

Proof:

$$\begin{aligned}\frac{d}{dt}E(p) &= \int p(-v^j\partial_j p + \mathcal{L}_0 p)dv \\ &= -\partial_j F^j(p) + \int p\mathcal{L}_0 p\, dv.\end{aligned}$$

In Proposition 1.1 it has been shown that on $\langle 1\rangle^\perp$ the operator $\mathcal{L}_0$ satisfies

$$\int p\mathcal{L}_0 p\, dv \le -\mu_2\|p\|_2^2.$$

For $p(t,x,.) \in \langle 1\rangle$ we have $\int p\mathcal{L}_0 p\, dv = 0$. Hence the entropy estimate follows. □

For now we fix (t,x) as a parameter and consider the dependence on v. For functions in $L^2(V)$ we aim to minimize the functional $E(u)$ with constraints of given moments m^{α_k} of order less or equal k:

$$G(u) = 0, \qquad \text{with} \quad G(u) = \int v^{\alpha_k}u(v)dv - m^{\alpha_k}.$$

Note that α_k defines a multi-index such that $G : L^2(V) \to \mathbb{R}^{N_k}$.

For minimization of E under the constraint $G = 0$ we use the framework of Lagrangian multipliers as presented e.g. in Zeidler [117]. If u_0 is a minimizer, then

$$\begin{aligned}E'(u_0) : L^2(V) \to \mathbb{R} : &\qquad h \mapsto \int u_0(v)h(v)dv \\ G'(u_0) : L^2(V) \to \mathbb{R}^{N_k} : &\qquad h \mapsto \int v^{\alpha_k}h(v)dv.\end{aligned}$$

Theorem 3.7 *Assume u_{min} is a minimizer, then there exist Lagrangian multipliers $\Lambda_{\alpha_k} \in \mathbb{R}^{N_k}$ such that all $\phi \in L^2(V)$ satisfy*

$$F'(u_{min})\phi + \Lambda_{\alpha_k}G'(u_{min})\phi = 0,$$

where the summation convention is applied for $\Lambda_{\alpha_k}G'(u_{min})\phi$, since $G'(u_{min})\phi \in \mathbb{R}^{N_k}$.

Proof: For the existence of Lagrangian multipliers we have to check two conditions (see Zeidler [117])

(i) For each $h \in L^2(V)$ with $G'(u_{\min})h = 0$ there exists a curve $\tilde{u}(s)$ such that $\tilde{u}'(0) = h$ and $\tilde{u}$ is admissible, which means that $\tilde{u}$ is differentiable at $s = 0$ and $G(u(s)) = 0$ for $s \in (-\varepsilon, \varepsilon)$ for some $\varepsilon > 0$.

(ii) The range $R(G'(u_{\min}))$ is closed.

We first check (i): Consider $h \in L^2(V)$ with $G'(u_{\min})h = 0$. Then

$$\int v^{\alpha_k} h(v) dv = 0^{\alpha_k}, \tag{3.15}$$

which means that the first k moments of h vanish identically (here 0^{α_k} denotes the zero of $\mathbb{R}^{N_k}$.) We define a curve

$$\tilde{u}(v,s) := p(v) + h(v)s$$

which satisfies

$$\frac{\partial}{\partial s}\tilde{u}(v,0) = h(v)$$

and

$$\begin{aligned} G(\tilde{u}(v,s)) &= \int v^{\alpha_k} p(v) dv + \int v^{\alpha_k} h(v) dv \; s - m^{\alpha_k} \\ &= 0^{\alpha_k}, \end{aligned}$$

with use of (3.15). Then $\tilde{u}(v,s)$ is admissible, i.e. It is tangential to relative minima of the functional E. Then indeed for each $h \in L^2(V)$ with $G'(u_{\min})h = 0$ there is an admissible curve $\tilde{u}$ and condition (i) is satisfied.
Condition (ii) is immediate in this case. Since $G'(u_{\min})$ is a linear mapping into a finite dimensional space, its range is closed. □

From Theorem 3.7 it follows that for all $\phi \in L^2(V)$ we get

$$\int u_{\min}(v)\phi(v) dv + \Lambda_{\alpha_k} \int v^{\alpha_k} \phi(v) \; dv = 0.$$

Hence the integrand vanishes pointwise and the minimizer satisfies:

$$u_{\min} = -\Lambda_{\alpha_k} \bar{v}^{\alpha_k}. \tag{3.16}$$

The first k moments of the minimizer $u_{\min}$ are given by the constraints $G(u_{\min}) = 0$, hence we obtain for $l \leq k$ $(i_1, \ldots, i_l) \in \{1, \ldots, n\}^l$

$$m^{i_1 \ldots i_l} = -\int v^{i_1} \cdots v^{i_l} \Lambda_{\alpha_k} \bar{v}^{\alpha_k} \, dv. \tag{3.17}$$

This is a linear system for the Lagrangian multiplier Λ_{α_k}. Since from Theorem 3.7 we know that this multiplier exists it must be a linear function of the first k moments. Hence there is a $N_k \times N_k$-matrix $\mathcal{B}$ with

$$\Lambda_{\alpha_k} = \left(\mathcal{B} m^{\alpha_k}\right)_{\alpha_k}. \tag{3.18}$$

With use of the notion of the velocity tensor $\bar{v}^{i_1\dots i_k}$ introduced above we can write the linear system (3.17) in explicit form.

$$\begin{aligned} m^0 &= -\Lambda_0\bar{v}^0 - \Lambda_j\bar{v}^j - \dots - \Lambda_{j_1\dots j_k}\bar{v}^{j_1\dots j_k} \\ m^i &= -\Lambda_0\bar{v}^i - \Lambda_j\bar{v}^{ij} - \dots - \Lambda_{j_1\dots j_k}\bar{v}^{ij_1\dots j_k} \\ &\vdots \\ m^{i_1\dots i_k} &= -\Lambda_0\bar{v}^{i_1\dots i_k} - \dots - \Lambda_{j_1\dots j_k}\bar{v}^{i_1\dots i_k j_1\dots j_k} \end{aligned} \tag{3.19}$$

In case of $V = sS^{n-1}$ the odd velocity tensors vanish identically (see Lemma 3.1), and the system decouples into two independent systems for odd and even multipliers.

If $k \in \mathbb{N}$ is even and $V = sS^{n-1}$ then we obtain for the even indices

$$\begin{aligned} m^0 &= -\Lambda_0\bar{v}^0 - \Lambda_{j_1j_2}\bar{v}^{j_1j_2} - \dots - \Lambda_{j_1\dots j_k}\bar{v}^{j_1\dots j_k} \\ m^{i_1i_2} &= -\Lambda_0\bar{v}^{i_1i_2} - \Lambda_{j_1j_2}\bar{v}^{i_1i_2j_1j_2} - \dots - \Lambda_{j_1\dots j_k}\bar{v}^{i_1i_2j_1\dots j_k} \\ &\vdots \\ m^{i_1\dots i_k} &= -\Lambda_0\bar{v}^{i_1\dots i_k} - \dots - \Lambda_{j_1\dots j_k}\bar{v}^{i_1\dots i_k j_1\dots j_k} \end{aligned} \tag{3.20}$$

and for the odd indices

$$\begin{aligned} m^i &= -\Lambda_j\bar{v}^{ij} - \dots - \Lambda_{j_1\dots j_{k-1}}\bar{v}^{ij_1\dots j_{k-1}} \\ &\vdots \\ m^{i_1\dots i_{k-1}} &= -\Lambda_j\bar{v}^{i_1\dots i_{k-1}j} - \dots - \Lambda_{j_1\dots j_{k-1}}\bar{v}^{i_1\dots i_{k-1}j_1\dots j_{k-1}}. \end{aligned} \tag{3.21}$$

In case of k odd and $V = sS^{n-1}$ we obtain the following two decoupled systems. For the even indices:

$$\begin{aligned} m^0 &= -\Lambda_0\bar{v}^0 - \dots - \Lambda_{j_1\dots j_{k-1}}\bar{v}^{j_1\dots j_{k-1}} \\ &\vdots \\ m^{i_1\dots i_{k-1}} &= -\Lambda_0\bar{v}^{i_1\dots i_{k-1}} - \dots - \Lambda_{j_1\dots j_{k-1}}\bar{v}^{i_1\dots i_{k-1}j_1\dots j_{k-1}} \end{aligned} \tag{3.22}$$

and for the odd indices

$$\begin{aligned} m^i &= -\Lambda_j\bar{v}^{ij} - \dots - \Lambda_{j_1\dots j_k}\bar{v}^{ij_1\dots j_k} \\ &\vdots \\ m^{i_1\dots i_k} &= -\Lambda_j\bar{v}^{i_1\dots i_k j} - \dots - \Lambda_{j_1\dots j_k}\bar{v}^{i_1\dots i_k j_1\dots j_k}. \end{aligned} \tag{3.23}$$

We will use these equations to consider explicit examples later.

The above systems of equations are invariant under exchange of pairs of indices. Hence it follows that

Lemma 3.8 *The Lagrangian multipliers $\Lambda^{i_1\dots i_k}$ are symmetric with respect to exchange of indices.*

Now we proceed with the general notion of (3.17) to find the general moment closure.

3.2.3 Moment Closure

We consider the unknown $(k+1)$-st moment of $u_{\min}$. Using (3.18), we get

$$\begin{aligned}\int v^{i_1}\cdots v^{i_{k+1}} u_{\min}(v)dv &= -\int v^{i_1}\cdots v^{i_{k+1}}\Lambda_{\alpha_k} v^{\alpha_k}\, dv \\ &= -(\mathcal{B}m^{\alpha_k})_{\alpha_k}\int v^{i_1}\cdots v^{i_{k+1}} v^{\alpha_k} dv \\ &= -m^{\alpha_k}\int v^{i_1}\cdots v^{i_{k+1}}(v^{\alpha_k}\mathcal{B}^T)_{\alpha_k} dv\end{aligned}$$

Hence the $(k+1)$-st moment of $u_{\min}$ is a linear combination of the lower order moments of the form

$$m^{i_1\dots i_{k+1}} = \int v^{i_1}\cdots v^{i_{k+1}} u_{\min}(v)dv = \mathcal{A}_{\alpha_k}^{i_1\dots i_{k+1}} m^{\alpha_k}, \tag{3.24}$$

with mappings $\mathcal{A}_{\alpha_k}^{i_1\dots i_{k+1}} : \mathbb{R}^{N_k} \to \mathbb{R}$ given by

$$\mathcal{A}_{\alpha_k}^{i_1\dots i_{k+1}} := \int v^{i_1}\cdots v^{i_{k+1}}(v^{\alpha_k}\mathcal{B}^T)_{\alpha_k}\, dv. \tag{3.25}$$

The next step to obtain the moment closure is to assume that the highest moment $m^{i_1\dots i_{k+1}}$ of $p(t,x,v)$ has approximately the same relation to the lower order moments as $u_{\min}$ has, and to replace $m^{i_1\dots i_k j}$ in (3.11) with (3.24). Since this is an approximation we switch notation to capital letters $M^{i_1\dots i_l}$ to distinguish from the original (exact) values $m^{i_1\dots i_l}$.

In case where the system (3.8), (3.10) and (3.11) is k-quasi closed (see Def. 3.4 and Lemma 3.5) we obtain the following closed system:

$$\begin{aligned} M_t^0 + \partial_j M^j &= 0 \\ M_t^i + \partial_j M^{ij} &= \mu(w^i - M^i) \\ &\vdots \\ M_t^{i_1\dots i_l} + \partial_j M^{i_1\dots i_l j} &= \mu(w^{i_1\dots i_l} - M^{i_1\dots i_l}) \\ &\vdots \\ M_t^{i_1\dots i_k} + \partial_j\left(\mathcal{A}_{\alpha_k}^{i_1\dots i_k j} M^{\alpha_k}\right) &= \mu(w^{i_1\dots i_k} - M^{i_1\dots i_k}),\end{aligned} \tag{3.26}$$

with $w^{\alpha_k} = w^{\alpha_k}(M^{\alpha_k})$ as given in Lemma 3.5.

If the moment system is not k-quasi closed, then the terms $w^{i_1\dots i_k}$ in (3.11) depend on the original distribution as well. Hence we also assume that they are appropriately approximated by using the minimizer $u_{\min}$ instead of p. This way they will depend on moments of order less or equal k. We carry out this approximation in equation (3.11) and obtain a closed system for approximations to the first k moments:

$$\begin{aligned} M_t^0 + \partial_j M^j &= 0 \\ M_t^i + \partial_j M^{ij} &= \mu(W^i - M^i) \\ &\vdots \\ M_t^{i_1\dots i_l} + \partial_j M^{i_1\dots i_l j} &= \mu(W^{i_1\dots i_l} - M^{i_1\dots i_l}) \\ &\vdots \\ M_t^{i_1\dots i_k} + \partial_j \left(\mathcal{A}_{\alpha_k}^{i_1\dots i_k j} M^{\alpha_k}\right) &= \mu(W^{i_1\dots i_k} - M^{i_1\dots i_k}), \end{aligned} \tag{3.27}$$

where for $1 \le l \le k$ we have *approximated T-modulated moments*

$$W^{i_1\dots i_l} := \int_V \int_V v^{i_1} \cdots v^{i_l} T(v, v') U(t, x, v') dv' dv \tag{3.28}$$

with an *approximative minimizer*

$$U(t, x, v) := -\Gamma_{\alpha_k} v_k^{\alpha}, \tag{3.29}$$

where the *approximated multiplier* are

$$\Gamma_{\alpha_k} = (\mathcal{B} M^{\alpha_k})_{\alpha_k}, \tag{3.30}$$

and $\mathcal{B}$ is given by (3.18).

Note that the system (3.27)-(3.30) indeed defines a closed system for M^{α_k}.

3.2.4 The Three-Moment Equations

In case of $k = 3$ and $n = 2$ and $V = sS^1$ we study the above procedure explicitly to find a closed system for the first three moments M^0, M^i, M^{i_1,i_2}, $i, i_1, i_2 \in \{1, 2\}$. The 3-moment system reads:

$$\begin{aligned} m_t^0 + \partial_j m^j &= 0 \\ m_t^i + \partial_j m^{ij} &= \mu(w^i - m^i), \qquad i = 1, 2 \\ m_t^{i_1 i_2} + \partial_j m^{i_1 i_2 j} &= \mu(w^{i_1 i_2} - m^{i_1 i_2}) \qquad i_1, i_2 = 1, 2. \end{aligned} \tag{3.31}$$

We use systems (3.22) and (3.23) to find expressions for the Lagrangian multipliers $\Lambda_0, \Lambda_i, \Lambda_{i_1 i_2}$. In the present case system (3.23) for odd indices is

$$\begin{pmatrix} m^1 \\ m^2 \end{pmatrix} = - \begin{pmatrix} \bar{v}^{11} & \bar{v}^{12} \\ \bar{v}^{21} & \bar{v}^{22} \end{pmatrix} \begin{pmatrix} \Lambda_1 \\ \Lambda_2 \end{pmatrix}. \tag{3.32}$$

Now, with use of Lemma 3.1, we obtain, with $\omega_0 = |S^1| = 2\pi$,

$$\bar{v}^{11} = \bar{v}^{22} = s^3\pi, \qquad \bar{v}^{12} = \bar{v}^{21} = 0.$$

Then (3.32) is immediately solved with

$$\Lambda_i = -\frac{1}{\pi s^3} m^i, \qquad \text{for } i = 1, 2. \tag{3.33}$$

The system (3.22) for the even indices reads in this case:

$$\begin{pmatrix} m^0 \\ m^{11} \\ m^{12} \\ m^{21} \\ m^{22} \end{pmatrix} = - \begin{pmatrix} \bar{v}^0 & \bar{v}^{11} & \bar{v}^{12} & \bar{v}^{21} & \bar{v}^{22} \\ \bar{v}^{11} & \bar{v}^{1111} & \bar{v}^{1112} & \bar{v}^{1121} & \bar{v}^{1122} \\ \bar{v}^{12} & \bar{v}^{1211} & \bar{v}^{1212} & \bar{v}^{1221} & \bar{v}^{1222} \\ \bar{v}^{21} & \bar{v}^{2111} & \bar{v}^{2112} & \bar{v}^{2121} & \bar{v}^{2122} \\ \bar{v}^{22} & \bar{v}^{2211} & \bar{v}^{2212} & \bar{v}^{2221} & \bar{v}^{2222} \end{pmatrix} \begin{pmatrix} \Lambda_0 \\ \Lambda_{11} \\ \Lambda_{12} \\ \Lambda_{21} \\ \Lambda_{22} \end{pmatrix}. \tag{3.34}$$

Again we use Lemma 3.1 to obtain explicit values for the velocity tensors. Especially in (3.6) we explicitely calculated the four-velocity tensor. In the present case the relevant constant is $c_4 = \frac{\pi}{4}$. Then the matrix in (3.34) is given by

$$\begin{pmatrix} s2\pi & s^3\pi & 0 & 0 & s^3\pi \\ s^3\pi & 3\alpha & 0 & 0 & \alpha \\ 0 & 0 & \alpha & \alpha & 0 \\ 0 & 0 & \alpha & \alpha & 0 \\ s^3\pi & \alpha & 0 & 0 & 3\alpha \end{pmatrix} \qquad \text{with } \alpha = s^5 \frac{\pi}{4}.$$

Hence the equations for the mixed indices decouple and due to symmetry (see Lemmata 3.2, 3.8) we have $m^{12} = m^{21}$ and $\Lambda_{12} = \Lambda_{21}$. Then it follows from (3.34) that

$$\Lambda_{12} = \Lambda_{21} = -\frac{2}{s^5\pi} m^{12}. \tag{3.35}$$

The remaining system for Λ_0, Λ_{11} and Λ_{22} reads

$$\begin{pmatrix} m^0 \\ m^{11} \\ m^{22} \end{pmatrix} = - \begin{pmatrix} s2\pi & s^3\pi & s^3\pi \\ s^3\pi & 3\alpha & \alpha \\ s^3\pi & \alpha & 3\alpha \end{pmatrix} \begin{pmatrix} \Lambda_0 \\ \Lambda_{11} \\ \Lambda_{22} \end{pmatrix}.$$

We denote the above matrix by J and observe that

$$\det(J) = \frac{\pi}{4} s^{11} \neq 0.$$

Hence J is invertible and we get

$$\begin{pmatrix} \Lambda_0 \\ \Lambda_{11} \\ \Lambda_{22} \end{pmatrix} = -J^{-1} \begin{pmatrix} m^0 \\ m^{11} \\ m^{22} \end{pmatrix}. \tag{3.36}$$

When we denote $J^{-1} = (\alpha_{ij})_{i,j\in\{1,2,3\}}$ then formula (3.18) can be written explicitly as

$$\begin{pmatrix} \Lambda_0 \\ \Lambda_1 \\ \Lambda_2 \\ \Lambda_{11} \\ \Lambda_{12} \\ \Lambda_{21} \\ \Lambda_{22} \end{pmatrix} = - \begin{pmatrix} \alpha_{11} & 0 & 0 & \alpha_{12} & 0 & 0 & \alpha_{13} \\ 0 & (\pi s^3)^{-1} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & (\pi s^3)^{-1} & 0 & 0 & 0 & 0 \\ \alpha_{21} & 0 & 0 & \alpha_{22} & 0 & 0 & \alpha_{23} \\ 0 & 0 & 0 & 0 & 2(\pi s^5)^{-1} & 2(\pi s^5)^{-1} & 0 \\ 0 & 0 & 0 & 0 & 2(\pi s^5)^{-1} & 2(\pi s^5)^{-1} & 0 \\ \alpha_{31} & 0 & 0 & \alpha_{32} & 0 & 0 & \alpha_{33} \end{pmatrix} \begin{pmatrix} m^0 \\ m^1 \\ m^2 \\ m^{11} \\ m^{12} \\ m^{21} \\ m^{22} \end{pmatrix} \tag{3.37}$$

Finally the minimizer $u_{\min}$ given in (3.16) reads

$$u_{\min} = -\Lambda_0 - \Lambda_j v^j - \Lambda_{j_1 j_2} v^{j_1} v^{j_2}. \tag{3.38}$$

3.2.5 Closure of the 3-Moment Equations

To close the system (3.31) for the first three moments m^0, m^i, m^{ij} we consider the third moment of the minimizer $u_{\min}$, given in (3.38). For $i_1, i_2, i_3 \in \{1, 2\}$ we obtain, with using the representation of $\bar{v}$:

$$\begin{aligned} m^{i_1 i_2 i_3}(u_{\min}) &= \int v^{i_1} v^{i_2} v^{i_3} u_{\min} dv \\ &= -\Lambda_0 \bar{v}^{i_1 i_2 i_3} - \Lambda_j \bar{v}^{i_1 i_2 i_3 j} - \Lambda_{j_1 j_2} v^{i_1 i_2 i_3 j_1 j_2} \\ &= \frac{1}{\pi s^3} \left(m^1 \bar{v}^{i_1 i_2 i_3 1} + m^2 \bar{v}^{i_1 i_2 i_3 2} \right). \end{aligned}$$

Then, with (3.6), we get

$$\begin{aligned} m^{111}(u_{\min}) &= \frac{1}{\pi s^3} \left(3\alpha m^1 \right) = \frac{3}{4} s^2 m^1 \\ m^{112}(u_{\min}) = m^{121}(u_{\min}) = m^{211}(u_{\min}) &= \frac{s^2}{4} m^2 \\ m^{122}(u_{\min}) = m^{212}(u_{\min}) = m^{221}(u_{\min}) &= \frac{s^2}{4} m^1 \\ m^{222}(u_{\min}) &= \frac{3}{4} s^2 m^2. \end{aligned}$$

The linear forms $\mathcal{A}^{i_1 i_2 i_3}$ defined in (3.25) are given by

$$\begin{aligned} A^{111} &= (0, 3s^2/4, 0, 0, 0, 0, 0) \\ A^{112} = A^{121} = A^{211} &= (0, 0, s^2/4, 0, 0, 0, 0) \\ A^{122} = A^{212} = A^{221} &= (0, s^2/4, 0, 0, 0, 0, 0) \\ A^{222} &= (0, 0, 3s^2/4, 0, 0, 0, 0), \end{aligned}$$

which are linear forms for the vector $m^{\alpha_2} = (m^0, m^1, m^2, m^{11}, m^{12}, m^{21}, m^{22})^T$.

The crucial term in (3.31) is $\partial_j m^{i_1 i_2 j}$. For the moments of $u_{\min}$ we get

$$\begin{aligned} \partial_1 m^{111}(u_{\min}) + \partial_2 m^{112}(u_{\min}) &= \frac{s^2}{4}\left(3\partial_1 m^1 + \partial_2 m^2\right) \\ \partial_1 m^{121}(u_{\min}) + \partial_2 m^{122}(u_{\min}) &= \frac{s^2}{4}\left(\partial_1 m^2 + \partial_2 m^1\right) \\ \partial_1 m^{211}(u_{\min}) + \partial_2 m^{212}(u_{\min}) &= \frac{s^2}{4}\left(\partial_1 m^2 + \partial_2 m^1\right) \\ \partial_1 m^{221}(u_{\min}) + \partial_2 m^{222}(u_{\min}) &= \frac{s^2}{4}\left(\partial_1 m^1 + 3\partial_2 m^2\right). \end{aligned}$$

Again we choose capital letters M^0, M^i, M^{ij} to finally close the moment system

$$\begin{aligned} M_t^0 + \partial_j M^j &= 0 \\ M_t^1 + \partial_1 M^{11} + \partial_2 M^{12} &= \mu(W^1 - M^1) \\ M_t^2 + \partial_1 M^{21} + \partial_2 M^{22} &= \mu(W^2 - M^2) \\ M_t^{11} + \tfrac{s^2}{4}\left(3\partial_1 M^1 + \partial_2 M^2\right) &= \mu(W^{11} - M^{11}) \\ M_t^{12} + \tfrac{s^2}{4}\left(\partial_1 M^2 + \partial_2 M^1\right) &= \mu(W^{12} - M^{12}) \\ M_t^{21} + \tfrac{s^2}{4}\left(\partial_1 M^2 + \partial_2 M^1\right) &= \mu(W^{21} - M^{21}) \\ M_t^{22} + \tfrac{s^2}{4}\left(\partial_1 M^1 + 3\partial_2 M^2\right) &= \mu(W^{22} - M^{22}), \end{aligned} \tag{3.39}$$

with

$$W^{i_1 \dots i_l} := \int_V \int_V v^{i_1} \cdots v^{i_l} T(v, v') U(t, x, v') dv'.$$

The approximative minimizer is

$$U(t, x, v) := -\Gamma_0 - \Gamma_j v^j - \Gamma_{j_1 j_2} v^{j_1} v^{j_2} \tag{3.40}$$

and the approximated multipliers are given by (3.37) with capital M^{α_2} instead of m^{α_2}.

It is clear that if system (3.31) is 2-quasi closed then we obtain (3.39) with w^{α_2} instead of W^{α_2}.

We consider some special cases:

1. Assume $T(v,v') = \frac{1}{\omega}$, with $\omega = |sS^1| = 2\pi s$. Then the moment system is 2-quasi closed (see Example 3.3) and we have

$$w^{\alpha_2} = \frac{\bar{v}^{i_1 \dots i_2}}{2\pi s} M^0.$$

Hence

$$\begin{aligned} w^0 &= M^0, & w^1 &= w^1 = 0, \\ w^{11} &= w^{22} = \frac{s^2}{2} M^0 & w^{12} &= w^{21} = 0. \end{aligned}$$

Then the closed moment system reads

$$\begin{aligned} M_t^0 + \partial_j M^j &= 0 \\ M_t^i + \partial_j M^{ij} &= -\mu M^i, \qquad i = 1,2 \\ M_t^{11} + \tfrac{s^2}{4}\left(3\partial_1 M^1 + \partial_2 M^2\right) &= \mu\left(\tfrac{s^2}{2} M^0 - M^{11}\right) \\ M_t^{12} + \tfrac{s^2}{4}\left(\partial_1 M^2 + \partial_2 M^1\right) &= -\mu M^{12} \\ M_t^{21} + \tfrac{s^2}{4}\left(\partial_1 M^2 + \partial_2 M^1\right) &= -\mu M^{21} \\ M_t^{22} + \tfrac{s^2}{4}\left(\partial_1 M^1 + 3\partial_2 M^2\right) &= \mu\left(\tfrac{s^2}{2} M^0 - M^{22}\right). \end{aligned} \tag{3.41}$$

2. We consider a scaling limit for large turning rate $\mu \to \infty$ but finite speed $s < \infty$. Then formally the last four equations of (3.41) become

$$M^{11} = M^{22} = \frac{s^2}{2} M^0, \qquad M^{12} = M^{21} = 0. \tag{3.42}$$

The whole system (3.41) reduces to

$$\begin{aligned} M_t^0 + \partial_j M^j &= 0 \\ M_t^i + \frac{s^2}{2}\partial_i M^0 &= -\mu M^i, \end{aligned}$$

which is exactly the two moment - or Cattaneo - approximation (2.13).

Remark 3.1 *The scaling considered here corresponds to the Chapman-Enskog scaling of the Boltzmann equation*

$$\varepsilon(p_t + v\nabla p) = Q(p,p),$$

where Q denotes the collision operator and the mean free path is assumed to be small $\approx O(\varepsilon)$. For the Boltzmann equation this scaling leads to the Navier-Stokes or Euler equations if the medium is compressible or incompressible, respectively. Here the Cattaneo approximation ranges on the same level.

3. It is important to investigate the classical parabolic limit. As shown earlier there are two ways to obtain the parabolic limit for transport equations. One is a parameter scaling of $s \to \infty, \mu \to \infty$ such that $\frac{s^2}{2\mu} \to D < \infty$, the other is to consider scaled space and time variables $\tau = \varepsilon^2 t$ and $\xi = \varepsilon x$. It is easily checked that the first limit is not appropriate for the study of (3.41), since an additional factor of s^2 appears in the equations for M^{11} and M^{22}. It is however useful to study the scaling of $\tau = \varepsilon^2 t$ and $\xi = \varepsilon x$. In these new coordinates the system (3.41) reads:

$$\begin{aligned}
\varepsilon^2 M^0_\tau + \varepsilon \partial_j M^j &= 0 \\
\varepsilon^2 M^i_\tau + \varepsilon \partial_j M^{ij} &= -\mu M^i, \qquad i = 1,2 \\
\varepsilon^2 M^{11}_\tau + \varepsilon \tfrac{s^2}{4} \left(3\partial_1 M^1 + \partial_2 M^2\right) &= \mu \left(\tfrac{s^2}{2} M^0 - M^{11}\right) \\
\varepsilon^2 M^{12}_\tau + \varepsilon \tfrac{s^2}{4} \left(\partial_1 M^2 + \partial_2 M^1\right) &= -\mu M^{12} \\
\varepsilon^2 M^{21}_\tau + \varepsilon \tfrac{s^2}{4} \left(\partial_1 M^2 + \partial_2 M^1\right) &= -\mu M^{21} \\
\varepsilon^2 M^{22}_\tau + \varepsilon \tfrac{s^2}{4} \left(\partial_1 M^1 + 3\partial_2 M^2\right) &= \mu \left(\tfrac{s^2}{2} M^0 - M^{22}\right).
\end{aligned} \tag{3.43}$$

Then the 0-order approximation to the last four equations is again (3.42). Hence again we obtain a Cattaneo system, but with scaled variables.

$$\begin{aligned}
\varepsilon^2 M^0_\tau + \varepsilon \partial_j M^j &= 0 \\
\varepsilon^2 M^i_\tau + \varepsilon \tfrac{s^2}{2} \partial_i M^0 &= -\mu M^i.
\end{aligned} \tag{3.44}$$

The first equation of (3.44) is equivalent with $M^0_\tau = -\partial_j \frac{M^j}{\varepsilon}$. To obtain an expression for $\frac{M^j}{\varepsilon}$ we write the second equation as

$$\varepsilon M^i_\tau + \frac{s^2}{2} \partial_i M^0 = -\mu \frac{M^i}{\varepsilon},$$

which formally gives for ε small:

$$\frac{M^i}{\varepsilon} = -\frac{s^2}{2\mu} \partial_i M^0.$$

This finally leads to the diffusion limit

$$M^0_\tau = \frac{s^2}{2\mu} \partial_i \partial^i M^0. \tag{3.45}$$

3.3 Steady States

For dissipative processes steady states are typical candidates for limit sets. Moreover the study of steady states for different levels of moment closure helps to get insight into the relation of different closures. Here we consider the example of constant speed $V = s \cdot S^{n-1}$ in two dimensions with uniformly distributed velocities $T(v, v') = \frac{1}{\omega}$.

3.3.1 Cattaneo-Approximation

The system for steady states of the Cattaneo approximation (2.13) is

$$\partial_j M^j = 0, \qquad \frac{s^2}{2\mu}\partial_j M^0 = -M^j, \quad \text{for} \quad j = 1, 2.$$

We introduce the second equation into the first and arrive at the Laplace equation

$$\frac{s^2}{2\mu}\Delta M^0 = 0, \quad \text{and} \quad M^j = -\frac{s^2}{2\mu}\partial_j M^0, \tag{3.46}$$

which describes exactly the steady states of the corresponding heat equation $M^0_t = \frac{s^2}{2\mu}\nabla M^0$.

3.3.2 The Three-Moment Closure

The system for stationary solutions of (3.41) is

$$\begin{aligned}
\partial_1 M^1 + \partial_2 M^2 &= 0 && (3.47)\\
\partial_1 M^{11} + \partial_2 M^{12} &= -\mu M^1 && (3.48)\\
\partial_1 M^{21} + \partial_2 M^{22} &= -\mu M^2 && (3.49)\\
\frac{s^2}{4}(3\partial_1 M^1 + \partial_2 M^2) &= \mu\left(\frac{s^2}{2}M^0 - M^{11}\right) && (3.50)\\
\frac{s^2}{4}(\partial_1 M^2 + \partial_2 M^1) &= -\mu M^{12} = -\mu M^{21} && (3.51)\\
\frac{s^2}{4}(\partial_1 M^1 + 3\partial_2 M^2) &= \mu\left(\frac{s^2}{2}M^0 - M^{22}\right). && (3.52)
\end{aligned}$$

We solve (3.50)-(3.52) for $M^{ij}, i, j = 1, 2$ and introduce these into (3.48) and (3.49), respectively.

$$\begin{aligned}
\partial_1\left(\frac{s^2}{2}M^0 - \frac{s^2}{4\mu}(3\partial_1 M^1 + \partial_2 M^2)\right) - \partial_2\left(\frac{s^2}{4\mu}(\partial_1 M^2 + \partial_2 M^1)\right) &= -\mu M^1\\
-\partial_1\left(\frac{s^2}{4\mu}(\partial_1 M^2 + \partial_2 M^1)\right) + \partial_2\left(\frac{s^2}{2}M^0 - \frac{s^2}{4\mu}(\partial_1 M^1 + 3\partial_2 M^2)\right) &= -\mu M^2.
\end{aligned}$$

Rearrangement leads to

$$\begin{aligned}
\frac{s^2}{4\mu}(3\partial_1\partial_1 + \partial_2\partial_2)M^1 + \frac{s^2}{4\mu}(\partial_1\partial_2 + \partial_2\partial_1)M^2 &= \mu M^1 + \frac{s^2}{2}\partial_1 M^0\\
\frac{s^2}{4\mu}(\partial_1\partial_2 + \partial_2\partial_1)M^1 + \frac{s^2}{4\mu}(\partial_1\partial_1 + 3\partial_2\partial_2)M^2 &= \mu M^2 + \frac{s^2}{2}\partial_2 M^0.
\end{aligned}$$

We solve this system explicitly using Fourier transformation. If (ξ_1, ξ_2) denote the dual parameters of (x_1, x_2), then the transformed system reads, with for now $d = \frac{s^2}{4\mu}$

$$\begin{aligned} d(-3\xi_1^2 - \xi_2^2)\hat{M}^1 - 2d\xi_1\xi_2\hat{M}^2 &= \mu\hat{M}^1 + \frac{s^2}{2}(-i\xi_1)\hat{M}^0 \\ -2d\xi_1\xi_2\hat{M}^1 + d(-\xi_1^2 - 3\xi_2^2)\hat{M}^2 &= \mu\hat{M}^1 + \frac{s^2}{2}(-i\xi_2)\hat{M}^0. \end{aligned}$$

We write this as a linear equation

$$LF = -i\frac{s^2}{2}\hat{M}^0 \begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix}, \tag{3.53}$$

with $L = (\hat{M}^1, \hat{M}^2)^T$ and

$$F = \begin{pmatrix} -\mu - d(3\xi_1^2 + \xi_2^2) & -2d\xi_1\xi_2 \\ -2d\xi_1\xi_2 & -\mu - d(\xi_1^2 + 3\xi_2^2) \end{pmatrix}.$$

We find for the determinant that

$$\det F = \mu^2 + 4\mu d(\xi_1^2 + \xi_2^2)^2 + 3d^2(\xi_1^2 + \xi_2^2)^2, \tag{3.54}$$

which is positive for each $(\xi_1, \xi_2) \in \mathbb{R}^2$ and $\mu > 0$. Hence (3.53) is uniquely solvable for each $(\xi_1, \xi_2) \in \mathbb{R}^2$. The solution is given by

$$\begin{pmatrix} \hat{M}^1 \\ \hat{M}^2 \end{pmatrix} = i\frac{s^2}{2}\frac{\mu + d(\xi_1^2 + \xi_2^2)}{\det F}\hat{M}^0 \begin{pmatrix} \xi_1 \\ \xi_2 \end{pmatrix}. \tag{3.55}$$

Fourier transformation of the first equation (3.47) gives $-i\xi_1\hat{M}^1 - i\xi_2\hat{M}^2 = 0$. Using (3.55) this reduces to the Laplace equation

$$-(\xi_1^2 + \xi_2^2)\hat{M}^0 = 0. \tag{3.56}$$

Then (M^1, M^2) are given by (3.55) and we can finally calculate the remaining functions from (3.50), (3.51) and (3.52)

$$\begin{aligned} M^{11} &= \tfrac{s^2}{2}M^0 - \tfrac{s^2}{4\mu}(3\partial_1 M^1 + \partial_2 M^2) \\ M^{12} &= M^{21} = -\tfrac{s^2}{4\mu}(\partial_1 M^2 + \partial_2 M^1) \\ M^{22} &= \tfrac{s^2}{2}M^0 - \tfrac{s^2}{4\mu}(\partial_1 M^1 + 3\partial_2 M^2). \end{aligned} \tag{3.57}$$

Lemma 3.9 *The steady states of the three moment problem for* $(M^0, M^i, M^{ij})_{i,j\in\{1,2\}}$ *are given as follows*

1. *$M^0(x)$ solves the Laplace equation $\Delta M^0(x) = 0$ on $\mathbb{R}^2$ with $\int M^0(x)dx = N$.*

2. *(M^1, M^2) are given from Fourier transformation of (3.55).*

3. *$(M^{ij})_{i,j\in\{1,2\}}$ are given by (3.57).*

Remark 3.2 1. *The steady states of the moments are obtained from the stationary solutions of a corresponding diffusion equation: $M^0_t = \Delta M^0$.*

2. *The same construction works for the nonlinear problem with*

$$M^0_t + \partial_j M^j = f(M^0).$$

Then the steady states of the three moment systems are related to a semilinear elliptic problem of the form

$$c\Delta M^0 = f(M^0)$$

with an appropriate diffusion constant $c > 0$.

3. *The author believes that at any level of moment closure the stationary solution can be constructed from the elliptic equation $\Delta M^0 = 0$. This, however, needs further exploration.*

4 Resting Phase Dynamics

In this Section we consider birth-death processes in connection with transport equations. The question is, how to model the interactions of birth/death and the random walk process. It is obvious that these processes are not independent in general.

At a stimulating discussion with L. Edelstein-Keshet, K.P. Hadeler, H. Othmer and others at a meeting at the IMA in Minneapolis, USA in May 99 we discussed how to design a model for animals that stop moving when they give birth. A reproduction term of the form: "an individual moving with velocity v gives birth to an individual moving with velocity v'", which we call instantaneous-birth*, seems unrealistic; or at least too simple. In this Chapter we consider a model where particles rest to give birth. We introduce a resting phase r where birth takes place. If reproductions and deaths occur on a slower time scale than the random walk, a singular perturbation analysis leads in a* parabolic limit *to reaction diffusion equations. We show that the inner solution relaxes to a homogeneous distribution and that the outer expansion is well described by a reaction-diffusion model with* effective *birth and death rates. We match inner and outer expansions and we prove that in the linear case the long time asymptotics are approximated by the outer expansion to second order in the perturbation parameter. In a discussion we consider conditions under which the assumption of instantaneous birth is appropriate. We consider a related parabolic model with resting phases. Moreover we discuss the relations of the present results to the known literature.*

4.1 The Model

We split the total population density $N(t,x)$ into a density $p(t,x,v)$ of individuals moving with velocity $v \in V$ and a density $r(t,x)$ for particles resting at $x \in \Omega$. The velocity set is assumed to be bounded with $\omega = |V|$ and symmetric of the form that $v \in V$ implies $-v \in V$. We study a model for (p,r) which bases on the following assumptions:

1. The pure movement process is a velocity jump process

$$p_t + v \cdot \nabla p = -\mu p + \mu \int T(v,v')p(.,.,v')dv'. \tag{4.1}$$

We assume that the kernel $T(v, v')$ satisfies the basic assumptions (T1)-(T4) given in Section 1.4.1. We denote the turning operator as $\mathcal{L}_0 := -\mu(I - \mathcal{T}_0)$ and Proposition 1.1 applies.

2. There is a constant rate $\alpha > 0$ such that individuals stop moving with that rate α.

3. At rest particles give birth at a rate $g(N) \geq 0$ (g for "gain").

4. Particles choose a velocity $v \in V$ with constant rate $\beta > 0$ and with equal distribution on V.

5. Death occurs for moving and resting particles at the same rate $l(N) \geq 0$[1]. (l for "loss").

For later use we define the pure kinetic birth-death process without any movement by

$$\dot{u} = f(u) := g(u)u - l(u)u.$$

The resting-phase transport model reads

$$p_t + v \cdot \nabla p = \mathcal{L}_0 p - \alpha p + \frac{\beta}{\omega} r - l(N)p \tag{4.2}$$

$$r_t = \alpha \int p(.,.,v)dv - \beta r + g(N)r - l(N)r. \tag{4.3}$$

where the total particle density N is given by

$$N(t,x) = \int p(t,x,v)dv + r(t,x).$$

We assume compactly supported initial data on $\Omega = \mathbb{R}^n$, which are L^2-integrable on $\mathbb{R}^n \times V$. Then the solution will have compact support as long as it exists.

We study the parabolic limit of (4.2,4.3) in the framework of singular perturbation theory and matching asymptotic expansions. For that purpose we identify appropriate scalings of space and time (parabolic scaling). As pointed out in [52], these scalings occur for biological populations quite naturally. For a given small quantity $\varepsilon > 0$ we consider fast and slow time scales, t and $\tau = \varepsilon^2 t$, respectively, on microscopic and macroscopic space scales x and $\xi = \varepsilon x$. In singular perturbation theory one splits the dynamic into two parts. The first part (*inner solution*) describes the relaxation of the initial data on the fast time scale t. The *outer solution* describes the long time behavior on the slow time scale τ. The initial data for the outer solution are however not directly specified by the initial data of the original problem (4.2, 4.3). This can be achieved by *matching* inner

[1] It might be of particular interest to study a higher death rate at rest due to predators or a lower death rate due to shelter.

and outer expansions in an intermediate region. Roughly speaking, the asymptotics of the inner solution for $t \to \infty$ defines the initial condition for the outer solution at $\tau = 0$.

We begin to study the outer solution $(\tilde{p}, \tilde{r})$ which leads to the diffusion limit equation (4.17). This gives approximations of second order in the perturbation parameter ε (Theorem 4.8). After that we study the inner solution and we illustrate that both parts match correctly.

4.2 The Outer Expansion

4.2.1 Scaling

In [52] we introduced the scaling of

$$\tau = \varepsilon^2 t, \qquad \xi = \varepsilon x,$$

for small $0 < \varepsilon \leq 1$.

We assume that birth and death occurs on a much larger scale as compared to the random walk process. There are many movements and many turnings at one incident of birth or death. Hence we assume a scaling of the form

$$f(u) = \varepsilon^a \tilde{f}(u)$$

with $a > 0$. In the study presented here it turns out that only the choice of $a = 2$ leads to a reaction diffusion limit equation (see the Remark at the discussion section). Then reactions take place on the diffusion scale (slowest scale) and we assume

$$f(u) = \varepsilon^2 \tilde{f}(u) = \varepsilon^2 (\tilde{g}(u)u - \tilde{l}(u)u).$$

System (4.2, 4.3) in the new variables reads

$$\varepsilon^2 \tilde{p}_\tau + \varepsilon v \cdot \nabla_\xi \tilde{p} = \mathcal{L}_0 \tilde{p} - \alpha \tilde{p} + \frac{\beta}{\omega} \tilde{r} - \varepsilon^2 \tilde{l}(\tilde{N}) \tilde{p} \tag{4.4}$$

$$\varepsilon^2 \tilde{r}_\tau = \alpha \int \tilde{p}(.,.,v) dv - \beta \tilde{r} + \varepsilon^2 \tilde{g}(\tilde{N}) \tilde{r} - \varepsilon^2 \tilde{l}(\tilde{N}) \tilde{r}, \tag{4.5}$$

where $\tilde{p}(\tau, \xi, v) = p(\tau/\varepsilon^2, \xi/\varepsilon, v), \tilde{r}(\tau, \xi) = r(\tau/\varepsilon^2, \xi/\varepsilon)$. We consider Hilbert expansions in ε up to order $k > 2$:

$$\tilde{p}(\tau, \xi, v) := \sum_{j=0}^{k} \varepsilon^j p_j(\tau, \xi, v), \qquad \tilde{r}(\tau, \xi) := \sum_{j=0}^{k} \varepsilon^j r_j(\tau, \xi)$$

$$\tilde{N}(\tau, \xi) := \sum_{j=0}^{k} \varepsilon^j N_j(\tau, \xi), \qquad N_j(\tau, \xi) = r_j(\tau, \xi) + \int p_j(\tau, \xi, v) dv, \quad 0 \leq j \leq k.$$

We expand the nonlinearities $\tilde{g}, \tilde{l}$ according to this representation:

$$\begin{aligned}\tilde{g}(\tilde{N}) &= \tilde{g}(N_0) + \tilde{g}'(N_0)(\sum_{j=1}^{k} \varepsilon^j N_j) + \text{l.o.t.} \\ \tilde{l}(\tilde{N}) &= \tilde{l}(N_0) + \tilde{l}'(N_0)(\sum_{j=1}^{k} \varepsilon^j N_j) + \text{l.o.t..}\end{aligned}$$

4.2.2 Formal Derivation of the Diffusion Limit

We introduce all of the above expansions into system (4.4, 4.5) and collect orders of ε. During this section we neglect the subscript ξ at the ∇-operator.

$$\varepsilon^0: \quad \begin{cases} 0 &= \mathcal{L}_0 p_0 - \alpha p_0 + \frac{\beta}{\omega} r_0 \\ 0 &= \alpha \int p_0 dv - \beta r_0 \end{cases} \tag{4.6}$$

$$\varepsilon^1: \quad \begin{cases} v \cdot \nabla p_0 &= \mathcal{L}_0 p_1 - \alpha p_1 + \frac{\beta}{\omega} r_1 \\ 0 &= \alpha \int p_1 dv - \beta r_1 \end{cases} \tag{4.7}$$

$$\varepsilon^2: \quad \begin{cases} p_{0,\tau} + v \cdot \nabla p_1 &= \mathcal{L}_0 p_2 - \alpha p_2 + \frac{\beta}{\omega} r_2 - \tilde{l}(N_0) p_0 \\ r_{0,\tau} &= \alpha \int p_2 dv - \beta r_2 + \tilde{g}(N_0) r_0 - \tilde{l}(N_0) r_0. \end{cases} \tag{4.8}$$

From (4.6) it follows that

$$r_0 = \frac{\alpha}{\beta} \int p_0 dv.$$

Hence the first equation of (4.6) reads

$$0 = \mathcal{L}_0 p_0 - \alpha p_0 + \frac{\alpha}{\omega} \int p_0 dv =: \mathcal{L}_\alpha p_0, \tag{4.9}$$

where the operator $\mathcal{L}_\alpha$ is given for $\alpha \geq 0$ and $\psi \in L^2(V)$ by

$$\mathcal{L}_\alpha \psi(v) = -(\mu + \alpha)\psi(v) + (\mu + \alpha) \int \left(\frac{\mu}{\mu + \alpha} T(v, v') + \frac{\alpha}{(\mu + \alpha)\omega} \right) \psi(v')\, dv'. \tag{4.10}$$

We denote the modified turning kernel by

$$T_\alpha(v, v') := \frac{\mu}{\mu + \alpha} T(v, v') + \frac{\alpha}{(\mu + \alpha)\omega} \tag{4.11}$$

and $\mathcal{T}_\alpha$ is the integral operator defined by T_α.

Lemma 4.1 *T_α satisfies conditions* (T1)-(T4).

Proof: Since T is assumed to satisfy (T1)-(T4) it satisfies $T \geq 0$. Hence for $\alpha > 0$ we have $T_\alpha(v, v') > 0$ for all $(v, v') \in V^2$. Then (T2) and the first condition of (T1) follow.
Integration of the kernel gives:

$$\int T_\alpha(v, v')dv = \frac{\mu}{\mu + \alpha} + \frac{\alpha}{\mu + \alpha} = 1 = \int T_\alpha(v, v')dv'.$$

Hence (T4) and the second condition in (T1) are satisfied. Moreover

$$\int\int T_\alpha^2(v, v')dvdv' = \left(\mu^2 \int\int T^2(v, v')dvdv' + 2\mu\alpha + \alpha^2\right)(\mu + \alpha)^{-2} < \infty.$$

Then (T1) is satisfied as well and it remains to check (T3):

$$\begin{aligned} \|\mathcal{T}_\alpha\|_{\langle 1\rangle^\perp} &= \sup_{\psi \in L^2(V), \|\psi\| = 1, \int \psi dv = 0} \left| \int \frac{\mu}{\mu + \alpha} T(v, v')\psi(v')dv' + \frac{\alpha}{(\mu + \alpha)\omega} \int \psi(v)dv \right| \\ &\leq \|\mathcal{T}_0\|_{\langle 1\rangle^\perp} < 1. \end{aligned}$$

□

Hence Proposition 1.1 applies for $\mathcal{L}_\alpha$ and we have

Corollary 4.2 *Assume* (T1)-(T4) *for* $T(v, v')$ *and let* $\mathcal{L}_\alpha$ *be defined by* (4.10) *for* $\alpha \geq 0$. *Then*

1. 0 *is a simple eigenvalue of* $\mathcal{L}_\alpha$ *and the corresponding eigenfunction is* $\phi(v) \equiv 1$.
2. *There is a decomposition* $L^2(V) = \langle 1\rangle \oplus \langle 1\rangle^\perp$ *and for all* $\psi \in \langle 1\rangle^\perp$

$$\int \psi \mathcal{L}_\alpha \psi dv \leq -\nu_\alpha \|\psi\|^2_{L^2(V)}, \quad \text{where} \quad \nu_\alpha \equiv (\mu + \alpha)(1 - \|\mathcal{T}_\alpha\|_{\langle 1\rangle^\perp}). \tag{4.12}$$

3. *All nonzero eigenvalues* λ *satisfy* $-2(\mu + \alpha) < Re\ \lambda \leq -\nu_\alpha < 0$, *and to within scalar multiples there is no other positive eigenfunction.*
4. $\|\mathcal{L}_\alpha\|_{\mathcal{L}(L^2(V), L^2(V))} \leq 2(\mu + \alpha)$.
5. $\mathcal{L}_\alpha$ *restricted to* $\langle 1\rangle^\perp \subset L^2(V)$ *has a linear inverse* $\mathcal{F}_\alpha$ *with norm*

$$\|\mathcal{F}_\alpha\|_{\mathcal{L}(\langle 1\rangle^\perp, \langle 1\rangle^\perp)} \leq \frac{1}{\nu_\alpha}. \tag{4.13}$$

Now we go back to consider the ε^j-systems for $j = 0, 1, 2$.
$\boldsymbol{\varepsilon^0}$ **:** With the above Corollary it follows from (4.9) that $p_0 = p_0(\tau, \xi)$ does not depend on velocity $v \in V$. Then

$$r_0 = \frac{\alpha}{\beta} \int p_0 dv = \frac{\alpha\omega}{\beta} p_0. \tag{4.14}$$

$\boldsymbol{\varepsilon^1}$: From the second equation of (4.7) it follows that $r_1 = \alpha/\beta \int p_1 dv$, hence in the first equation of (4.7) the operator $\mathcal{L}_\alpha$ appears again:

$$v \cdot \nabla p_0 = \mathcal{L}_\alpha p_1.$$

This equation is solvable since

$$\int (v \cdot \nabla p_0) dv = \int v dv \cdot \nabla p_0 = 0.$$

Then

$$p_1 = \mathcal{F}_\alpha (v \cdot \nabla p_0), \quad \text{with} \quad \mathcal{F}_\alpha := \left(\mathcal{L}_\alpha|_{\langle 1 \rangle^\perp} \right)^{-1}. \tag{4.15}$$

Since $\mathcal{F}_\alpha$ is one-to-one on $\langle 1 \rangle^\perp$ we have $\int p_1 dv = 0$ and then $r_1 = 0$.

$\boldsymbol{\varepsilon^2}$: From the second equation of (4.8) we obtain

$$\frac{\beta}{\omega} r_2 = \frac{1}{\omega} \left(\alpha \int p_2 dv + \tilde{g}_0 r_0 - \tilde{l}_0 r_0 - r_{0,\tau} \right),$$

where for now we write $\tilde{g}_0 := \tilde{g}(N_0)$ and similarly for $\tilde{l}_0$. With (4.14) we get

$$\frac{\beta}{\omega} r_2 = \frac{\alpha}{\omega} \int p_2 dv + \frac{\alpha}{\beta} \left(\tilde{g}_0 p_0 - \tilde{l}_0 p_0 - p_{0,\tau} \right).$$

We introduce this expression into the first equation of (4.8):

$$p_{0,\tau} + v \cdot \nabla p_1 = \mathcal{L}_\alpha p_2 + \frac{\alpha}{\beta} (\tilde{g}_0 - \tilde{l}_0) p_0 - \frac{\alpha}{\beta} p_{0,\tau} - \tilde{l}_0 p_0. \tag{4.16}$$

The solvability condition with respect to $\mathcal{L}_\alpha$ reads, with use of (4.15),

$$\int \left(1 + \frac{\alpha}{\beta} \right) p_{0,\tau} dv + \nabla \cdot \int v \mathcal{F}_\alpha v dv \nabla p_0 = \frac{\alpha}{\beta} (\tilde{g}_0 - \tilde{l}_0) \int p_0 dv - \tilde{l}_0 \int p_0 dv.$$

Since p_0 does not depend on velocity $v \in V$ this equation becomes

$$\omega \left(1 + \frac{\alpha}{\beta} \right) p_{0,\tau} + \nabla \cdot \int v \mathcal{F}_\alpha v dv \cdot \nabla p_0 = \tilde{g}_0 \frac{\alpha}{\beta} \omega p_0 - \tilde{l}_0 \left(1 + \frac{\alpha}{\beta} \right) \omega p_0.$$

Now $\tilde{g}_0 = \tilde{g}(N_0)$ and

$$N_0 = r_0 + \omega p_0 = \left(1 + \frac{\alpha}{\beta} \right) \omega p_0.$$

Finally the parabolic limit equation reads

$$N_{0,\tau} = \nabla D_{\alpha,\beta} \nabla \, N_0 + \frac{\alpha}{\alpha + \beta} \tilde{g}(N_0) N_0 - \tilde{l}_0(N_0) N_0 \tag{4.17}$$

with diffusion tensor

$$D_{\alpha,\beta} := -\frac{\beta}{\omega(\alpha+\beta)} \int v\mathcal{F}_\alpha v \, dv. \tag{4.18}$$

Hence we obtain the effective birth-rate reduced by a factor $\alpha/(\alpha+\beta)$. This factor describes the mean fraction of the population which is at rest at any time. For the diffusion tensor we will discuss special cases in more detail in the discussion section 4.4.

If $N_0(\tau,\xi)$ satisfies (4.17) then (4.16) is solvable for p_2 and we get

$$\begin{aligned} p_2(\tau,\xi,v) &= \mathcal{F}_\alpha\left(p_{0,\tau} + v\cdot\nabla p_1 - \frac{\alpha}{\beta}(\tilde{g}_0 - \tilde{l}_0)p_0 + \frac{\alpha}{\beta}p_{0,\tau} + \tilde{l}_0 p_0\right) \\ &= \mathcal{F}_\alpha\left(\left(1+\frac{\alpha}{\beta}\right)p_{0,\tau} + v\cdot\nabla p_1 - \frac{\alpha}{\beta}\tilde{g}_0 p_0\left(1+\frac{\alpha}{\beta}\right)\tilde{l}_0 p_0\right) \\ &= \mathcal{F}_\alpha\left(\frac{1}{\omega}N_{0,\tau} + v\cdot\nabla\mathcal{F}_\alpha(v\cdot\nabla p_0) - \frac{\alpha}{\omega(\alpha+\beta)}\tilde{g}_0 N_0 + \frac{1}{\omega}\tilde{l}_0 N_0\right) \\ &= \mathcal{F}_\alpha\left(\frac{1}{\omega}\nabla D_{\alpha,\beta}\nabla N_0 + \frac{\beta}{\omega(\alpha+\beta)}\, v\cdot\nabla\mathcal{F}_\alpha(v\cdot\nabla N_0)\right). \end{aligned} \tag{4.19}$$

Then $\int p_2 dv = 0$ and

$$\begin{aligned} r_2 &= \frac{\alpha}{\beta^2}\left(\tilde{g}_0 p_0 - \tilde{l}_0 p_0 - p_{0,\tau}\right) \\ &= \frac{\alpha}{\omega\beta(\alpha+\beta)}\left(\frac{\beta}{\alpha+\beta}\tilde{g}_0 N_0 - \nabla D_{\alpha,\beta}\nabla N_0\right). \end{aligned} \tag{4.20}$$

We showed how to formally obtain a parabolic limit equation from a regular perturbation expansion. Next we study the accuracy of an approximation which can be gained from the limit equation. To be more specific we need additional assumptions.

4.2.3 Assumptions (A1)-(A4)

(A1) $f \in C^1(\mathbb{R})$, $g, l \in C_b^1(\mathbb{R})$ and $l(N^*) \geq g(N^*)$ for some $N^* > 0$.

(A2) The initial data

$$p(0,x,v) = \varphi(x,v), \qquad r(0,x) = \psi(x)$$

are spatially compactly supported with $\int \varphi(x,v)dv + \psi(x) \leq N^*$, $\varphi(x,.) \in L^2(V)$ for all $x \in \mathbb{R}^n$ and $\varphi(.,v) \in C^{0,\sigma}(\mathbb{R}^n)$ for almost all $v \in V$ and some $0 < \sigma < 1$.

(A3) $T > 0$ is fixed.

(A4) $V = sS^{n-1}$ or $V = B_s(0)$ for some $s > 0$.

With these assumptions we will be able to obtain approximations of order ε^2 in intervals of the form $\theta/\varepsilon^2 < \tau \leq T/\varepsilon^2$ on compact sets $\Omega \subset \mathbb{R}^n$. First we study the full resting-phase transport system.

4.2.4 Existence for the Resting-Phase Transport System

As shown in Section 2.2 the shift operator $\Phi = -v \cdot \nabla$ generates a strongly continuous unitary group on $L^2(\mathbb{R}^n \times V)$. (see also Dautray, Lions [25] Ch XXI, section 2, Prop 1.).
The nonlinearities are of the form $g(\varphi)\psi, l(\varphi)\psi$ with $\varphi, \psi \in L^2(\mathbb{R}^n \times V)$ with bounded and differentiable rates g and l. Hence $g(\varphi)\psi, l(\varphi)\psi \in L^2(\mathbb{R}^n \times V)$. Moreover the mappings $((\varphi, \psi) \mapsto g(\varphi)\psi)$ and $((\varphi, \psi) \mapsto l(\varphi)\psi)$ are globally Lipschitz continuous on both $L^2(\mathbb{R}^n \times V)^2$ and $H^1(\mathbb{R}^n \times V)^2$. The turning operator $\mathcal{L}_0$ is linear and compact hence local and global existence of solutions to (4.2, 4.3) follows from standard Perron-iteration and perturbation arguments (see e.g. Taylor [113] or Pazy [93]).

Theorem 4.3 *Assume* (T1)-(T4) *and* (A1)-(A4). *For each pair of initial data* φ, ψ *with* $\varphi \in D(\Phi)$ *and* $\psi \in L^2(\mathbb{R}^n)$ *with* $\varphi(., v), \psi \in L^1(\mathbb{R}^n)$ *there is a unique solution* (p, r) *of* (4.2, 4.3) *with*

$$p \in C^1([0,\infty), L^2(\mathbb{R}^n \times V)) \cap C^0([0,\infty), D(\Phi)), \quad r \in C^1([0,\infty), L^2(\mathbb{R}^n))$$

and $p(0, .) = \varphi$ *and* $r(0) = \psi$.

Next we show a global L^2-estimate for p_0. For that purpose we need some information on mean values of p. Let

$$\begin{aligned} \check{p}(t,x) &:= \int p(t,x,v)dv \qquad \bar{p}(t) := \int \check{p}(t,x)dx, \\ \bar{r}(t) &:= \int r(t,x)dx, \qquad \bar{N}(t) := \int N(t,x)dx = \bar{p}(t) + \bar{r}(t). \end{aligned} \tag{4.21}$$

Lemma 4.4

$$\bar{N}(t) \le \bar{N}(0)e^{\|g\|_\infty t}. \tag{4.22}$$

Proof: Integration of system (4.2, 4.3) with respect to space and velocity gives

$$\begin{aligned} \bar{p}_t &= -\alpha\bar{p} + \beta\bar{r} - \int l(N)\check{p}\, dx \\ \bar{r}_t &= \alpha\bar{p} - \beta\bar{r} + \int g(N)r\, dx - \int l(N)r\, dx. \end{aligned} \tag{4.23}$$

Note that due to $\int T(v, v')dv = 1$ the V-integral of $\mathcal{L}_0 p$ vanished. The above equations add to

$$\bar{N}_t = \int g(N)r\, dx - \int l(N)(r + \check{p})dx.$$

where the last term is non positive. Then $\bar{N}_t \le \|g\|_\infty \bar{N}$ and we obtain (4.22). □

Proposition 4.5 *Assume* (A1)-(A4). *Let* (p, r) *denote a solution of* (4.2, 4.3). *Then for each* t *with* $0 < t \le T$ *there is a constant* $c_1 = c_1(\alpha, \beta, \omega, \mu, \min\{l\}, \|g\|_\infty, T)$ *such that*

$$\|p(t, ., .)\|_{L^2(\mathbb{R}^n \times V)} \le c_1 \bar{N}(0).$$

Proof: With use of (4.2) we obtain

$$\begin{aligned}\frac{d}{dt}\frac{1}{2}\int p^2 dv &= \int p\left(-v\cdot\nabla p + \mathcal{L}_0 p - \alpha p + \frac{\beta}{\omega} r - l(N)p\right) dv \\ &= -\nabla\cdot\frac{1}{2}\int v p^2 dv + \int p\mathcal{L}_0 p\, dv - \alpha\int p^2 dv + \frac{\beta}{\omega}\int p\, dv\, r - l(N)\int p^2 dv.\end{aligned}$$

Since the term $\int p\mathcal{L}_0 p\, dv \leq 0$ (see Proposition 1.1) integration of the above equation with respect to space gives

$$\frac{d}{dt}\frac{1}{2}\|p\|^2_{L^2(\mathbb{R}^n\times V)} \leq -\alpha\|p\|^2_{L^2(\mathbb{R}^n\times V)} + \frac{\beta}{\omega}\bar{N}^2 - \min\{l\}\|p\|^2_{L^2(\mathbb{R}^n\times V)}.$$

Here we used Lemma 4.4 and the fact that $\int(\int p dv\, r)dx \leq \bar{N}^2$. With use of Gronwall's Lemma and Lemma 4.4 the assertion follows. □

4.2.5 Regularity Properties of the Limit Equation

Here we study regularity properties of the parabolic limit initial value problem

$$\begin{aligned}N_{0,\tau} &= \nabla D_{\alpha,\beta}\nabla N_0 + \tfrac{\alpha}{\alpha+\beta}\tilde{g}(N_0)N_0 - \tilde{l}(N_0)N_0, \\ N_0(0,\xi) &= \int\varphi(\xi,v)dv + \psi(\xi).\end{aligned} \tag{4.24}$$

Lemma 4.6 *The interval $\Gamma := [0, N^*]$ is positively invariant for solutions of* (4.24).

Proof: A result of Chuey, Conley, Smoller [23] applies. □

Proposition 4.7 *For ϑ with $0 < \vartheta < T$ we have*

$$(i) \qquad \sup_{\vartheta\leq\tau\leq T}\|D^2 N_0(\tau,.)\|_\infty \leq K_{\vartheta,T}\|N_0(0,.)\|_{C^{0,\sigma}},$$

$$(ii) \qquad \sup_{\vartheta\leq\tau\leq T}\|N_{0,\tau}(\tau,.)\|_\infty \leq \kappa_{\alpha,\beta}K_{\vartheta,T}\|N_0(0,.)\|_{C^{0,\sigma}} + c_3 N^*,$$

where

$$\begin{aligned}K_{\vartheta,T} &= c_2\left(\vartheta^{\sigma/2-1} + T^{\sigma/2}2^{[2TK_1(N^*)]+1}\right). \\ c_3 &= \frac{\alpha}{\alpha+\beta}\|\tilde{g}\|_{C^0(\Gamma)} + \|\tilde{l}\|_{C^0(\Gamma)} \\ \kappa_{\alpha,\beta} &= \frac{\beta s^2}{\omega(\alpha+\beta)\nu_\alpha},\end{aligned}$$

c_2 is defined by (4.25) *and $K_1(N^*)$ is given by* (4.29).

Proof: Since $A := \nabla D_{\alpha,\beta} \nabla$ defines a strongly elliptic sectorial operator (see [52], Lemma 3.3) it generates an analytic contraction semigroup on $C^{2+\sigma}(\mathbb{R}^n)$ ([70]). Moreover, for $\phi \in C^{0,\sigma}(\mathbb{R}^n)$ which does not grow faster than $e^{c|x|^2}$ for $|x| \to \infty$ we have the regularity property that

$$\|D^2(e^{A\tau}\phi)\|_\infty \leq c_2 \tau^{\sigma/2-1} \|\phi\|_{C^{0,\sigma}} \tag{4.25}$$

(See [70] chapter IV, 11 formula (11.6)). Note that for compactly supported initial data the solution $N_0(\tau, \xi)$ of (4.24) has exactly the correct growth behavior as $|x| \to \infty$. This can be seen from the representation of the solution with fundamental solutions (see e.g. [70]).

From the limit equation (4.24) we obtain

$$N_0(\tau,\xi) = e^{A\tau} N_0(0,\xi) + \int_0^\tau e^{A(\tau-\theta)} \left(\frac{\alpha}{\alpha+\beta} \tilde{g}(N_0) N_0 - \tilde{l}(N_0) N_0 \right) d\theta \tag{4.26}$$

which leads to

$$\|N_0(\tau,.)\|_{C^{0,\sigma}} \leq \|N_0(0,.)\|_{C^{0,\sigma}} + \int_0^\tau \left\| \frac{\alpha}{\alpha+\beta} \tilde{g}(N_0) N_0 - \tilde{l}(N_0) N_0 \right\|_{C^{0,\sigma}} d\theta. \tag{4.27}$$

The norm $\|.\|_{C^{0,\sigma}}$ is defined as $\|.\|_{C^{0,\sigma}} = \|.\|_\infty + [.]_\sigma$, where $[.]_\sigma$ denotes the usual Hölder seminorm. For now we define

$$h(N) := \frac{\alpha}{\alpha+\beta} \tilde{g}(N) - \tilde{l}(N)$$

and obtain

$$\|h(N_0) N_0\|_\infty \leq \|h\|_{C^0(\Gamma)} \|N_0\|_\infty. \tag{4.28}$$

To find a bound for the Hölder seminorm we consider $x \neq y \in \mathbb{R}^n$ and we get

$$\begin{aligned} \frac{h(N(x))N(x) - h(N(y))N(y)}{|x-y|^\sigma} &= \frac{h(N(x)) - h(N(y))}{|N(x) - N(y)|} N(x) \frac{|N(x) - N(y)|}{|x-y|^\sigma} \\ &\quad + h(N(y)) \frac{|N(x) - N(y)|}{|x-y|^\sigma} \\ &\leq \left(\|h\|_{C^1(\Gamma)} N^* + \|h\|_{C^0(\Gamma)} \right) \|N\|_{C^{0,\sigma}}. \end{aligned}$$

Hence from (4.27) and (4.28) we obtain

$$\|N_0(\tau,.)\|_{C^{0,\sigma}} \leq \|N_0(0,.)\|_{C^{0,\sigma}} + \tau \left(\|h\|_{C^1(\Gamma)} N^* + 2\|h\|_{C^0(\Gamma)} \right) \sup_{0 \leq \theta \leq \tau} \|N_0(\theta,.)\|_{C^{0,\sigma}}.$$

We denote

$$K_1(N^*) := \|h\|_{C^1(\Gamma)} N^* + 2\|h\|_{C^0(\Gamma)} \tag{4.29}$$

and choose

$$\tau_0 = \frac{1}{2K_1(N^*)}. \tag{4.30}$$

Then we have

$$\sup_{0\le\theta\le\tau_0} \|N_0(\theta,.)\|_{C^{0,\sigma}} \le 2\|N_0(0,.)\|_{C^{0,\sigma}}.$$

This estimate can be iterated such that for any $k \in \mathbb{N}$ we have

$$\sup_{0\le\theta\le k\tau_0} \|N_0(\theta,.)\|_{C^{0,\sigma}} \le 2^k\|N_0(0,.)\|_{C^{0,\sigma}}. \tag{4.31}$$

With the regularity property mentioned above (4.25) we obtain

$$\begin{aligned}\|D^2N_0(\tau,.)\|_\infty &\le c_2\tau^{\sigma/2-1}\|N_0(0,.)\|_{C^{0,\sigma}} + c_2\int_0^\tau (\tau-\theta)^{\sigma/2-1}\,\|h(N_0)N_0\|_{C^{0,\sigma}}\,d\theta \\ &\le c_2\tau^{\sigma/2-1}\|N_0(0,.)\|_{C^{0,\sigma}} + c_2\tau^{\sigma/2}K_1(N^*)\sup_{0\le\vartheta\le\tau}\|N_0(\vartheta,.)\|_{C^{0,\sigma}}\end{aligned}$$

Then for $0 < \vartheta \le T$ it follows from (4.31) that

$$\sup_{\vartheta\le\tau\le T}\|D^2N_0(\tau,.)\|_\infty \le c_2\vartheta^{\sigma/2-1}\|N_0(0,.)\|_{C^{0,\sigma}} + c_2T^{\sigma/2}K_1(N^*)2^k\|N_0(0,.)\|_{C^{0,\sigma}},$$

with $k = [T/\tau_0] + 1$. This proves (i) of the above Proposition.

To obtain (ii) we apply this estimate directly to the equation (4.24) and we use the fact that

$$\|\nabla D_{\alpha,\beta}\nabla N_0(\tau,.)\|_\infty \le \kappa_{\alpha,\beta}\|D^2N_0(\tau,.)\|_\infty.$$

□

4.2.6 Approximation Property of the Outer Solution

Theorem 4.8 *Let the assumptions* (A1)-(A4) *be satisfied and assume* $\tilde{g} \ge 0$ *and* $\tilde{l} > 0$ *are constant with* $(\tilde{g}-\tilde{l})/\tilde{l} \ne \beta$. *Suppose:*

1. *The pair* $(p(t,x,v), r(t,x))$ *solves the resting-phase transport system* (4.2, 4.3) *for* $0 \le t \le T$ *with homogeneous initial conditions* $p(0,x,v) = \varphi(x), r(0,x) = \psi(x)$.

2. $N_0(\tau,\xi)$ *solves the parabolic limit initial value problem* (4.24) *in* $C^{0,\sigma}(\mathbb{R}^n)$.

3. $$p_0(\tau,\xi) := \frac{\beta}{\omega(\alpha+\beta)}N_0(\tau,\xi), \qquad r_0(\tau,\xi) := \frac{\alpha}{\alpha+\beta}N_0(\tau,\xi).$$

4.

$$p_1(\tau,\xi,v) := \mathcal{F}_\alpha(v\cdot\nabla p_0(\tau,\xi)), \qquad r_1(\tau,\xi,v) := 0.$$

We define

$$P(\tau,\xi,v) := p_0(\tau,\xi) + \varepsilon p_1(\tau,\xi,v), \qquad R(\tau,\xi) := r_0(\tau,\xi).$$

Then for each ϑ with $0<\vartheta<T$ and each compact set $\Omega\subset\mathbb{R}^n$ there is a constant

$$c_4 = c_4(|\Omega|, T, \vartheta, \alpha, \beta, \nu_\alpha, s, N^*, \bar N(0), \|N_0(0,.)\|_{C^{0,\sigma}})$$

such that for all t with $\vartheta/\varepsilon^2 < t \le T/\varepsilon^2$ we have

$$\|p(t,x,.) - P(t,x,.)\|_{L^2(\Omega\times V)} + \|r(t,.) - R(t,.)\|_\infty \le c_4\varepsilon^2. \tag{4.32}$$

Proof: We define the residuum (A,B) by

$$\tilde p(\tau,\xi,v) - P(\tau,\xi,v) = \varepsilon^2 A(\tau,\xi,v) \quad\text{and}\quad \tilde r(\tau,\xi) - R(\tau,\xi) = \varepsilon^2 B(\tau,\xi)$$

and we show that A and B are bounded in appropriate norms, independently of ε.

The functions p_0, p_1, r_0 and r_1 are chosen to satisfy the ε^0- and ε^1-systems (4.6), (4.7), respectively. It remains to study the ε^2-system for A and B:

$$p_{0,\tau} + v\cdot\nabla p_1 = \mathcal{L}_0 A - \alpha A + \frac{\beta}{\omega}B - \tilde l(\tilde N)\tilde p \tag{4.33}$$

$$r_{0,\tau} = \alpha\int A dv - \beta B + \tilde g(\tilde N)\tilde r - \tilde l(\tilde N)\tilde r. \tag{4.34}$$

The solvability of this system for A and B leads to

$$\int A dv = \frac{\tilde g - \tilde l}{\tilde l} B. \tag{4.35}$$

It follows from (4.34) that

$$r_{0,\tau} = \left(\frac{\tilde g - \tilde l}{\tilde l} - \beta\right) B + \tilde g(\tilde N)\tilde r - \tilde l(\tilde N)\tilde r. \tag{4.36}$$

Hence

$$\|B(t,.)\|_\infty \le \left(\frac{\tilde g - \tilde l}{\tilde l} - \beta\right)^{-1} \left[\left(\|\tilde g\|_\infty + \|\tilde l\|_\infty\right)\bar N(t) + \frac{\alpha}{\alpha+\beta}\|N_{0,\tau}(\tau,.)\|_\infty\right] \tag{4.37}$$

where $\bar N(t)$ has been defined in (4.21). With Lemma 4.4 and with Proposition 4.7(ii) there is an ε-independent constant c_5 such that

$$\|B(t,.)\|_\infty \le c_5.$$

To find an estimate for A we solve (4.34) for B and introduce it into (4.33) to obtain

$$\mathcal{L}_\alpha A = p_{0,\tau} + v \cdot \nabla \mathcal{F}_\alpha (v \cdot \nabla p_0) - \frac{\tilde{g}(\tilde{N})\tilde{r}}{\omega} + \tilde{l}(\tilde{N}) \left(\frac{\tilde{r}}{\omega} + \tilde{p} \right) + \frac{1}{\omega} r_{0,\tau}, \tag{4.38}$$

with $\mathcal{L}_\alpha$ from (4.10) and $\mathcal{F}_\alpha$ from Corollary 4.2. We study L^2-norms. For the last term we get

$$\begin{aligned} \left\| \frac{\tilde{r}}{\omega} + \tilde{p} \right\|^2_{L^2(\mathbb{R}^n \times V)} &= \int \frac{\tilde{r}}{\omega} \left(\frac{\tilde{r}}{\omega} + 2 \int \tilde{p}\, dv \right) + \|\tilde{p}\|^2_{L^2} \\ &\leq \frac{2}{\omega^2} \bar{N}(\tau)^2 + c_1^2 \bar{N}(0)^2 \\ &\leq c_6 \bar{N}(0)^2, \end{aligned} \tag{4.39}$$

where we used Lemma 4.4, Proposition 4.5 and the fact that $\tilde{r}(\tau,\xi) + \int \tilde{p}(\tau,\xi,v)dv \leq \bar{N}(\tau)$. The constant c_6 is given by

$$c_6 := \frac{2}{\omega^2} e^{2\|g\|_\infty T} + c_1.$$

From (4.38) it follows that for all compact sets $\Omega \in \mathbb{R}^n$ we have

$$\begin{aligned} \|\mathcal{L}_\alpha A(\tau,.,.)\|^2_{L^2(\Omega \times V)} \leq\ & \omega|\Omega| \|N_{0,\tau}(\tau,.)\|^2_\infty + \omega \|\mathcal{F}_\alpha\|^2 s^2 |\Omega| \|D^2 p_0(\tau,.)\|^2_\infty \\ & + \frac{1}{\omega} \|\tilde{g}\|^2_\infty \bar{N}(\tau)^2 + \|\tilde{l}\|^2_\infty \left\| \frac{\tilde{r}(\tau,.)}{\omega} + \tilde{p}(\tau,.,.) \right\|^2_{L^2}. \end{aligned}$$

With use of Proposition 4.7, Lemma 4.4 and the above estimate (4.39) we arrive at

$$\begin{aligned} \|\mathcal{L}_\alpha A(\tau,.,.)\|^2_{L^2(\Omega \times V)} \leq\ & \omega|\Omega| \left(\kappa_{\alpha,\beta} K_{\vartheta,T} \|N_0(\tau,.)\|_{C^{0,\sigma}} + K_2(N^*) \right)^2 \\ & + \frac{\omega|\Omega| s^2}{\nu_\alpha} K_{\vartheta,T} \|N_0(\tau,.)\|_{C^{0,\sigma}} \\ & + \frac{1}{\omega} \|\tilde{g}\|^2_\infty e^{2\|g\|_\infty T} \bar{N}(0)^2 + c_6 \|\tilde{l}\|^2_\infty \bar{N}(0)^2, \end{aligned}$$

which is bounded independent of ε. We denote the right hand side by

$$c_7 = c_7(|\Omega|, T, \vartheta, \alpha, \beta, \nu_\alpha, s, N^*, \bar{N}(0), \|N_0(0,.)\|_{C^{0,\sigma}}).$$

Finally we split A according to

$$A = \frac{1}{\omega} \int A dv + \tilde{A}.$$

Then $\mathcal{L}_\alpha A = \mathcal{L}_\alpha \tilde{A} = Z \in \langle 1 \rangle^\perp$ and $\mathcal{F}_\alpha Z = \tilde{A}$. For $\tilde{A}$ we obtain

$$\|\tilde{A}(\tau,.,.)\|^2_{L^2(\Omega \times V)} = \|\mathcal{F}_\alpha Z\|^2_2 \leq \|\mathcal{F}_\alpha\|^2 \|Z\|^2_2 \leq \frac{c_7}{\nu_\alpha^2}.$$

Hence $\|\tilde{A}(\tau,.,.)\|_{L^2(\Omega\times V)} \leq \sqrt{c_7}/\nu_\alpha$. Since $\int Adv$ is bounded by B via (4.35) a upper bound for A results.
Finally we switch to the original time and space variables (t,x) and obtain the assertion of the Theorem. □

Remark 4.1 *We can not expect to get the strong approximation property as in Theorem 4.8 for nonlinear rates $\tilde{g}(N), \tilde{l}(N)$. For most relevant nonlinear cases the transport system (4.2, 4.3) and the parabolic limit (4.24) both will have a global compact attractor. It is however not clear how these attractors are related. If, for example, the attractor of the parabolic limit equation is chaotic, then trajectories are sensitive to perturbations. Each approximation of solutions will fail after a certain time. Even if the diffusion limit has a stable limit-cycle it is not clear that solutions of the transport model and the corresponding parabolic approximation enter the limit cycle with exactly the same phase. To get more insight into the nonlinear case one has to consider upper and lower semi-continuity of the corresponding attractors.*

4.3 Inner Expansion and Matching

For the inner expansion we consider the original fast time scale t and the macroscopic space scale ξ. Then $\hat{p}(t,\xi,v) = p(t,x/\varepsilon,v)$ and $\hat{r}(t,\xi) = r(t,x/\varepsilon)$ satisfy the initial value problem

$$\begin{aligned} \hat{p}_t + \varepsilon v\cdot\nabla\hat{p} &= \mathcal{L}_0\hat{p} - \alpha\hat{p} + \tfrac{\beta}{\omega}\hat{r} - \varepsilon^2\hat{l}(\hat{N})\hat{p} \\ \hat{r}_t &= \alpha\int\hat{p}dv - \beta\hat{r} + \varepsilon^2\hat{g}(\hat{N})\hat{r} - \varepsilon^2\hat{l}(\hat{N})\hat{r} \\ \hat{p}(0,\xi,v) = \varphi(\xi/\varepsilon,v) &\qquad \hat{r}(0,\xi) = \psi(\xi/\varepsilon), \end{aligned} \tag{4.40}$$

where $\hat{N} = \int\hat{p}dv + \hat{r}$ and $\hat{l}(\hat{N}) = \tilde{l}(\tilde{N}(\varepsilon^2 t,\xi))$ and $\hat{g}(\hat{N}) = \tilde{g}(\tilde{N}(\varepsilon^2 t,\xi))$.

Again we study expansions in ε

$$\hat{p}(t,\xi,v) := \sum_{j=0}^{k}\varepsilon^j\hat{p}_j(t,\xi,v), \qquad \hat{r}(t,\xi) := \sum_{j=0}^{k}\varepsilon^j\hat{r}_j(t,\xi)$$

$$\hat{N}(t,\xi), := \sum_{j=0}^{k}\varepsilon^j\hat{N}_j(t,\xi), \qquad \hat{N}_j(t,\xi) = \hat{r}_j(t,\xi) + \int\hat{p}_j(t,\xi,v)dv, \quad 0\leq j\leq k,$$

and we collect orders of ε of order zero only:

$$\varepsilon^0: \qquad \left\{\begin{array}{rcl} \hat{p}_{0,t} &=& \mathcal{L}_0\hat{p}_0 - \alpha\hat{p}_0 + \frac{\beta}{\omega}\hat{r}_0 \\ \hat{r}_{0,t} &=& \alpha\int\hat{p}_0dv - \beta\hat{r}_0 \end{array}\right. . \tag{4.41}$$

We show that the functional

$$\mathcal{E}(p,r) := \frac{\omega}{2}\int p^2 dv + r\int p dv + \frac{r^2}{2}$$

is a Lyapunov function of the integro-differential system (4.41).

Theorem 4.9 *For solutions* $(\hat{p}_0, \hat{r}_0)$ *of* (4.41) *we have*

$$\frac{d}{dt}\mathcal{E}(\hat{p}_0,\hat{r}_0) \le -\alpha\omega\int\left(\hat{p}_0 - \frac{1}{\omega}\int \hat{p}_0 dv'\right)^2 dv.$$

Proof:

$$\begin{aligned}\frac{d}{dt}\frac{\omega}{2}\int \hat{p}_0^2 dv &= \omega\int \hat{p}_0\mathcal{L}_0\hat{p}_0 dv - \omega\alpha\int\hat{p}_0^2 dv + \beta\int\hat{p}_0 dv\ \hat{r}_0\\ &\le -\alpha\omega\int\hat{p}_0^2 dv + \beta\hat{r}_0\int\hat{p}_0 dv\end{aligned}$$

$$\begin{aligned}\frac{d}{dt}\left(\hat{r}_0\int\hat{p}_0 dv\right) &= \left(\alpha\int\hat{p}_0 dv - \beta\hat{r}_0\right)\int\hat{p}_0 dv + \hat{r}_0\left(\int\mathcal{L}_0\hat{p}_0 dv - \alpha\int\hat{p}_0 dv + \frac{\beta}{\omega}\int\hat{r}_0 dv\right)\\ &= \alpha\left(\int\hat{p}_0 dv\right)^2 - (\alpha+\beta)\hat{r}_0\int\hat{p}_0 dv + \beta\hat{r}_0^2,\end{aligned}$$

$$\frac{d}{dt}\frac{r_0^2}{2} = \alpha\hat{r}_0\int\hat{p}_0 dv - \beta\hat{r}_0^2.$$

From these inequalities it follows that

$$\begin{aligned}\frac{d}{dt}\mathcal{E}(\hat{p}_0,\hat{r}_0) &\le -\omega\alpha\hat{p}_0^2 dv + \alpha\left(\int\hat{p}_0 dv\right)^2\\ &= -\alpha\omega\int\left(\hat{p}_0 - \frac{1}{\omega}\int\hat{p}_0 dv'\right)^2 dv.\end{aligned}$$

□

For now we abbreviate the mean value by

$$\phi_0(t,\xi) := \int\hat{p}_0(t,\xi,v')dv'.$$

Since $\mathcal{E}$ is a Lyapunov function we have

$$\lim_{t\to\infty}\|\hat{p}_0(t,\xi,.) - \frac{1}{\omega}\phi_0(t,\xi)\|_2 = 0.$$

Hence in the limit of $\tau \to \infty$ the function $\hat{p}_0$ does not depend on v. Then the asymptotic behavior of (4.41) is determined by the system

$$\begin{aligned} \phi_{0,t} &= -\alpha\phi_0 + \beta\hat{r}_0 \\ \hat{r}_{0,t} &= \alpha\phi_0 - \beta\hat{r}_0. \end{aligned} \tag{4.42}$$

The mass $\hat{N}(\xi) = \phi_0(\xi) + \hat{r}_0(\xi)$ is preserved and the steady state $(\beta/(\alpha+\beta)\hat{N}, \alpha/(\alpha+\beta)\hat{N})$ is asymptotically stable. The initial data of the original problem (see (A2)) determine $\hat{N}$:

$$\hat{N}(\xi) = \int \varphi(\xi, v)dv + \psi(\xi).$$

Hence the limit of the inner solution $(\hat{p}_0, \hat{r}_0)$ for $t \to \infty$ is given by

$$\begin{aligned} \hat{P}_0(\xi) &= \tfrac{\beta}{\omega(\alpha+\beta)} \left(\int \varphi(\xi, v')dv' + \psi(\xi)\right) \\ \hat{R}_0(\xi) &= \tfrac{\alpha}{\alpha+\beta} \left(\int \varphi(\xi, v')dv' + \psi(\xi)\right). \end{aligned} \tag{4.43}$$

Matching: To match inner and outer solutions we use the asymptotic limit of the inner solution (4.43) as initial condition for the outer solution. These are homogeneous in v, as was expected for the outer solution. The corresponding initial condition for the parabolic limit $N_0(\tau, \xi)$ is then given by

$$N_0(0, \xi) = \omega\hat{P}_0(\xi) + \hat{R}_0(\xi) = \int \varphi(\xi, v)dv + \psi(\xi). \tag{4.44}$$

This matches exactly the initial conditions of the outer expansion which we used in (4.24).

4.4 Discussion

4.4.1 Perturbations of Homogeneous Initial Data

In this Section we show that solutions of the resting phase transport equation (4.2, 4.3) for initial data of the form $p(0, x, v) = \varphi(x) + \varepsilon\varphi_1(x, v)$ are of order ε compared to the solution of the corresponding homogeneous problem with $p(0, x, v) = \varphi(x)$.

Theorem 4.10 *Assume* (A1)-(A4). *Suppose that*

1. (r, p) *solves* (4.2, 4.3) *with initial conditions* $p(0, x, v) = \varphi(x) + \varepsilon\varphi_1(x, v)$ *and* $r(0, x) = \psi(x)$ *with* $\int_V \varphi_1(x, v)dv = 0$.

2. (a, b) *solves* (4.2, 4.3) *with initial conditions* $a(0, x, v) = \varphi(x)$ *and* $b(0, x) = \psi(x)$.

Then for each T there is a constant c_8 such that for all $t \leq T$

$$\|p(t,.,.) - a(t,.,.)\|_{L^2(\mathbb{R}^n \times V)} + \|r(t,.) - b(t,.)\|_\infty \leq \varepsilon c_8 \|\varphi_1\|_{D(\mathcal{A})}.$$

Proof: We study the difference $y := p - a$, $z := r - b$ and we denote $N(t,x) := \int p(t,x,v)dv + r(t,x)$ and $M(t,x) := \int a(t,x,v)dv + b(t,x)$. Then (y,z) solves

$$\begin{aligned} y_t + v \cdot \nabla y &= \mathcal{L}_0 y - \alpha y + \frac{\beta}{\omega} z - l(N)p + l(M)a \\ z_t &= \alpha \int_V y\, dv - \beta z + g(N)r - g(M)b - l(N)r + l(M)b \\ y(0,x,v) &= \varepsilon \varphi_1(x,v) \\ z(0,x) &= 0. \end{aligned}$$

Since $N - M = \int (p-a)dv + r - b = \int y\, dv - z$, we rewrite this system as

$$\begin{aligned} y_t + v \cdot \nabla y &= \mathcal{L}_0 y - \alpha y + \frac{\beta}{\omega} z - l(N)y - a\frac{l(N) - l(M)}{N - M}\left(\int y\, dv + z\right) \\ z_t &= \alpha \int_V y\, dv - \beta z + g(N)z + b\frac{g(N) - g(M)}{N - M}\left(\int y\, dv + z\right) \\ &\quad -l(N)z - b\frac{l(N) - l(M)}{N - M}\left(\int y\, dv + z\right) \\ y(0,x,v) &= \varepsilon \varphi_1(x,v) \\ z(0,x) &= 0. \end{aligned}$$

The functions g and l are supposed to be uniformly bounded in C^1. Hence the above system defines a linear evolution equation for (y,z), where the operator $\mathcal{A}$ is perturbed by a bounded, time and space dependent, multiplication operator. We know already that the initial value problem is solvable since the solutions (p,r) and (a,b) exist. Hence there is a bounded solution operator $\mathcal{Q}(t,x) : D(\Phi) \times L^2(\mathbb{R}^n) \to L^2(\mathbb{R}^n \times V) \times L^2(\mathbb{R}^n)$ such that the solution can be written as

$$\begin{pmatrix} y(t,x,v) \\ z(t,x) \end{pmatrix} = \mathcal{Q}(t,x) \begin{pmatrix} \varepsilon \varphi_1(x,v) \\ 0 \end{pmatrix}.$$

Then the assertion follows with $c_8 := \sup_{t \leq T} \|\mathcal{Q}\|_{\mathcal{L}(D(\Phi), L^2)}$. □

4.4.2 Small Proportion of the Population in Resting Phase

In case of $\alpha \to 0$ individuals do not stop moving and hence in our model they cannot reproduce. For the relevant operators and parameters we observe that for $\alpha \to 0$ (we

will not specify any norms for convergence of these operators).

$$\begin{aligned} \mathcal{L}_\alpha = -(\mu+\alpha)I + (\mu+\alpha)\mathcal{T}_\alpha &\longrightarrow -\mu I + \mu\mathcal{T}_0 \\ \mathcal{F}_\alpha &\longrightarrow \mathcal{F}_0 \\ D_{\alpha,\beta} &\longrightarrow D_0 = -\frac{1}{\omega}\int v\mathcal{F}_0 v dv \\ N_0 &\longrightarrow \omega p_0 \end{aligned}$$

Then the limit equation (4.17) reduces to

$$N_{0,\tau} = \nabla D_0 \nabla N_0 - \tilde{l}(N_0)N_0$$

which is a reaction-diffusion equation for the pure death process with diffusion tensor D_0 as in the cases studied in [52].

4.4.3 Large Proportion of the Population in Resting Phase

There is a large proportion of the population in the resting phase if α is large and β is small. In that case $\alpha/(\alpha+\beta) \approx 1$ and the limit equation (4.17) becomes

$$N_{0,\tau} = \nabla D_{\alpha,\beta} \nabla N_0 + \tilde{f}(N_0). \tag{4.45}$$

The complement factor $\beta/(\alpha+\beta)$ is small, which shows that the modified diffusion tensor $D_{\alpha,\beta}$ given by (4.18) is small. To be more specific we consider an example:
Example: $V = sS^{n-1}$, $T = 1/\omega$: Then $T_\alpha = 1/\omega$ and the pseudo inverse $\mathcal{F}_\alpha$ is a multiplication operator by $-(\mu+\alpha)^{-1}$. Then

$$D_{\alpha,\beta} = \frac{\beta}{\omega(\alpha+\beta)}\int vv\, dv \frac{1}{\mu+\alpha} = \frac{s^2}{(\mu+\alpha)n}\frac{\beta}{\alpha+\beta}I.$$

Then the isotropic limit equation reads

$$N_{0,\tau} = d_\alpha \Delta N_0 + \tilde{f}(N_0), \quad \text{with} \quad d_\alpha = \frac{s^2}{(\mu+\alpha)n}\frac{\beta}{\alpha+\beta}. \tag{4.46}$$

For $\alpha = 0$ this reduces to $d_0 = \frac{s^2}{\mu n}$. Hence increasing α reduces the motility.

Remark 4.2 *It is easy to see that birth-death terms of order less or higher then ε^2 will not lead to a limit equation like* (4.17)*:*

1. *For perturbations of the form $f(u) = \varepsilon\tilde{f}(u)$ the nonlinearity f would enter into the turning operator $\mathcal{L}_\alpha$ in the equation for ε^1. Then no longer a linear problem results and we cannot apply the framework of Fredholm operators as used here.*

2. *For higher order perturbations $f(u) = \varepsilon^3\tilde{f}(u)$ the nonlinearity would not enter at all and the limiting equation would be linear to second order with vanishing reaction part.*

4.4.4 A Parabolic Model with Resting Phase

It is illustrating to compare the foregoing results with a model where particle movement is described by an uncorrelated random walk (Brownian motion). We keep the assumptions of Section 4.1 with the exception of assumption 1. Instead we assume now that

1'. *The movement of the population is described by the diffusion equation* $u_t = d\Delta u$, $d > 0$.

Then the parabolic model with resting phase reads

$$\begin{aligned} u_t &= d\Delta u - \alpha u + \beta r - l(N)u \\ r_t &= \alpha u + g(N)r - \beta r - l(N)r \\ N(t,x) &= u(t,x) + r(t,x) \end{aligned} \tag{4.47}$$

We consider the same scaling a above for the outer expansion

$$\tau = \varepsilon^2 t, \qquad \xi = \varepsilon x, \qquad f(u) = \varepsilon^2 \tilde{f}(u).$$

Then the scaled system reads.

$$\begin{aligned} \varepsilon^2 u_\tau &= \varepsilon^2 d\Delta_\xi u - \alpha u + \beta r - \varepsilon^2 \tilde{l}(N)u \\ \varepsilon^2 r_\tau &= \alpha u + \varepsilon^2 \tilde{g}(N)r - \beta r - \varepsilon^2 \tilde{l}(N)r. \end{aligned} \tag{4.48}$$

Again we consider expansions in ε for $k > 2$.

$$u(\tau,\xi) = \sum_{j=0}^{k} \varepsilon^j u_j(\tau,\xi), \qquad r(\tau,\xi) = \sum_{j=0}^{k} \varepsilon^j r_j(\tau,\xi),$$
$$N(\tau,\xi) = \sum_{j=0}^{k} \varepsilon^j N_j(\tau,\xi), \qquad N_j = u_j + r_j.$$

A comparison of orders of ε leads to the following systems

$$\varepsilon^0: \qquad \begin{aligned} -\alpha u_0 + \beta r_0 &= 0 \\ \alpha u_0 - \beta r_0 &= 0 \end{aligned} \tag{4.49}$$

$$\varepsilon^1: \qquad \begin{aligned} -\alpha u_1 + \beta r_1 &= 0 \\ \alpha u_1 - \beta r_1 &= 0 \end{aligned} \tag{4.50}$$

$$\varepsilon^2: \qquad \begin{aligned} u_{0,\tau} &= d\Delta u_0 - \tilde{l}(N_0)u_0 - \alpha u_2 + \beta r_2 \\ r_{0,\tau} &= \alpha u_2 - \beta r_2 + \tilde{g}(N_0)r_0 - \tilde{l}(N_0)r_0 \end{aligned} \tag{4.51}$$

From (4.49) it follows that $r_0 = \frac{\alpha}{\beta} u_0$, hence $N_0 = \frac{\alpha+\beta}{\beta} u_0$. We solve the second equation of (4.51) for $-\alpha u_2 + \beta r_2$ and use this in the first equation of (4.51) to obtain a single equation for N_0:

$$N_{0,\tau} = \frac{\beta d}{\alpha+\beta} \Delta N_0 + \frac{\alpha}{\alpha+\beta} \tilde{g}(N_0) N_0 - \tilde{l}(N_0) N_0. \tag{4.52}$$

This equation shows exactly the same scaling in α and β as (4.17) and (4.18). The reproduction rate is scaled by the mean proportion of the population which is at rest and the motility is scaled by the mean proportion which is moving.

5 Chemotaxis and Density Control

In this chapter we study a version of the Patlak-Keller-Segel model where the chemotactic velocity depends on both, the external signal and the local population density. A parabolic quasilinear strongly coupled system follows. Motivated by reasonable biological assumptions we assume that the chemotactic response is turned off at high cell concentrations. The response to high population densities prevents overcrowding. We prove local and global existence in time of classical solutions. Numerical simulations show interesting phenomena of pattern formation and formation of stable aggregates, which are similar to the patterns observed in Section 2.6.3 and are presented in [53].

5.1 Introduction

We consider the following parabolic chemotaxis system

$$\begin{aligned} u_t &= \nabla(\nabla u - V(u,v)\nabla v) \\ v_t &= \mu\Delta v + g(u,v) \\ u(0,.) &= u_0, \quad v(0,.) = v_0. \end{aligned} \tag{5.1}$$

on a C^3-differentiable, compact Riemannian manifold $(\mathcal{M}, (\gamma^{\alpha\beta})_{\alpha\beta})$ without boundary. This class includes a 1-D interval with periodic boundary conditions or in 2-D a torus (e.g $\mathbb{R}^2/\mathbf{Z}^2$). From solutions to homogeneous Neumann boundary conditions on intervals in 1 (or 2) dimensions we can construct solutions with periodic boundary conditions on a domain of double (four times) the size. Hence also Neumann boundary conditions on intervals in 1- and 2-D are included here.

The function $u(t,x)$ describes the particle density at time t, at position $x \in \bar{\Omega}$; $v(t,x)$ is the density of the external signal. The *chemotactic velocity* V is assumed to be bounded and the function $g(u,v)$ describes production and degradation of the external stimulus.

We will show global existence of classical solutions for

$$V(u,v) = u\beta(u)\chi(v), \tag{5.2}$$

where $\beta, \chi \in C^3$ satisfy the following conditions

$$\begin{aligned} &\text{(i)} && \chi > 0 \\ &\text{(ii)} && \beta(0) > 0, \text{ there exists an } \bar{u} > 0 \text{ such that } \beta(\bar{u}) = 0 \\ & && \text{and } \beta(u) > 0 \text{ for } 0 < u < \bar{u}. \end{aligned} \tag{5.3}$$

For the production term $g(u,v)$ we assume that it has birth-death structure, i.e., we assume $g \in C^2(\mathbb{R}^2)$ and

$$g(u,v) = g_1(u,v)u - g_2(u,v)v, \tag{5.4}$$

with bounded death rate $g_2 \geq \delta > 0$ and with birth rate $g_1 \geq 0$. Then there exists a $\bar{v} > 0$ such that

$$g(u,\bar{v}) \leq 0 \quad \text{for all} \quad 0 \leq u \leq \bar{u}. \tag{5.5}$$

The standard example for V is

$$V_0(u,v) = \chi u(1-u) \tag{5.6}$$

and for g it is the linear function

$$g_0(u,v) = \gamma u - \delta v, \quad \gamma \geq 0, \delta > 0, \tag{5.7}$$

which has been used in the related literature as well. In contrast to previous studies of parabolic chemotaxis equations, we assume that the chemotactic velocity is bounded. The case of $V(u,v) = u\chi(v)$ has been studied in great detail in the literature. Finite time blow-up of solutions has, in particular, captured much attention (see the references in Section 1.2.3). When the solution blows up, the model is no longer valid and another process is assumed to start (i.e., formation of a fruiting body or differentiation into several cell types). In biological processes of aggregation and cell movement, however, developmental phases do not necessarily occur sequentially. For example, cell specification of embryonic cells or prespore/prestalk cells in *Dictyostelium* can occur prior to or during periods of cell movement. More pertinently, the cAMP signaling mechanism responsible for initial aggregation of *Dictyostelium* is also thought to play a major role in the subsequent developmental stages (for example, slug formation or culmination [73]). Bearing this in mind, it is preferable to develop a simple chemotaxis model (like (5.1)) excluding blow up and permitting global existence independently of thresholds or of space dimensions.

In fact, a steady state analysis of (5.1) together with the assumptions (5.3) shows that stationary non constant patterns are possible for sufficiently large χ. In $1-D$ the steady state analysis leads to

$$u_x = u\beta(u)\chi(v)v_x,$$

implying that a stationary solution $u(x)$ has an extremum when $u = 0$ or $u = \bar{u}$ or $v_x = 0$. Thus the distribution will be flat about $u = 0$ and $u = \bar{u}$, which has indeed been observed in numerical simulations (see [53]). A detailed bifurcation analysis of steady states for a similar system to (5.1) can be found in Schaaf [98] and for the classical model in Senba and Suzuki [105].

Another approach to global existence of solutions to a chemotaxis equation, with V linear in u, has been considered by Gajewski and Zacharias [38], and independently by Nagai *et al.* [83] and Biler [13]. They use a Lyapunov function to demonstrate global existence in the subcritical case (i.e., small enough χ). Here we require no such restriction on the size of χ, nor do we have dependence on the space dimension for global existence.

Chemotactic systems of the type (5.1) can be derived from a biased random walk model whereby the probability of a particle jumping is modulated by an extracellular signal and by the local population density. In particular, specific conditions for the chemotactic velocity can be derived from realistic assumptions based on how cells detect and interpret environmental cues. Some bacteria, for example, are known to secrete a chemical signal which allows to locally detect the population density (*quorum sensing molecules* [29]). Other examples, which lead to the functional form of V as studied here, include mechanical inhibition of signal transduction due to interactions between cell boundaries of neighboring cells or competition of attraction and repulsion mechanisms. We give several example in [90].

The main result of this chapter is the existence of global in time solutions as presented in Theorem 5.7. The proof of global existence relies on the existence of an invariant region Γ as shown in Theorem 5.2. To our knowledge, the known literature on quasilinear parabolic systems does not provide a result on local existence which would fit exactly to (5.1). Hence we start our analysis by showing local in time existence using a fixed point argument. In case of a bounded region Ω with Dirichlet boundary conditions the results of Amann [6] on local existence could be applied if $V < 2\sqrt{\mu}$. This condition guarantees that the equation is of parabolic type. As demonstrated below we need no condition of that kind. We will study solutions (u, v), where v is contained in a slightly better regularity class then u (see the definitions of $\mathcal{X}_u, \mathcal{X}_v$ below). Then the cross diffusion term in (5.1) appears as a lower order term, compared to the second derivative of u. Hence it can be treated as a perturbation. This approach uses the fact, that the generator of (5.1) is of tridiagonal type and we make use of regularity properties of the equation for the signal v. The regularity properties of the heat equation semigroup have been summarized in Taylor [113], see Lemma 5.1.

5.2 Local and Global Existence

We study classical solutions of (5.1) for some $t_0 > 0$ in spaces

$$\mathcal{X}_u := C([0,t_0), W^{\sigma,p}(\mathcal{M})), \qquad \mathcal{X}_v := C([0,t_0), W^{\sigma+\alpha,p}(\mathcal{M})),$$

with

$$1 < \sigma < 2, \quad 1 < \alpha < 2, \quad 2 < \sigma + \alpha < 3, \quad \max\left\{\frac{n}{\sigma-1}, \frac{n}{2-\sigma}\right\} < p. \tag{5.8}$$

For this choice of parameters we have a Sobolev imbedding $W^{\sigma,p} \to C_b^1$ (see [1]).

Equation (5.1) falls into the class of quasilinear systems with cross-diffusion. However, in its present form there is no existence result in the literature which applies directly. The works of Ladyžhenskaja, Solonnikov and Ural'ceva [70] and Amann [6] are standard sources in this field.

We will construct solutions using a contraction mapping argument. This involves intensive use of the following regularity properties of the solution semigroup $e^{\Delta t}$ of the heat equation $u_t = \Delta u$ on $\mathcal{M}$.

Lemma 5.1 (Taylor, [113] p. 274)
For all $p \geq q > 0$ and $s \geq r$ we have

$$e^{\Delta t} : W^{r,q}(\mathcal{M}) \to W^{s,p}(\mathcal{M}), \quad \textit{with norm} \quad Ct^{-\kappa},$$

where κ is given by

$$\kappa = \frac{n}{2}\left(\frac{1}{q} - \frac{1}{p}\right) + \frac{1}{2}(s-r).$$

Our analysis starts by identifying an invariant region Γ for solutions in $\mathcal{X}_u \times \mathcal{X}_v$. We proceed to show a number of appropriate *a-priori* estimates which enable a contraction mapping argument for local existence. Moreover, these estimates demonstrate bounds which grow polynomially in time, leading to global existence.

For simplicity of notation, we shall denote all constants by C, even though they might have different values in the same estimate. Of course, all constants used below depend on the metric $(\gamma^{\alpha\beta})_{\alpha\beta}$ of $\mathcal{M}$. We will omit the argument $(\mathcal{M})$ of the Sobolev spaces $W^{\sigma,p}$ and we denote the norms by $\|.\|_{\sigma,p}$.

5.2.1 Invariant Region

The zero of the chemotactic velocity $V(u,v)$ at $u = \bar{u}$ permits us to find an invariant region for (u,v) in $\mathbb{R}^2$. This a-priori L^∞-estimate is the key ingredient to obtain global existence in time.

Theorem 5.2 *Assume* (5.2)–(5.4) *Then the region*

$$\Gamma := \{(u,v) \in \mathbb{R}^2 : 0 \le u \le \bar{u},\ 0 \le v \le \bar{v}\}$$

is positively invariant for solutions of (5.1).

Proof: We explicitly prove the existence of an upper limit $(\bar{u}, \bar{v})$. The proof of non-negativity uses the same construction.

Let $(u,v) \in \mathcal{X}_u \times \mathcal{X}_v$ be a solution of (5.1). We define

$$u^+(t,x) := \begin{cases} u(t,x) - \bar{u}, & \text{if} \quad u(t,x) > \bar{u}, \\ 0, & \text{otherwise.} \end{cases}$$

For each time t, where $0 \le t \le t_0$, we split the manifold $\mathcal{M}$ into three disjoint sets $\mathcal{M} = J_-(t) + J_0(t) + J_+(t)$:

$$\begin{aligned} J_-(t) &:= \{x \in \mathcal{M} : u(t,x) < \bar{u}\} \\ J_0(t) &:= \{x \in \mathcal{M} : u(t,x) = \bar{u}\} \\ J_+(t) &:= \{x \in \mathcal{M} : u(t,x) > \bar{u}\}. \end{aligned}$$

Since $u(t,.) \in W^{\sigma,p}$ for $\sigma > 1, p > n/2$, it is continuously differentiable (by the Sobolev imbedding). Thus, the above sets are measurable and $\partial J_+(t)$ is a differentiable submanifold. We can write

$$\begin{aligned} \frac{d}{dt}\frac{1}{2}\|u^+(t,.)\|_2^2 &= \int_{J_-(t)} u^+ u_t^+ dx + \int_{J_0(t)} u^+ u_t^+ dx + \int_{J_+(t)} u^+ u_t^+ dx \\ &= \int_{J_+(t)} (u - \bar{u}) u_t^+ \, dx \end{aligned}$$

since, on $J_0 \cup J_-$, we have $u^+ = 0$. The set $J_+(t)$ is open and u is continuous in time t. Then for each $x \in J_+(t)$ there exists an $\varepsilon > 0$ such that $u(\vartheta, x) > \bar{u}$ for all $\vartheta \in (t-\varepsilon, t+\varepsilon)$. Hence $u_t^+ = u_t$ on $J_+(t)$. Then with the first equation of (5.1) we obtain

$$\begin{aligned} \frac{d}{dt}\frac{1}{2}\|u^+(t,.)\|_2^2 &= \int_{J_+(t)} (u - \bar{u}) \left(\nabla(\nabla u - V(u,v)\nabla v)\right) dx \\ &= -\int_{J_+(t)} (\nabla u)^2 + \int_{\partial J_+(t)} (u - \bar{u})(\nabla u \cdot \nu) dS \\ &\quad + \int_{J_+(t)} \nabla u V(u,v) \nabla v \, dx - \int_{\partial J_+(t)} (u - \bar{u}) V(u,v)(\nabla v \cdot \nu) dS, \end{aligned}$$

where ν denotes the outer normal on $\partial J_+(t)$. On the boundary of $J_+(t)$ we have $u = \bar{u}$, and the boundary integrals vanish. Thus,

$$\frac{d}{dt}\frac{1}{2}\|u^+(t,.)\|_2^2 = -\int_{J_+(t)} (\nabla u)^2 + \int_{J_+(t)} \nabla u V(u,v) \nabla v \, dx. \tag{5.9}$$

As we are interested in solutions inside Γ only, we allow V outside Γ to be modified into

$$\tilde{V}(u,v) := \begin{cases} V(u,v), & \text{if} \quad u \le \bar{u} \\ 0, & \text{else} \end{cases},$$

which is continuous at $\bar{u}$. Then for solutions of (5.1), with $\tilde{V}$ instead of V, the estimate (5.9) can be reduced to

$$\frac{d}{dt}\|u^+(t,.)\|_2^2 \le 0.$$

If initially $u_0^+ = 0$, then $u^+(t,.) = 0$ for all times of existence. Since $V \equiv \tilde{V}$ on Γ, the same conclusion holds for (5.1) with the original V.

To prove the upper bound of v we define

$$v^+(t,x) := \begin{cases} v(t,x) - \bar{v}, & \text{if} \quad v(t,x) > \bar{v}, \\ 0, & \text{else.} \end{cases}$$

We again split $\mathcal{M}$ according to $v <, =, > \bar{v}$ and consider $\frac{d}{dt}\frac{1}{2}\|v^+(t,.)\|_2^2$. Here

$$\frac{d}{dt}\|v^+(t,.)\|_2^2 \le 0$$

follows directly. This proves $v(t,x) \le \bar{v}$, if initially $v_0(x) \le \bar{v}$.
The non-negativity property, $u \ge 0, v \ge 0$, can be shown by a similar construction. □

5.2.2 A-priori estimates

We study first the second equation of (5.1).

Theorem 5.3 *Assume* (5.2)-(5.4) *and* p, σ, α *are as given in* (5.8). *Then solutions* $(u,v) \in \mathcal{X}_u \times \mathcal{X}_v$, *with* $(u(t,x), v(t,x)) \in \Gamma$, *of* (5.1) *satisfy:*

$$\|v\|_{\mathcal{X}_v} \le \|v_0\|_{\sigma+\alpha,p} + C_0 t_0^{1-h}\left(\|u\|_{\mathcal{X}_u} + \|u\|_{\mathcal{X}_u}^2 + \|v\|_{\mathcal{X}_v}\right), \tag{5.10}$$

where $h = \frac{1}{2}(\sigma + \alpha - 1)$ *and the constant* $C_0 > 0$ *depends according to*

$$C_0 = C_0\left(\sigma, \alpha, p, \bar{u}, \|g_1\|_{C^1(\Gamma)}\right). \tag{5.11}$$

Proof: With use of semigroup notation $T_\mu(t) := e^{\mu\Delta t}$, we can write the solution of $v_t = \mu\Delta v + g(u,v)$, $v(0,x) = v_0(x)$ formally as

$$\begin{aligned} v(t) &= T_\mu(t)v_0 + \int_0^t T_\mu(t-s)g_1(u,v)u\,ds - \int_0^t T_\mu(t-s)g_2(u,v)v\,ds \\ &\le T_\mu(t)v_0 + \int_0^t T_\mu(t-s)g_1(u,v)u\,ds. \end{aligned} \tag{5.12}$$

Here we have made use of $g_2 \geq 0$, $v \geq 0$ and the fact that $T_\mu(t)$ is positive. From Lemma 5.1, we obtain $T_\mu(t) : W^{1,p} \to W^{\sigma+\alpha,p}$ with norm Ct^{-h}, where $h := \frac{1}{2}(\sigma + \alpha - 1)$ and $C = C(\sigma, \alpha)$. From the assumptions on σ and α it follows that $0 < h < 1$. Then we obtain (suppressing the arguments (t, x) or $(s, .)$ of the dependent functions u, v)

$$\begin{aligned}
\|v\|_{\mathcal{X}_v} &\leq \|v_0\|_{\sigma+\alpha,p} + Ct_0^{1-h} \sup_{0\leq t\leq t_0} \|g_1(u,v)u\|_{1,p} \\
&\leq \|v_0\|_{\sigma+\alpha,p} \\
&\quad + Ct_0^{1-h} \sup_t \{\|g_1 u\|_p + \|(g_1)_u \nabla u\, u\|_p + \|(g_1)_v \nabla v\, u\|_p + \|g_1 \nabla u\|_p\} \quad (5.13) \\
&\leq \|v_0\|_{\sigma+\alpha,p} \\
&\quad + Ct_0^{1-h} \|g_1\|_{C^1(\Gamma)} \sup_t \{\|u\|_p + \|u\nabla u\|_p + \|u\nabla v\|_p + \|\nabla u\|_p\}\,. \quad (5.14)
\end{aligned}$$

Here we use the notation that the p-norm of a vector valued function $\varphi(x) \in \mathbb{R}^n$ is given by $\|\varphi\|_p = \left(\sum_{i=1}^n \|\varphi_i\|_p^p\right)^{1/p}$.

Since $\sigma > 1$, we have $\|u\|_p + \|\nabla u\|_p \leq \|u\|_{\sigma,p}$ and $\|u\nabla u\|_p \leq C\|u\|_{\sigma,p}^2$. We choose some $\tilde{q}$ with $1 \leq \tilde{q} \leq \frac{n}{n-p}$ and we denote the dual exponent by $\tilde{p}$ ($\tilde{p}^{-1} + \tilde{q}^{-1} = 1$). Then from Hölder's inequality it follows that $\|u\nabla v\|_p \leq \|u\|_{\tilde{p}p}\|v\|_{1,\tilde{q}p}$. Moreover, we have the Sobolev imbedding $W^{2,p} \to W^{1,\tilde{q}p}$. Finally, from the existence of an invariant region Γ, it follows that there is a constant $C > 0$ such that $\|u\|_{\tilde{p}p} \leq C\bar{u}$, where $C = C(\tilde{q}, p)$. This gives $\|u\nabla v\|_p \leq C\bar{u}\|v\|_{2,p}$. Then each term in (5.14) is controlled and (5.10) follows. □

With this estimate, we can derive several auxiliary inequalities which will be useful in the sequel.

Corollary 5.4 *Assume the conditions of the above Theorem.*

1. *For a choice of* $t_0 \leq (\frac{1}{2C_0})^{\frac{1}{1-h}}$, *we obtain*

$$\|v\|_{\mathcal{X}_v} \leq C_1 \left(\|v_0\|_{\sigma+\alpha,p} + \|u\|_{\mathcal{X}_u} + \|u\|_{\mathcal{X}_u}^2\right), \quad (5.15)$$

   where $C_1 = 2\max\{1, C_0 t_0^{1-h}\}$.

2. *For the contraction mapping argument later we require the following: Given two functions* $\varphi_1, \varphi_2 \in \mathcal{X}_u$, *the corresponding solutions* $v_j = v_j(\varphi_j)$ *of* $v_{j,t} = \mu\Delta v_j + g(\varphi_j, v_j)$, $v_j(0) = v_0$, *for* $j = 1, 2$ *satisfy*

$$\|v_1 - v_2\|_{\mathcal{X}_v} \leq C_2 \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}, \quad (5.16)$$

   for some constant $C_2(C_0, \bar{v}, \|\varphi_1\|_{\mathcal{X}_u}, \|\varphi_2\|_{\mathcal{X}_u}, t_0) > 0$ *for sufficiently small* t_0 *(e.g.,* t_0 *satisfies* (5.17) *below).*

Proof: The estimate (5.15) follows directly from (5.10) by the specific choice of t_0.

To show (5.16), we consider the difference $\Psi := v_1 - v_2$. This satisfies

$$\Psi_t = \mu\Delta\Psi + g(\varphi_2, v_2)\Psi + (G_1 - G_2)v_1, \quad \Psi(0) = 0,$$

where $G_i = g(\varphi_i, v_i)$, $i = 1, 2$. For Ψ, estimate (5.14) must be supplemented by the term

$$+Ct_0^{1-h} \sup_t \|(G_1 - G_2)v_1\|_p \leq Ct_0^{1-h}\|g\|_{C^1(\Gamma)} \left(\|\varphi_1 - \varphi_2\|_{\mathcal{X}_u} + \|v_1 - v_2\|_{\mathcal{X}_v}\right) \|v_1\|_p.$$

From the existence of the invariant region Γ we have $\|v_1\|_p \leq C_p\bar{v}$. The quadratic term in (5.10) can be estimated as

$$\|\varphi_1 - \varphi_2\|^2_{\mathcal{X}_u} \leq \left(\|\varphi_1\|_{\mathcal{X}_u} + \|\varphi_2\|_{\mathcal{X}_u}\right) \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}.$$

Then it follows that

$$\|v_1 - v_2\|_{\mathcal{X}_v} \leq Ct_0^{1-h} \left(\|\varphi_1 - \varphi_2\|_{\mathcal{X}_u} + \|v_1 - v_2\|_{\mathcal{X}_v}\right).$$

Assuming

$$t_0 \leq \left(\frac{1}{2C}\right)^{\frac{1}{1-h}}, \tag{5.17}$$

we obtain (5.16) with an appropriate C. □

Remark 5.1 *If, moreover, $(g_1)_u = 0$ (which includes the classical example of $g_0 = \gamma u - \delta v$) then*

$$\|v\|_{\mathcal{X}_v} \leq C_1 \left(\|v_0\|_{\sigma+\alpha,p} + \|u\|_{\mathcal{X}_u}\right). \tag{5.18}$$

Under the condition $(g_1)_u = 0$, the term containing $u\nabla u$ in (5.13) vanishes identically, the corresponding term $\|u\|^2_{\mathcal{X}_u}$ in estimate (5.10) also vanishes and (5.18) follows from (5.15).

We now proceed with our analysis by attending to the first equation of (5.1).

Theorem 5.5 *Assume* (5.2)-(5.4) *and p, σ, α as given by* (5.8). *For solutions $(u, v) \in \mathcal{X}_u \times \mathcal{X}_v$ of* (5.1) *with values in Γ, there exist constants C_3, C_4, C_5 (given by* (5.33)*) such that*

$$\|u\|_{\mathcal{X}_u} \leq 2\left(\|u_0\|_{\sigma,p} + C_3 t_0^{1-\frac{\sigma}{2}}\|v\|_{\mathcal{X}_v} + C_4 t_0^{1-b}\|v\|^2_{\mathcal{X}_v} + C_5 t_0^{\frac{\sigma(1-c)}{\sigma-1}}\|v\|^{\frac{\sigma}{\sigma-1}}_{\mathcal{X}_v}\right), \tag{5.19}$$

where

$$b = \frac{n}{2p} + \frac{\sigma}{2}, \qquad c = \frac{n(\sigma-1)}{2p} + \frac{\sigma}{2}. \tag{5.20}$$

Proof: We again use the semigroup approach, $T(t) = e^{\Delta t}$, to solve for u:

$$u(t) = T(t)u_0 - \int_0^t T(t-s)V(u,v)\Delta v\, ds, \tag{5.21}$$

$$- \int_0^t T(t-s)V_v(u,v)(\nabla v)^2\, ds \tag{5.22}$$

$$- \int_0^t T(t-s)V_u(u,v)\nabla u \nabla v\, ds \tag{5.23}$$

where V_u, V_v denote the partial derivatives of V with respect to u, v, respectively. We assume $v \in \mathcal{X}_v$ and consider these three terms separately.

Term (5.21): We use the regularity Lemma 5.1 for

$$T(t) : L^p \to W^{\sigma,p} \quad \text{with norm} \quad C_\sigma t^{-\sigma/2} \tag{5.24}$$

and obtain

$$\begin{aligned} \left\| \int T(t-s)V\Delta v\, ds \right\|_{\sigma,p} &\leq C_\sigma t_0^{1-\sigma/2} \sup_{0\leq t\leq t_0} \|V\Delta v\|_p \\ &\leq C_\sigma t_0^{1-\sigma/2} \|V\|_\Gamma \sup_{0\leq t\leq t_0} \|v(t,.)\|_{2,p}, \end{aligned} \tag{5.25}$$

where $C_\sigma = C_\sigma(\sigma, p)$ and $\|V\|_\Gamma$ denotes the supremum norm on $\Gamma \subset \mathbb{R}^2$.

Term (5.22): Here we use the regularity Lemma 5.1 for

$$T(t) : L^{p/2} \to W^{\sigma,p} \quad \text{with norm} \quad C_b t^{-b}, \tag{5.26}$$

where b is given in (5.20). From the parameter conditions (5.8) it follows that $b < 1$. We obtain

$$\begin{aligned} \left\| \int T(t-s)V_v(\nabla v)^2\, ds \right\|_{\sigma,p} &\leq C_b t_0^{1-b} \sup_{0\leq t\leq t_0} \|V_v(\nabla v)^2\|_{\frac{p}{2}} \\ &\leq C_b t_0^{1-b} \|V_v\|_\Gamma \sup_{0\leq t\leq t_0} \|v(t,.)\|_{1,p}^2 \end{aligned} \tag{5.27}$$

Term (5.23): It turns out to be much more difficult to obtain an appropriate estimate for the product $\nabla u \nabla v$. We start by using Young's inequality to get:

$$\begin{aligned} \|\nabla u \nabla v\|_{p/\sigma} &\leq \left\| \frac{\varepsilon}{\sigma}(\nabla u)^\sigma + \frac{1}{q\varepsilon^{q/\sigma}}(\nabla v)^q \right\|_{p/\sigma} \\ &\leq \frac{\varepsilon}{\sigma}\|u\|_{1,p}^\sigma + \frac{1}{q\varepsilon^{q/\sigma}}\|\nabla v\|_{p/(\sigma-1)}^{\frac{\sigma}{\sigma-1}}, \end{aligned}$$

where $q = \frac{\sigma}{\sigma-1}$ and some $\varepsilon > 0$. We use the interpolation inequality ([113], p. 22, Prop. 6.2)

$$\|u\|_{\theta\sigma,p} \leq C(\theta)\|u\|_{\sigma,p}^\theta \|u\|_p^{1-\theta}$$

for $\theta \in (0,1)$. If we choose $\theta = \sigma^{-1}$, we get

$$\|u\|_{1,p}^{\sigma} \le C(\sigma)\|u\|_{\sigma,p}\|u\|_p^{\sigma-1}. \tag{5.28}$$

As Γ is a bounded invariant region, there exists a constant $C = C(p,\sigma)$ such that

$$\|u\|_p^{\sigma-1} \le C\bar{u}^{\sigma-1}. \tag{5.29}$$

Finally we use $T(t) : L^{p/\sigma} \to W^{\sigma,p}$ with norm $C_c t^{-c}$, where c is as given in (5.20). It is easily verified from (5.8) that $c < 1$. Thus,

$$\begin{aligned}
\left\| \int_0^t T(t-s) V_u \nabla u \nabla v \, ds \right\|_{\sigma,p} &\le C_c t_0^{1-c} \sup_{0\le t\le t_0} \|(V_u \nabla u \nabla v)(t,.)\|_{p/\sigma} \\
&\le C_c t_0^{1-c} \|V_u\|_\Gamma \sup_{0\le t\le t_0} \left(\frac{\varepsilon}{\sigma} \|u\|_{\sigma,p} \bar{u}^{\sigma-1} + \frac{1}{q\varepsilon^{q/\sigma}} \|\nabla v\|_{p/(\sigma-1)}^{\frac{\sigma}{\sigma-1}} \right) \\
&\le C_6 t_0^{1-c} \|V_u\|_\Gamma \left(\frac{\varepsilon}{\sigma} \|u\|_{\mathcal{X}_u} + \frac{1}{q\varepsilon^{q/\sigma}} \|v\|_{\mathcal{X}_v}^{\frac{\sigma}{\sigma-1}} \right),
\end{aligned} \tag{5.30}$$

where $C_6 = C_6(C_c, \bar{u})$.

We collect estimates (5.25, 5.27, 5.30):

$$\begin{aligned}
\|u\|_{\mathcal{X}_u} \le\ & \|u_0\|_{\sigma,p} + C_\sigma t_0^{1-\frac{\sigma}{2}} \|V\|_\Gamma \|v\|_{\mathcal{X}_v} + C_b t_0^{1-b} \|V_v\|_\Gamma \|v\|_{\mathcal{X}_v}^2 + \\
& C_6 t_0^{1-c} \|V_u\|_\Gamma \left(\frac{\varepsilon}{\sigma} \|u\|_{\mathcal{X}_u} + \frac{1}{q\varepsilon^{\frac{q}{\sigma}}} \|v\|_{\mathcal{X}_v}^{\frac{\sigma-1}{\sigma}} \right).
\end{aligned} \tag{5.31}$$

For given $t_0 > 0$ we choose

$$\varepsilon = \frac{\sigma}{2t_0^{1-c}\|V_u\|_\Gamma C_6}. \tag{5.32}$$

Then, from (5.31), estimate (5.19) follows with constants C_3, C_4, C_5 given by:

$$C_3 = C_\sigma \|V\|_\Gamma, \qquad C_4 = C_b \|V_v\|_\Gamma, \qquad C_5 = C_6 \left(\frac{2\|V_u\|_\Gamma C_6}{\sigma} \right)^{\frac{1}{\sigma-1}}. \tag{5.33}$$

□

5.2.3 Local Existence

Theorem 5.6 *Assume* (5.2) – (5.4) *and* p, σ, α *as given by* (5.8). *For each initial datum* $u_0 \in W^{\sigma,p}$, $v_0 \in W^{\sigma+\alpha,p}$ *with* $(u_0(x), v_0(x)) \in \Gamma$ *for all* $x \in \mathcal{M}$, *there exists a* $t_0 > 0$ *and a unique solution* $(u,v) \in \mathcal{X}_u \times \mathcal{X}_v$ *of* (5.1).

Proof: We use a fixed-point argument. Consider $\varphi \in \mathcal{X}_u$ with $\varphi(0) = u_0$ and let $v = v(\varphi)$ denote the corresponding solution of the v-equation:

$$v_t = \mu\Delta v + g(\varphi, v), \qquad v(0) = v_0. \tag{5.34}$$

For this v we define $u = u(v(\varphi))$ to be the corresponding solution of

$$u_t = \nabla(\nabla u - V(u,v)\nabla v), \qquad u(0) = u_0 = \varphi(0). \tag{5.35}$$

These solutions exist by standard theory and the a-priori estimates (5.10) and (5.19). Moreover, the above estimates show that this procedure defines a map $Q : \mathcal{X}_u \to \mathcal{X}_u, Q\varphi := u(v(\varphi))$. We first show that for t_0 sufficiently small, Q maps a ball

$$\mathcal{B}_m := \{\varphi \in \mathcal{X}_u |\ \varphi(t) \in B_m(0), 0 \le t \le t_0\}, \qquad m := 2\|u_0\|_{\sigma,p} + 1.$$

into itself. Indeed, if we combine the estimates (5.19) and (5.15) we obtain

$$\begin{aligned}
\|Q\varphi\|_{\mathcal{X}_u} &\le 2\Big(\|u_0\|_{\sigma,p} + C_3C_1t_0^{1-\frac{\sigma}{2}}\left(\|v_0\|_{\sigma+\alpha,p} + \|\varphi\|_{\mathcal{X}_u} + \|\varphi\|_{\mathcal{X}_u}^2\right) \\
&\quad + C_4C_1^2t_0^{1-b}\left(\|v_0\|_{\sigma+\alpha,p} + \|\varphi\|_{\mathcal{X}_u} + \|\varphi\|_{\mathcal{X}_u}^2\right)^2 \\
&\quad + C_5C_1^{\frac{\sigma-1}{\sigma}}t_0^{\frac{\sigma(1-c)}{\sigma-1}}\left(\|v_0\|_{\sigma+\alpha,p} + \|\varphi\|_{\mathcal{X}_u} + \|\varphi\|_{\mathcal{X}_u}^2\right)^{\frac{\sigma}{\sigma-1}}\Big) \\
&\le 2\|u_0\|_{\sigma,p} + 1,
\end{aligned}$$

for small enough t_0.

Now we demonstrate that at small times, Q is a contraction. Consider $\varphi_1, \varphi_2 \in \mathcal{X}_u$ and let v_i for $i = 1, 2$ denote the corresponding solutions of the v-equation (5.34). Then the difference $Q\varphi_1 - Q\varphi_2$ satisfies:

$$\begin{aligned}
Q\varphi_1 - Q\varphi_2 &= -\int_0^t T(t-s)(V_1\Delta v_1 - V_2\Delta v_2)ds, && (5.36)\\
&\quad -\int_0^t T(t-s)(V_{1,v}(\nabla v_1)^2 - V_{2,v}(\nabla v_2)^2)ds && (5.37)\\
&\quad -\int_0^t T(t-s)(V_{1,u}\nabla u_1\nabla v_1 - V_{2,u}\nabla u_2\nabla v_2)ds, && (5.38)
\end{aligned}$$

where $V_i := V(\varphi_i, v_i)$ for $i = 1, 2$ and $V_{i,u}, V_{i,v}$ denote partial derivatives with respect to u and v, respectively. Again we study each term separately.

Term (5.36): Using (5.24) and (5.16), for t_0 small enough we get

$$\begin{aligned}
&\left\|\int_0^t T(t-s)(V_1\Delta v_1 - V_2\Delta v_2)ds\right\|_{\sigma,p} \\
&\le C_\sigma t^{1-\frac{\sigma}{2}}\left(\|V_1 - V_2\|_\Gamma \sup_{0\le\vartheta\le t}\|\Delta v_1(\vartheta,.)\|_p + \|V_2\|_\Gamma \sup_{0\le\vartheta\le t}\|\Delta v_1 - \Delta v_2\|_p\right) \\
&\le Ct^{1-\frac{\sigma}{2}}\|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}, && (5.39)
\end{aligned}$$

where $C = C(C_2, C_\sigma, \|V\|_{C^1(\Gamma)}, \|\varphi_1\|_{\mathcal{X}_u}, \|\varphi_2\|_{\mathcal{X}_u})$.
Term (5.37): Here we use (5.26) to obtain

$$\begin{aligned} & \left\| \int_0^t T(t-s)(V_{1,v}(\nabla v_1)^2 - V_{2,v}(\nabla v_2)^2 ds \right\|_{\sigma,p} \\ \leq\ & Ct^{1-b} \sup_{0\leq\vartheta\leq t} \left(\|V_{1,v} - V_{2,v}\|_\Gamma \|(\nabla v_1)^2\|_{p/2} + \|V_{2,v}\|_\Gamma \|(\nabla v_1)^2 - (\nabla v_2)^2\|_{p/2} \right). \end{aligned}$$

With Hölder's inequality we get

$$\|(\nabla v_1)^2 - (\nabla v_2)^2\|_{p/2} \leq \|\nabla v_1 + \nabla v_2\|_p \|\nabla v_1 - \nabla v_2\|_p.$$

With estimate (5.16) this leads to

$$\left\| \int_0^t T(t-s)(V_{1,v}(\nabla v_1)^2 - V_{2,v}(\nabla v_2)^2 ds \right\|_{\sigma,p} \leq Ct^{1-b} \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}, \tag{5.40}$$

where $C = C(C_2, C_b, \|V\|_{C^1(\Gamma)}, \|v_1\|_{1,p}, \|v_2\|_{1,p}, \|\varphi_1\|_{\mathcal{X}_u}, \|\varphi_2\|_{\mathcal{X}_u})$.
Term (5.38): Once again, we use (5.24) and (5.16):

$$\begin{aligned} & \left\| \int_0^t T(t-s)(V_{1,u}\nabla u_1 \nabla v_1 - V_{2,u}\nabla u_2 \nabla v_2) ds \right\|_{\sigma,p} \\ \leq\ & Ct^{1-\frac{\sigma}{2}} \sup_{0\leq\vartheta\leq t} \{ \|(V_{1,u} - V_{2,u})\nabla\varphi_1 \nabla v_1\|_p + \|V_{2,u}(\nabla\varphi_1 - \nabla\varphi_2)\nabla v_1\|_p \qquad (5.41) \\ & + \|V_{2,u}\nabla\varphi_2(\nabla v_1 - \nabla v_2)\|_p \} \\ \leq\ & Ct^{1-\frac{\sigma}{2}} \|V\|_{C^1(\Gamma)} \sup_{0\leq\vartheta\leq t} \{ \|\nabla\varphi_1\|_p \|\nabla v_1\|_\infty \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u} \qquad (5.42) \\ & + \|\nabla v_1\|_\infty \|\nabla\varphi_1 - \nabla\varphi_2\|_p + \|\nabla\varphi_2\|_p \|\nabla v_1 - \nabla v_2\|_\infty \} \\ \leq\ & Ct^{1-\frac{\sigma}{2}} \|\varphi_1 - \varphi_2\|_{\mathcal{X}_u}, \qquad (5.43) \end{aligned}$$

where $C = C(C_2, C_\sigma, \|V\|_{C^1(\Gamma)}, \|v_1\|_{\mathcal{X}_v}, \|v_2\|_{\mathcal{X}_v}, \|\varphi_1\|_{\mathcal{X}_u}, \|\varphi_2\|_{\mathcal{X}_u})$. □

5.2.4 Global Existence

In the above estimates we saw that all bounds grow, at most, algebraically in time t_0. We will use this to show global in time existence. The procedure uses the successive application of the regularity properties of the heat equation (e.g. as given in Lemma 5.1). Starting form the known L^∞ estimates (invariant region), we develop higher order estimates for v which lead to better estimates for u. Here we work with an additional set of parameters, $(\tilde{\sigma}, \nu)$ such that one iteration step of this procedure is sufficient. At each iteration we gain an order of $\tilde{\sigma}$. For the original parameters (σ, α) we would have to use more iterations to get the same result.

Theorem 5.7 *Assume* (5.2) – (5.4) *and* p, σ, α *as given by* (5.8). *For each initial datum* $u_0 \in W^{\sigma,p}$, $v_0 \in W^{\sigma+\alpha,p}$ *with* $(u_0(x), v_0(x)) \in \Gamma$ *for all* $x \in \mathcal{M}$, *there exists a unique global solution*

$$(u, v) \in C([0, \infty), W^{\sigma,p} \times W^{\sigma+\alpha,p})$$

of (5.1).

Proof: We start with the global L^∞ estimate (i.e. the invariant region Γ) to successively derive higher order estimates. For technical reasons we choose parameters $\tilde{\sigma} > 0$ and $\nu > 0$ such that

$$2 > \tilde{\sigma} > \max\left\{\sigma, \frac{5}{3}\right\} \tag{5.44}$$

$$2 - \tilde{\sigma} < \nu < \frac{\tilde{\sigma} - 1}{2} \tag{5.45}$$

$$1 - \nu + \tilde{\sigma} = \sigma + \alpha. \tag{5.46}$$

It is easy to check that these three conditions can be simultaneously satisfied.

Lemma 5.8 *There exists a constant* $\kappa_1 = \kappa_1(\tilde{\sigma}, p, \bar{u}, \bar{v}, \|g\|_{C^1(\Gamma)})$ *such that the solution of Theorem 5.6 satisfies*

$$\|v\|_{\tilde{\sigma},p} \leq \|v_0\|_{\tilde{\sigma},p} + \kappa_1 t_0^{1-\frac{\tilde{\sigma}}{2}} =: K_1(t_0). \tag{5.47}$$

Proof: We consider the solution of the v-equation as represented by (5.12) and we use (5.24) with $\tilde{\sigma}$ replacing σ. □

Now, with use of $T_\mu(t) : W^{1-\nu-\tilde{\sigma},p} \to W^{1-\nu,p}$ with norm $C_{\tilde{\sigma}} t^{-\tilde{\sigma}/2}$, we obtain from $u(t) = T(t)u_0 - \int T(t-s)\nabla(V\nabla v)ds$ that

$$\|u(t)\|_{1-\nu,p} \leq \|u_0\|_{1-\nu,p} + C_{\tilde{\sigma}} t^{1-\frac{\tilde{\sigma}}{2}} \sup_{0 \leq \vartheta \leq t} \|\nabla(V\nabla v)\|_{1-\nu-\tilde{\sigma},p}.$$

Since $\nu > 2 - \tilde{\sigma}$ we have $2 - \nu - \tilde{\sigma} < 0$. Then there is a constant $C = C(\tilde{\sigma}, \nu)$ such that

$$\|\nabla(V\nabla v)\|_{1-\nu-\tilde{\sigma},p} \leq C\|V\nabla v\|_{2-\nu-\tilde{\sigma},p}$$

and we get

$$\begin{aligned} \|u(t)\|_{1-\nu,p} &\leq \|u_0\|_{1-\nu,p} + Ct^{1-\frac{\tilde{\sigma}}{2}} \sup_{0 \leq \vartheta \leq t} \|V\nabla v\|_{2-\nu-\tilde{\sigma},p} \\ &\leq \|u_0\|_{1-\nu,p} + Ct^{1-\frac{\tilde{\sigma}}{2}} \|V\|_\Gamma \sup_{0 \leq \vartheta \leq t} \|v\|_{1,p}. \end{aligned}$$

We apply Lemma 5.8 to show

$$\|u(t)\|_{1-\nu,p} \leq \|u_0\|_{1-\nu,p} + Ct^{1-\frac{\tilde{\sigma}}{2}} \|V\|_\Gamma K_1(t_0) \quad =: K_2(t_0)$$

We use this estimate to get a better estimate for v, than in the previous Lemma 5.8. Since on the compact set Γ the function $h(u,v) = g_1(u,v)u$ is uniformly bounded in $C^2(\Gamma)$, it follows that the map $h : W^{1-\nu,p} \to W^{1-\nu,p}$ is Lipschitz continuous, where the Lipschitz constant is bounded by $H := \|h\|_{C^2(\Gamma)}$. Then , from (5.12), it follows that

$$\begin{aligned} \|v(t)\|_{1-\nu+\tilde{\sigma},p} &\leq \|v_0\|_{1-\nu+\tilde{\sigma},p} + Ct^{1-\frac{\tilde{\sigma}}{2}} \sup_{0\leq\vartheta\leq t} \|g_1(u,v)u\|_{1-\nu,p} \\ &\leq \|v_0\|_{1-\nu+\tilde{\sigma},p} + Ct^{1-\frac{\tilde{\sigma}}{2}} \sup_{0\leq\vartheta\leq t} \|h\|_{C^2(\Gamma)}\|u\|_{1-\nu,p} \\ &\leq \|v_0\|_{1-\nu+\tilde{\sigma},p} + Ct^{1-\frac{\tilde{\sigma}}{2}} HK_2(t_0) \end{aligned} \tag{5.48}$$

To complete the proof of global existence we use (5.46). Then from (5.48) it follows that

$$\|v\|_{\mathcal{X}_v} \leq \|v_0\|_{\sigma+\alpha,p} + Ct_0^{1-\frac{\tilde{\sigma}}{2}} K_2(t_0) =: K_3(t_0). \tag{5.49}$$

Hence $\|v\|_{\mathcal{X}_v}$ grows, at most, algebraically in time with maximal order of $2-\tilde{\sigma}$.

Finally, to estimate $\|u\|_{\mathcal{X}_u}$, we consider (5.31). For each time $t_0 > 0$ we choose $\varepsilon = \varepsilon(t_0)$ according to (5.32), and obtain (5.19). With use of (5.49) we observe that

$$\|u\|_{\mathcal{X}_u} \leq 2\left(\|u_0\|_{\sigma,p} + C_3 t_0^{1-\frac{\sigma}{2}} K_3(t_0) + C_4 t_0^{1-b} K_3(t_0)^2 + C_5 t_0^{\frac{\sigma(1-c)}{\sigma-1}} K_3(t_0)^{\frac{\sigma-1}{\sigma}}\right),$$

which also grows algebraically in time. Global existence in $\mathcal{X}_u \times \mathcal{X}_v$ follows.

□

Note that $\|u\|_{\mathcal{X}_u} + \|v\|_{\mathcal{X}_v}$ grows at most with t^2.

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