

BIOMIXING BY CHEMOTAXIS AND ENHANCEMENT OF BIOLOGICAL REACTIONS

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ABSTRACT. Many processes in biology involve both reactions and chemotaxis. However, to the best of our knowledge, the question of interaction between chemotaxis and reactions has not yet been addressed either analytically or numerically. We consider a model with a single density function involving diffusion, advection, chemotaxis, and absorbing reaction. The model is motivated, in particular, by studies of coral broadcast spawning, where experimental observations of the efficiency of fertilization rates significantly exceed the data obtained from numerical models that do not take chemotaxis (attraction of sperm gametes by a chemical secreted by egg gametes) into account. We prove that in the framework of our model, chemotaxis plays a crucial role. There is a rigid limit to how much the fertilization efficiency can be enhanced if there is no chemotaxis but only advection and diffusion. On the other hand, when chemotaxis is present, the fertilization rate can be arbitrarily close to being complete provided that the chemotactic attraction is sufficiently strong.

1. INTRODUCTION

Our goal in this paper is to study the effect chemotactic attraction may have on reproduction processes in biology. A particular motivation for this study comes from the phenomenon of coral broadcast spawning. Broadcast spawning is a fertilization strategy used by various benthic invertebrates (sea urchins, anemones, corals) whereby males and females release sperm and egg gametes into the surrounding flow. The gametes are positively buoyant, and rise to the surface of the ocean. The sperm and egg are initially separated by the ambient water, and effective mixing is necessary for successful fertilization. The fertilized gametes form larva, which is negatively buoyant and tries to attach to the bottom of the ocean floor to start a new colony. For the coral spawning problem, field measurements of the fertilization rates are rarely below 5%, and are often as high as 90% [8, 15, 24, 28]. On the other hand, numerical simulations based on the turbulent eddy diffusivity [4] predict fertilization rates of less than 1% due to the strong dilution of gametes. The turbulent eddy diffusivity approach involves two scalars that react and diffuse with the effective diffusivity taking the presence of the flow into account. It is well known, however, that the geometric structure of the fluid flow lost in the turbulent diffusivity approach can be important for improving the reaction rate (in the physical and engineering literature see [22, 26, 27]; in the mathematical literature see [16, 3, 13, 9, 14] for further references). Recent work of Crimaldi, Hartford, Cadwell and Weiss [6, 7] employed a more sophisticated model, taking into account the instantaneous details of the advective transport

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not captured by the eddy diffusivity approach. These papers showed that vortex stirring can generally enhance the reaction rate, perhaps accounting for some of the discrepancy between the numerical simulations and experiment.

However, there is also experimental evidence that chemotaxis plays a role in coral fertilization: eggs release a chemical that attracts sperm [1, 2, 18, 19]. Mathematically, chemotaxis has been extensively studied in the context of modeling mold and bacterial colonies. Since the original work of Patlak [23] and Keller-Segel [11, 12] where the first PDE model of chemotaxis was introduced, there has been an enormous amount of effort devoted to the possible blow up and regularity of solutions, as well as the asymptotic behavior and other properties (see [25] for further references). However, we are not aware of any rigorous or even computational work on the effects of chemotaxis for improved efficiency of biological reactions.

In this paper, we take the first step towards systematical study of this phenomenon, by analyzing rigorously a single partial differential equation modeling the fertilization process:

$$\partial_t \rho + u \cdot \nabla \rho = \Delta \rho + \chi \nabla(\rho \nabla(\Delta)^{-1} \rho) - \rho^q, \quad \rho(x, 0) = \rho_0(x), \quad x \in \mathbb{R}^d. \quad (1.1)$$

Here, in the simplest approximation, we consider just one density, $\rho(x, t) \geq 0$, corresponding to the assumption that the densities of sperm and egg gametes are identical. The vector field u in (1.1) models the ambient ocean flow, is divergence free, regular and prescribed, independent of ρ . The second term on the right is the standard chemotactic term, in the same form as it appears in the (simplified) Keller-Segel equation (see [25]). This term describes the tendency of $\rho(x, t)$ to move along the gradient of the chemical whose distribution is equal to $-\Delta^{-1} \rho$. This is an approximation to the full Keller-Segel system based on the assumption of chemical diffusion being much faster than diffusion of gamete densities. The term $(-\rho^q)$ models the reaction (fertilization). We do not account for the product of the reaction – fertilized eggs – which drop out of the process. We are interested in the behavior of

$$m_0(t) = \int_{\mathbb{R}^d} \rho(x, t) dx,$$

which is the total fraction of the unfertilized eggs by time t . It is easy to see that $m_0(t)$ is monotone decreasing. High efficiency fertilization corresponds to $m_0(t)$ becoming small with time, as almost all egg gametes are fertilized. We prove the following results.

Theorem 1.1. *Let $\rho(x, t)$ solve (1.1) with a divergence free $u(x, t) \in C^\infty(\mathbb{R}^d \times [0, \infty))$ and initial data $\rho_0 \geq 0 \in \mathcal{S}(\mathbb{R}^d)$ (the Schwartz class). Assume that $qd > d + 2$, and the chemotaxis is absent: $\chi = 0$. Then there exists a constant μ_0 depending only on q, d and $\rho_0(x)$ but not on $u(x, t)$ such that $m_0(t) \geq \mu_0$ for all $t \geq 0$.*

Remarks. 1. Observe that the constant μ_0 does not depend on u . No matter how strong the flow is or how it varies in time and space, it cannot enhance the reaction rate beyond a certain definitive limit. Moreover, some flows may have a negative effect on the reaction rate, increasing the leftover L^1 -norm of ρ .

2. The condition $qd > d + 2$ does not include the most natural case of $d = q = 2$. Dimension two corresponds to the surface of the ocean, and $q = 2$ corresponds to the product of egg and sperm densities. Our preliminary calculations show, however, that the mathematics of $d = q = 2$ case

is different and more subtle. Then the L^1 norm of ρ for sufficiently rapidly decaying initial data goes to zero but only very slowly in time. The difference between chemotactic and chemotactic-free equation (1.1) in this case is likely to manifest itself in the time scales of the fertilization process: in the presence of chemotaxis the L^1 norm goes to zero much faster. We will address this issue in a separate publication, to keep the present paper as transparent as possible.

3. The condition that $\rho_0 \in \mathcal{S}$ can of course be weakened. What we need is the initial data that is decaying sufficiently quickly and is minimally regular. Similarly, the condition that u is smooth can be weakened to, say, C^1 without much difficulty.

4. By $u \in C^\infty(\mathbb{R} \times [0, \infty))$ we mean that bounds on every derivative of u are uniform over all $x \in \mathbb{R}^d \times [0, t]$, for every $t > 0$.

On the other hand, in the presence of chemotaxis, we have

Theorem 1.2. *Let $\rho(x, t)$ solve (1.1) with a divergence free $u(x, t) \in C^\infty(\mathbb{R}^d \times [0, \infty))$ and fixed initial data $\rho_0 \geq 0 \in \mathcal{S}$. Assume that $d = 2$, and q is a positive integer greater than 2. Then we have that $m_0(t) \rightarrow c(\chi, \rho_0, u) > 0$ as $t \rightarrow \infty$, but $c(\chi, \rho_0, u) \rightarrow 0$ as $\chi \rightarrow \infty$, with q , ρ_0 and u fixed.*

Remarks. 1. We prove more (see Theorem 4.2). Here we stated the result in the simplest form to avoid technicalities.

2. In general, solutions of the chemotaxis equation are known to form singularities in a finite time for some initial data (see [25] for references). However, we will prove that in the presence of the reaction term $-\rho^q$ with $q > 2$, solutions always remain regular for regular initial data.

3. The case $d > 2$ is mathematically different and it is not clear that the L^1 norm may become arbitrarily small in this case even with strong chemotaxis aid. There appears to be a genuine mathematical reason why coral gametes rise to the surface instead of trying to find each other in the three-dimensional ocean!

Hence our model implies that the chemotactic term, as opposed to the flow and diffusion alone, can account for highly efficient fertilization rates that are observed in nature. Moreover, Theorems 1.1 and 1.2 suggest that the presence of chemotaxis may be a necessary and crucial aspect of the fertilization process. Of course, a more realistic model of the process is a system of equations involving two different densities. We will show that even for the system case, the flow can only have a limited effect on fertilization efficiency, similarly to our simple model. It is possible that in the system case the flow and chemotaxis can play supplementary role, with flow acting on larger and chemotaxis on smaller length scales. The influence of chemotaxis in the system setting, and investigation of quadratic reaction term are left for a later study.

2. THE REACTION-ADVECTION-DIFFUSION CASE

In this section, we prove Theorem 1.1. Consider equation (1.1) with $\chi = 0$:

$$\partial_t \rho + u \cdot \nabla \rho = \Delta \rho - \rho^q, \quad \rho(x, 0) = \rho_0(x). \quad (2.1)$$

As the first step, observe that by comparison principle, $\rho(x, t) \leq b(x, t)$, where

$$\partial_t b + u \cdot \nabla b = \Delta b, \quad b(x, 0) = \rho_0(x). \quad (2.2)$$

Also, note that since $\rho(x, t) \geq 0$,

$$\partial_t \|\rho(\cdot, t)\|_{L^1} = \partial_t \int_{\mathbb{R}^d} \rho(x, t) dx = - \int_{\mathbb{R}^d} \rho^q(x, t) dx \geq - \int_{\mathbb{R}^d} b^q(x, t) dx.$$

Therefore, the behavior of the L^q norm of b can be used for estimating decay of the L^1 norm of ρ . We have the following lemma, similar in spirit (and proof) to Lemma 3.1 of [9].

Lemma 2.1. *There exists $C = C(d)$ that, in particular, does not depend on the flow u , such that*

$$\|b(\cdot, t)\|_{L^2} \leq \min(\|b_0\|_{L^2}, Ct^{-d/4}\|b_0\|_{L^1}), \quad \|b(\cdot, t)\|_{L^\infty} \leq \min(\|b_0(x)\|_{L^\infty}, Ct^{-d/2}\|b_0\|_{L^1}). \quad (2.3)$$

Proof. By Nash inequality [20], we have

$$\|b\|_{L^2}^{1+\frac{2}{d}} \leq C(d)\|b\|_{L^1}^{2/d}\|\nabla b\|_{L^2}.$$

Multiplying (2.2) by b , integrating, and using incompressibility of u , we get

$$\frac{1}{2}\partial_t \|b\|_{L^2}^2 = -\|\nabla b\|_{L^2}^2 \leq -C\frac{\|b\|_{L^2}^{2+\frac{4}{d}}}{\|b\|_{L^1}^{\frac{4}{d}}} = -C\frac{\|b\|_{L^2}^{2+\frac{4}{d}}}{\|b_0\|_{L^1}^{\frac{4}{d}}}.$$

We used the conservation of the L^1 -norm of b in the last step. Set $z(t) = \|b(\cdot, t)\|_{L^2}^2$. Then

$$z'(t) \leq -Cz(t)^{1+\frac{2}{d}}\|b_0\|_{L^1}^{-\frac{4}{d}}.$$

Solving this differential inequality, we get

$$z(t) \leq \left(\frac{2Ct}{d\|b_0\|_{L^1}^{4/d}} + \frac{1}{\|b_0\|_{L^2}^{4/d}} \right)^{-d/2},$$

implying

$$\|b(\cdot, t)\|_{L^2}^2 \leq \min(\|b_0\|_{L^2}^2, C(d)t^{-d/2}\|b_0\|_{L^1}^2)$$

since the L^p norms of b are non-increasing. This gives the first inequality in (2.3).

The second inequality in (2.3) follows from a simple duality argument using incompressibility of u . Indeed, consider $\theta(x, s)$, a solution of

$$\partial_s \theta + u(x, t-s) \cdot \nabla \theta = \Delta \theta, \quad \theta(x, 0) = \theta_0(x) \in \mathcal{S}.$$

A direct calculation shows that

$$\frac{d}{ds} \int_{\mathbb{R}^d} b(x, s)\theta(x, t-s) dx = 0.$$

When $s = t$, we get

$$\left| \int_{\mathbb{R}^d} b(x, t)\theta_0(x) dx \right| \leq \|b(x, t)\|_{L^2} \|\theta_0\|_{L^2} \leq C(d)t^{-d/4}\|b_0\|_{L^1} \|\theta_0\|_{L^2}.$$

For $s = 0$, this implies

$$\left| \int_{\mathbb{R}^d} b_0(x)\theta(x, t) dx \right| \leq C(d)t^{-d/4}\|b_0\|_{L^1} \|\theta_0\|_{L^2}$$

for every $b_0, \theta_0 \in \mathcal{S}$. Hence

$$\|\theta(x, t)\|_{L^\infty} \leq C(d)t^{-d/4}\|\theta_0\|_{L^2} \quad (2.4)$$

for every $\theta_0 \in L^2$. To finish the proof of the Lemma, given $t > 0$, note that

$$\|b(x, t)\|_{L^\infty} \leq C(d)(t/2)^{-d/4}\|b(x, t/2)\|_{L^2} \leq C(d)t^{-d/2}\|b_0\|_{L^1}.$$

Here in the second step we used (2.4) and adjusted $C(d)$. □

For a more precise estimate on the residual mass μ_0 , we need one more lemma.

Lemma 2.2. *Assume that $\rho(x, t)$ solves (2.1) with a smooth bounded incompressible u and $\rho_0 \in \mathcal{S}$. Then for every $t > 0$ we have*

$$\frac{\|\rho(x, t)\|_{L^p}}{\|\rho(x, t)\|_{L^1}} \leq \frac{\|\rho_0\|_{L^p}}{\|\rho_0\|_{L^1}},$$

for all $1 \leq p \leq \infty$.

Proof. For $p = 1$ the result is immediate. Consider some $1 < p < \infty$, and look at

$$\begin{aligned} \frac{\partial}{\partial t} \left(\frac{\int_{\mathbb{R}^d} \rho^p dx}{\left(\int_{\mathbb{R}^d} \rho dx\right)^p} \right) &= p \left(\int_{\mathbb{R}^d} \rho dx \right)^{-p-1} \\ &\times \left[\int_{\mathbb{R}^d} \rho^{p-1} (-u \cdot \nabla \rho + \Delta \rho - \rho^q) dx \int_{\mathbb{R}^d} \rho dx - \int_{\mathbb{R}^d} \rho^p dx \int_{\mathbb{R}^d} (-u \cdot \nabla \rho + \Delta \rho - \rho^q) dx \right] \end{aligned}$$

Consider the term in the second line above, which after integration by parts simplifies to

$$\left(-(p-1) \int_{\mathbb{R}^d} \rho^{p-2} |\nabla \rho|^2 dx - \int_{\mathbb{R}^d} \rho^{q+p-1} dx \right) \int_{\mathbb{R}^d} \rho dx + \int_{\mathbb{R}^d} \rho^p dx \int_{\mathbb{R}^d} \rho^q dx.$$

This does not exceed

$$- \int_{\mathbb{R}^d} \rho^{q+p-1} dx \int_{\mathbb{R}^d} \rho dx + \int_{\mathbb{R}^d} \rho^p dx \int_{\mathbb{R}^d} \rho^q dx,$$

which is less than or equal to zero by an application of Hölder's inequality.

The $p = \infty$ case follows by a limiting procedure since $\rho(x, t) \in \mathcal{S}$ for all t . □

We are ready to prove Theorem 1.1.

Proof of Theorem 1.1. The idea of the proof is very simple. We will show that if L^1 -norm of ρ at some time t_0 is sufficiently small then for all times $t > t_0$ the L^1 -norm of $\rho(x, t)$ can not drop below $\|\rho(t_0)\|_{L^1}/2$. This shows that $\rho(x, t)$ can not tend to zero as $t \rightarrow +\infty$.

Recall that for every t ,

$$\partial_t \int_{\mathbb{R}^d} \rho(x, t) dx = - \int_{\mathbb{R}^d} \rho(x, t)^q dx \geq - \int_{\mathbb{R}^d} b(x, t)^q dx,$$

where b is given by (2.2). By Lemma 2.1 and Hölder's inequality,

$$\int_{\mathbb{R}^d} b(x, t)^q dx \leq C \min \left(\|\rho_0\|_{L^q}^q, t^{-\frac{d(q-1)}{2}} \|\rho_0\|_{L^1}^q \right).$$

Thus, for every $\tau > 0$,

$$\begin{aligned} \int_{t_0}^{\infty} dt \int_{\mathbb{R}^d} b(x, t)^q dx &\leq C(d) \left(\|\rho(\cdot, t_0)\|_{L^q}^q \tau + \|\rho(\cdot, t_0)\|_{L^1} \int_{t_0+\tau}^{\infty} t^{-\frac{d(q-1)}{2}} dt \right) \\ &\leq C(d, q) \left(\|\rho(\cdot, t_0)\|_{L^\infty}^{q-1} \|\rho(\cdot, t_0)\|_{L^1} \tau + \|\rho(\cdot, t_0)\|_{L^1}^q \tau^{\frac{d+2-qd}{2}} \right). \end{aligned} \quad (2.5)$$

We used the assumption $qd > d + 2$ when evaluating integral in time.

Assume, on the contrary, that the L^1 norm of ρ does go to zero for some u . Consider some time $t_0 > 0$ when $\|\rho(\cdot, t_0)\|$ is sufficiently small (we'll have a precise bound later). Using Lemma 2.2 and (2.5), we see that further decrease of the L^1 norm from that level is bounded by

$$\|\rho(\cdot, t_0)\|_{L^1} - \|\rho(\cdot, t)\|_{L^1} \leq C(d, q) \left(\frac{\|\rho_0\|_{L^\infty}^{q-1}}{\|\rho_0\|_{L^1}^{q-1}} \|\rho(\cdot, t_0)\|_{L^1}^q \tau + \|\rho(\cdot, t_0)\|_{L^1}^q \tau^{\frac{d+2-qd}{2}} \right), \quad (2.6)$$

for all $\tau > 0$. Choosing τ to minimize the expression (2.6), we find that for every $t > t_0$,

$$\|\rho(\cdot, t_0)\|_{L^1} - \|\rho(\cdot, t)\|_{L^1} \leq C(q, d) \|\rho(\cdot, t_0)\|_{L^1}^q \left(\frac{\|\rho_0\|_{L^\infty}}{\|\rho_0\|_{L^1}} \right)^{\frac{qd-d-2}{d}}. \quad (2.7)$$

If $\|\rho(t)\|_{L^1} \rightarrow 0$ as $t \rightarrow +\infty$, we may choose t_0 so that

$$C(q, d) \|\rho(\cdot, t_0)\|_{L^1}^{q-1} \left(\frac{\|\rho_0\|_{L^\infty}}{\|\rho_0\|_{L^1}} \right)^{\frac{qd-d-2}{d}} \leq \frac{1}{2}.$$

Then we get that

$$\|\rho(\cdot, t)\|_{L^1} \geq \frac{1}{2} \|\rho(\cdot, t_0)\|_{L^1} \geq \mu_0(q, d, \rho_0) \equiv \min \left(\frac{1}{2} \|\rho_0\|_{L^1}, \frac{1}{2^{\frac{q}{q-1}} C(q, d)^{\frac{1}{q-1}}} \left(\frac{\|\rho_0\|_{L^1}}{\|\rho_0\|_{L^\infty}} \right)^{1 - \frac{2}{d(q-1)}} \right)$$

for every $t > t_0$. This is a contradiction to the assumption $\|\rho(t)\|_{L^1} \rightarrow 0$ as $t \rightarrow +\infty$. This argument can also be used to define μ_0 in the statement of the theorem. \square

3. THE REACTION-ADVECTION-DIFFUSION CASE: A SYSTEM

In this section we show that the results of Section 2 largely extend to a more general model. Consider the following system

$$\partial_t s = (u \cdot \nabla) s + \kappa_1 \Delta s - (se)^{q/2}, \quad s(x, 0) = s_0(x) \quad (3.1)$$

$$\partial_t e = (u \cdot \nabla) e + \kappa_2 \Delta e - (se)^{q/2}, \quad e(x, 0) = e_0(x). \quad (3.2)$$

Here $s(x, t)$ and $e(x, t)$ are sperm and egg densities respectively. The following analog of Theorem 1.1 holds.

Theorem 3.1. *Let $s(x, t), e(x, t)$ solve (3.1), (3.2) with divergence free $u(x, t) \in C^\infty(\mathbb{R}^d \times [0, \infty))$ and initial data $s_0, e_0 \in S$. Assume that $qd > d + 2$, $q > 2$ and the chemotaxis is absent: $\chi = 0$. Then there exists a constant μ_1 depending only on q, d and $e_0(x), s_0(x)$ such that the L^1 norms of $s(x, t)$ and $e(x, t)$ remain greater than μ_1 for all times.*

Remark. The condition $q > 2$ can be omitted if $\|s_0\|_{L^1} = \|e_0\|_{L^1}$.

Proof. As before, we know that $s(x, t) \leq \bar{s}(x, t)$ and $e(x, t) \leq \bar{e}(x, t)$ where \bar{s}, \bar{e} solve (2.2) the with initial data s_0 and e_0 , and the diffusion coefficients κ_1 and κ_2 , respectively. Lemma 2.1 can still be used to control \bar{s}, \bar{e} . Instead of Lemma 2.2, we will use a cruder bound.

Observe that if $\|e_0\|_{L^1} \neq \|s_0\|_{L^1}$, then the L^1 norm that is larger initially remains larger than the other norm. Hence, assume without loss of generality that $\|e_0\|_{L^1} \leq \|s_0\|_{L^1}$ and focus on the decay of $\|e(\cdot, t)\|_{L^1}$. Let us estimate the decay after some time t_0 :

$$\begin{aligned} & \left| \int_{t_0}^{\infty} dt \int_{\mathbb{R}^d} s(x, t)^{q/2} e(x, t)^{q/2} dx \right| \leq \\ & \left| \int_{t_0}^{t_0+\tau} dt \int_{\mathbb{R}^d} s(x, t)^{q/2} e(x, t)^{q/2} dx \right| + \left| \int_{t_0+\tau}^{\infty} dt \int_{\mathbb{R}^d} s(x, t)^{q/2} e(x, t)^{q/2} dx \right| \\ & \leq \tau \|s(\cdot, t_0)\|_{L^\infty}^{q/2} \|e(\cdot, t_0)\|_{L^\infty}^{\frac{q}{2}-1} \|e(\cdot, t_0)\|_{L^1} + \int_{t_0+\tau}^{\infty} \|s(\cdot, t)\|_{L^q}^{q/2} \|e(\cdot, t)\|_{L^q}^{q/2} dt \\ & \leq \tau \|s_0\|_{L^\infty}^{q/2} \|e_0\|_{L^\infty}^{\frac{q}{2}-1} \|e(\cdot, t_0)\|_{L^1} + C\tau^{1-\frac{d(q-1)}{2}} \|s_0\|_{L^1}^{q/2} \|e(\cdot, t_0)\|_{L^1}^{q/2}. \end{aligned} \quad (3.3)$$

Choosing τ to minimize (3.3) leads to

$$\|e(\cdot, t_0)\|_{L^1} - \|e(\cdot, t)\|_{L^1} \leq C(q, d) \|s_0\|_{L^\infty}^{\frac{q(qd-d-2)}{2d(q-1)}} \|s_0\|_{L^1}^{\frac{q}{d(q-1)}} \|e_0\|_{L^\infty}^{\frac{(q-2)(qd-d-2)}{2d(q-1)}} \|e(\cdot, t_0)\|_{L^1}^{1+\frac{q-2}{d(q-1)}}. \quad (3.4)$$

Suppose that $\|e(\cdot, t)\|_{L^1}$ does go to zero as $t \rightarrow \infty$. Choose t_0 so that $C\|e(x, t_0)\|_{L^1}^{\frac{q-2}{d(q-1)}} < \frac{1}{2}$ (where C is the constant in front of $\|e(\cdot, t_0)\|_{L^1}^{1+\frac{q-2}{d(q-1)}}$ in (3.4)). In this case, due to (3.4), the L^1 of $e(x, t)$ can never drop below half of its value at t_0 . This is a contradiction. \square

4. REACTION ENHANCEMENT BY CHEMOTAXIS

In this section, we will show that chemotaxis, as opposed to a divergence free fluid flow, can, in principle, make reaction as efficient as needed. We consider the equation

$$\partial_t \rho = \Delta \rho - (u \cdot \nabla) \rho + \chi \nabla(\rho \nabla(\Delta)^{-1} \rho) - \rho^q, \quad \rho(x, 0) = \rho_0(x). \quad (4.1)$$

We will prove that the large time limit of the L^1 norm of $\rho(x, t)$ goes to zero as chemotaxis coupling increases. On the other hand, we will also prove lower bounds showing that the L^1 norm does not go to zero as $t \rightarrow \infty$ for each fixed coupling. Before we state the main results of this section, there is an auxiliary issue we need to settle. In general, solutions to the chemotaxis equation may lose regularity in a finite time (see e.g. [25] for further references). As Theorem 4.1 below shows, this does not happen with the additional negative reaction term $-\rho^q$, $q > 2$ in the right hand side: solutions with smooth initial data stay smooth. We will work with initial data which is concentrated in a finite region, in particular, with a finite second moment. As we will see, this property is also preserved by the evolution. Let us define

$$\|f\|_{M_n} = \int_{\mathbb{R}^d} (|\nabla f| + |f(x)|)(1 + |x|^n) dx.$$

Let H^s denote the standard Sobolev spaces in \mathbb{R}^d . Define a Banach space $K_{s,n}$ with the norm $\|f\|_{K_{s,n}} = \|f\|_{H^s} + \|f\|_{M_n}$. Then we have

Theorem 4.1. *Assume that $q > 2$, $n > 0$ and $s > d/2 + 1$ are integers and $\rho_0 \in K_{s,n}$. Suppose that $u \in C^\infty(\mathbb{R}^d \times [0, \infty))$ is divergence free. Then there exists a unique solution $\rho(x, t)$ of the equation (4.1) in $C(K_{s,n}, [0, \infty)) \cap C^\infty(\mathbb{R}^d \times (0, \infty))$.*

The proof of Theorem 4.1 uses fairly standard techniques; we sketch it in Appendix I.

First, we prove the bound showing reaction enhancement by chemotaxis. Let us define

$$m_2 = \min_{x_0} \int_{\mathbb{R}^d} |x - x_0|^2 \rho_0(x) dx.$$

Theorem 4.2. *Let $d = 2$, and suppose that $u \in C^\infty(\mathbb{R}^d \times [0, \infty))$ is divergence free. Assume that $q > 2$, $s > d/2 + 1$ and $n \geq 2$ are integers and $\rho(x, t)$ solves (4.1) with $\rho_0 \geq 0 \in K_{s,n}$. Then*

a. If $u = 0$, then $\lim_{t \rightarrow \infty} \|\rho(\cdot, t)\|_{L^1} \leq 2\chi^{-1}$. More precisely, for every $\tau > 0$, we have

$$\|\rho(\cdot, \tau)\|_{L^1} \leq \frac{2}{\chi} \left(1 + \sqrt{1 + \frac{\chi m_2}{4\tau}} \right). \quad (4.2)$$

b. If $u \neq 0$, then $\lim_{t \rightarrow \infty} \|\rho(\cdot, t)\|_{L^1} \leq C(u, m_2)\chi^{-2/3}$. Moreover, for $0 \leq \tau \leq \chi^{1/3}$ we have

$$\|\rho(\cdot, \tau)\|_{L^1} \leq C(u, m_2)(\chi\tau)^{-1/2}. \quad (4.3)$$

Remark. Note, in particular, that if $u = 0$, the level $\|\rho(\cdot, \tau)\|_{L^1} \sim \chi^{-1}$ will be reached in at most $\tau \sim \chi$, while the level $\sim \chi^{-1/2}$ is reached in at most $\tau \sim 1$. If $u \neq 0$, the upper bound on the time scale to reach the L^1 norm level $\sim \chi^{-1/2}$ is also $\tau \sim 1$.

Proof. Since $\rho_0 \in K_{s,n}$, there exists x_0 such that $\int_{\mathbb{R}^2} |x - x_0|^2 \rho_0(x) dx = m_2$. Set $x_0 = 0$ for simplicity. Consider

$$\partial_t \int_{\mathbb{R}^2} |x|^2 \rho dx = \int_{\mathbb{R}^2} |x|^2 (u \cdot \nabla) \rho dx + \int_{\mathbb{R}^2} |x|^2 \Delta \rho dx + \chi \int_{\mathbb{R}^2} |x|^2 \nabla(\rho \nabla \Delta^{-1} \rho) dx - \int_{\mathbb{R}^2} |x|^2 \rho^q dx. \quad (4.4)$$

Observe that due to $\nabla \cdot u = 0$,

$$\int_{\mathbb{R}^2} |x|^2 (u \cdot \nabla) \rho dx = -2 \int_{\mathbb{R}^2} (x \cdot u) \rho dx,$$

and in dimension two

$$\int_{\mathbb{R}^2} |x|^2 \Delta \rho dx = 4 \int_{\mathbb{R}^2} \rho dx.$$

For the chemotaxis term, we have

$$\int_{\mathbb{R}^2} |x|^2 \nabla(\rho \nabla \Delta^{-1} \rho) dx = -2 \int_{\mathbb{R}^2 \times \mathbb{R}^2} \int_{\mathbb{R}^2} \frac{x \cdot (x - y)}{|x - y|^2} \rho(x, t) \rho(y, t) dx dy = - \left(\int_{\mathbb{R}^2} \rho dx \right)^2.$$

In the last step, we used symmetrization in x, y . Due to Theorem 4.1, all integrations by parts are justified for all $t \geq 0$. Therefore, we can recast (4.4) as

$$\partial_t \int_{\mathbb{R}^2} |x|^2 \rho dx = -2 \int_{\mathbb{R}^2} (x \cdot u) \rho dx + 4 \int_{\mathbb{R}^2} \rho dx - \chi \left(\int_{\mathbb{R}^2} \rho dx \right)^2 - \int_{\mathbb{R}^2} |x|^2 \rho^q dx. \quad (4.5)$$

First let us set $u = 0$ in (4.5). Suppose that $\|\rho(\cdot, t)\|_{L^1} \geq Y$ for all $t \in [0, \tau]$, and $Y \geq 4/\chi$. It follows from (4.5) that we need $\tau Y(\chi Y - 4) \leq m_2$ to avoid contradiction. This quadratic inequality translates into (4.2).

Now, assume that u is an arbitrary smooth divergence free vector field. In this case, we further estimate

$$\left| \int_{\mathbb{R}^2} x \cdot u \rho \, dx \right| \leq \|u\|_{L^\infty}^2 \chi^\beta \int_{\mathbb{R}^2} \rho \, dx + \chi^{-\beta} \int_{\mathbb{R}^2} |x|^2 \rho \, dx,$$

with $\beta > 0$ to be chosen. Then, it follows from (4.5) that

$$\partial_t \int_{\mathbb{R}^2} |x|^2 \rho \, dx < 2\chi^{-\beta} \int_{\mathbb{R}^2} |x|^2 \rho \, dx + \left(4 + 2\chi^\beta \|u\|_{L^\infty}^2 - \chi \int_{\mathbb{R}^2} \rho \, dx \right) \int_{\mathbb{R}^2} \rho \, dx,$$

and thus

$$\partial_t \left(e^{-2\chi^{-\beta}t} \int_{\mathbb{R}^2} |x|^2 \rho \, dx \right) < e^{-2\chi^{-\beta}t} \left(4 + 2\chi^\beta \|u\|_{L^\infty}^2 - \chi \int_{\mathbb{R}^2} \rho \, dx \right) \int_{\mathbb{R}^2} \rho \, dx. \quad (4.6)$$

Assume now that for all $t \in [0, \tau]$, we have $\|\rho(\cdot, t)\|_{L^1} \geq Y > 0$, and that

$$Y \geq \frac{2}{\chi} (2 + \chi^\beta \|u\|_{L^\infty}^2).$$

Then, the integral in time of the right hand side in (4.6) over $[0, \tau]$ can be estimated from above by

$$\int_0^\tau e^{-2\chi^{-\beta}t} Y \left(4 + 2\chi^\beta \|u\|_{L^\infty}^2 - \chi Y \right) dt = \left(1 - e^{-2\chi^{-\beta}\tau} \right) Y \chi^\beta \left(2 + \chi^\beta \|u\|_{L^\infty}^2 - \chi Y/2 \right). \quad (4.7)$$

Setting $\tau = \chi^\beta$, we see that to avoid a contradiction, we need

$$(1 - e^{-2}) \chi^\beta Y \left(\chi Y - 4 - 2\chi^\beta \|u\|_{L^\infty}^2 \right) \leq 2m_2. \quad (4.8)$$

An elementary computation shows that the optimal choice that makes Y the smallest is $\beta = 1/3$. Solving this quadratic inequality, we find that $\|\rho(\cdot, \tau = \chi^{1/3})\|_{L^1}$ cannot exceed $c(u, m_2) \chi^{-2/3}$. More generally, for $0 < \tau < \chi^{1/3}$, we get from (4.7) the bound

$$\|\rho(\cdot, \tau)\|_{L^1} \leq C(u, m_2) (\chi \tau)^{-\frac{1}{2}}.$$

□

Next we prove a result in the opposite direction, showing that at least some estimates of Theorem 4.2 scale sharply in χ .

Theorem 4.3. *Let $d = 2$, and suppose that $u \in C^\infty(\mathbb{R}^d \times [0, \infty))$ is divergence free. Assume that $q > 2$, $s > d/2 + 1$ and $n \geq 2$ are integers and $\rho(x, t)$ solves (4.1) with $\rho_0 \geq 0 \in K_{s,n}$. Then $\lim_{t \rightarrow \infty} \|\rho(\cdot, t)\|_{L^1} > 0$. Moreover, for some initial data ρ_0 , $\|\rho(\cdot, t)\|_{L^1}$ remains above $c(q, \rho_0) \chi^{-1}$ for all times.*

Proof. Recall that $\partial_t \int_{\mathbb{R}^2} \rho(x, t) \, dx = - \int_{\mathbb{R}^2} \rho(x, t)^q \, dx$. Let us derive estimates on $\|\rho\|_{L^q}$. Multiplying (4.1) by ρ^{q-1} and integrating, we obtain

$$\frac{1}{q} \partial_t \int_{\mathbb{R}^2} \rho^q \, dx = \int_{\mathbb{R}^2} \rho^{q-1} \Delta \rho \, dx + \chi \int_{\mathbb{R}^2} \rho^{q-1} \nabla \cdot (\rho \nabla \Delta^{-1} \rho) \, dx - \int_{\mathbb{R}^2} \rho^{2q-1} \, dx. \quad (4.9)$$

Observe that

$$\int_{\mathbb{R}^2} \rho^{q-1} \nabla \cdot (\rho \nabla \Delta^{-1} \rho) dx = -(q-1) \int_{\mathbb{R}^2} \rho^{q-1} \nabla \rho \cdot \nabla \Delta^{-1} \rho dx = \frac{q-1}{q} \int_{\mathbb{R}^2} \rho^{q+1} dx.$$

The last equality is obtained by integration by parts. Thus, we can rewrite (4.9) as

$$\partial_t \int_{\mathbb{R}^2} \rho^q dx = -\frac{4(q-1)}{q} \int_{\mathbb{R}^2} |\nabla \rho^{q/2}|^2 dx + \chi(q-1) \int_{\mathbb{R}^2} \rho^{q+1} dx - q \int_{\mathbb{R}^2} \rho^{2q-1} dx. \quad (4.10)$$

Let us introduce $v = \rho^{q/2}$, and recall a Gagliardo-Nirenberg type inequality

$$\|v\|_{L^{2+\alpha}} \leq C(d, \alpha) \|\nabla v\|_{L^2}^{\frac{2}{2+\alpha}} \|v\|_{L^{\frac{2d}{\alpha}}}^{\frac{\alpha}{2+\alpha}}, \quad (4.11)$$

which is valid for all $\alpha > 0$, $d \geq 1$. In our case, we set $\alpha = 2/q$, and inequality (4.11) translates into

$$\int_{\mathbb{R}^2} \rho^{q+1} dx \leq C(q) \int_{\mathbb{R}^2} |\nabla \rho^{q/2}|^2 dx \int_{\mathbb{R}^2} \rho dx.$$

Observe that $\alpha d/2 < 1$. While inequalities of this kind are well known to the experts [17], the references that include the case of exponents less than one are not common. For the sake of completeness, we provide a sketch of a simple proof of inequality (4.11) in Appendix II. Therefore, from (4.10) we can conclude that

$$\partial_t \int_{\mathbb{R}^2} \rho^q dx \leq -\frac{q-1}{q} \int_{\mathbb{R}^2} |\nabla \rho^{q/2}|^2 dx \left(4 - C(q)\chi \int_{\mathbb{R}^2} \rho dx\right) - q \int_{\mathbb{R}^2} \rho^{2q-1} dx.$$

Now, suppose that $C(q)\chi \int_{\mathbb{R}^2} \rho(x, t) dx$ drops below 2 at some time t_0 . Then, for all later times, we get

$$\partial_t \int_{\mathbb{R}^2} \rho^q dx \leq -C(q) \int_{\mathbb{R}^2} |\nabla \rho^{q/2}|^2 dx \quad (4.12)$$

(we use $C(q)$ for a positive constant depending only on q that may change from line to line). Let us recall another Gagliardo-Nirenberg inequality

$$\|v\|_{L^2}^{1+\frac{2}{d(q-1)}} \leq C(q, d) \|\nabla v\|_{L^2} \|v\|_{L^{\frac{2d}{q}}}^{\frac{2}{d(q-1)}}. \quad (4.13)$$

Applying it in (4.12) with $v = \rho^{q/2}$ in $d = 2$ leads to

$$\partial_t \int_{\mathbb{R}^2} \rho^q dx \leq -C(q) \left(\int_{\mathbb{R}^2} \rho^q dx\right)^{1+\frac{1}{q-1}} \left(\int_{\mathbb{R}^2} \rho dx\right)^{-\frac{q}{q-1}}.$$

Solving this differential inequality, and using the fact that $\int_{\mathbb{R}^2} \rho dx$ is monotone decreasing, leads to

$$\int_{\mathbb{R}^2} \rho(x, t)^q dx \leq \min \left(\int_{\mathbb{R}^2} \rho(x, t_0)^q dx, C(q)(t-t_0)^{-q+1} \left(\int_{\mathbb{R}^2} \rho(x, t_0) dx\right)^q \right).$$

Then the argument identical to that in the proof of Theorem 1.1 implies that

$$\inf_t \int_{\mathbb{R}^2} \rho(x, t) dx \geq \min \left(\frac{1}{2} \|\rho(\cdot, t_0)\|_{L^1}, C(q) \left(\frac{\|\rho(\cdot, t_0)\|_{L^1}}{\|\rho(\cdot, t_0)\|_{L^\infty}} \right)^{q-2} \right) \quad (4.14)$$

(observe that the proof of Lemma 2.2 goes through when $C(q)\chi \int_{\mathbb{R}^2} \rho(x, t) dx < 2$). Since we have a uniform upper bound for $\|\rho(x, t)\|_{L^\infty}$ (see Lemma 5.6 below), (4.14) implies the first statement of the theorem. Moreover, we can always take initial data such that $t_0 = 0$, and the L^∞ norm of ρ_0 is sufficiently small, making the bound on the right hand side of (4.14) equal to $c(q)\chi^{-1}$. This proves the second statement of the theorem. \square

5. APPENDIX I: GLOBAL EXISTENCE OF SMOOTH SOLUTIONS

Here we prove Theorem 4.1. We begin with the construction of a local solution in an appropriate space. We will consider arbitrary dimension d . Recall that

$$\|f\|_{M_n} = \int_{\mathbb{R}^d} (|\rho(x)| + |\nabla \rho(x)|)(1 + |x|^n) dx,$$

and the Banach space $K_{s,n}$ is defined by the norm $\|f\|_{K_{s,n}} = \|f\|_{M_n} + \|f\|_{H^s}$. First, we need a simple lemma on the heat semigroup action in this space.

Lemma 5.1. *Assume that $\rho_0 \in K_{s,n}$, with $s \geq 0, n \geq 0$. Then we have*

$$\|e^{t\Delta} \rho_0\|_{M_n} \leq C(1 + t^{n/2})\|\rho_0\|_{M_n}, \quad \|\nabla e^{t\Delta} \rho_0\|_{M_n} \leq C(t^{-1/2} + t^{(n-1)/2})\|\rho_0\|_{M_n}; \quad (5.1)$$

$$\|e^{t\Delta} \rho_0\|_{H^s} \leq \|\rho_0\|_{H^s}, \quad \|\nabla e^{t\Delta} \rho_0\|_{H^s} \leq Ct^{-1/2}\|\rho_0\|_{H^s}. \quad (5.2)$$

As a consequence,

$$\|e^{t\Delta} \rho_0\|_{K_{s,n}} \leq C(1 + t^{n/2})\|\rho_0\|_{K_{s,n}}, \quad \|\nabla e^{t\Delta} \rho_0\|_{K_{s,n}} \leq C(t^{-1/2} + t^{(n-1)/2})\|\rho_0\|_{K_{s,n}}. \quad (5.3)$$

The proof of Lemma 5.1 is elementary and we omit it.

Next, we set up the contraction mapping argument for local existence. We will use the Banach space $X_{s,n}^T \equiv C(K_{s,n}, [0, T])$ with a sufficiently small $T > 0$. Let us rewrite the equation (4.1) in an integral form using the Duhamel principle.

$$\rho(x, t) = e^{t\Delta} \rho_0(x) + \int_0^t e^{(t-s)\Delta} (\nabla \cdot (u\rho) - \rho^q + \nabla \cdot (\rho \nabla \Delta^{-1} \rho)) ds. \quad (5.4)$$

Let us denote

$$B_t(\rho) \equiv \int_0^t e^{(t-s)\Delta} (\nabla \cdot (u\rho) - \rho^q + \nabla \cdot (\rho \nabla \Delta^{-1} \rho)) ds.$$

We need the following auxiliary estimates.

Lemma 5.2. *Assume that q, s, n are positive integers and $s > \frac{d}{2} + 1$. Let $f, g \in K_{s,n}$. Then*

$$\|f^q - g^q\|_{H^s} \leq C(\|f\|_{H^s}^{q-1} + \|g\|_{H^s}^{q-1})\|f - g\|_{H^s} \quad (5.5)$$

$$\|f \nabla \Delta^{-1} f - g \nabla \Delta^{-1} g\|_{H^s} \leq C(\|f\|_{H^s} + \|g\|_{H^s})\|f - g\|_{H^s} \quad (5.6)$$

$$\|f^q - g^q\|_{M_n} \leq C(\|f\|_{H^s}^{q-1} + \|g\|_{H^s}^{q-1})\|f - g\|_{M_n} \quad (5.7)$$

$$\|f \nabla \Delta^{-1} f - g \nabla \Delta^{-1} g\|_{M_n} \leq C(\|f\|_{H^s} + \|g\|_{H^s})(\|f - g\|_{M_n} + \|f - g\|_{H^s}). \quad (5.8)$$

All constants in the inequalities may depend only on q, d, s and n .

Proof. All these estimates are fairly straightforward. The estimate (5.5) follows from writing $f^q - g^q = (f - g)(f^{q-1} + \dots + g^{q-1})$ and the fact that H^s is an algebra when $s > d/2$ (see, e.g. [29]). The estimate (5.6) follows from a similar argument. The third inequality (5.7) is proved by the same expansion and use of Sobolev imbedding implying $\|f\|_{L^\infty} + \|\nabla f\|_{L^\infty} \leq C\|f\|_{H^s}$ and similar bounds for g . Finally, to prove the last inequality (5.8), write

$$f\nabla\Delta^{-1}f - g\nabla\Delta^{-1}g = (f - g)\nabla\Delta^{-1}f + g(\nabla\Delta^{-1}f - \nabla\Delta^{-1}g).$$

Integral of the right hand side expression against $(1 + |x|^n)$ does not exceed

$$\|f - g\|_{M_n}\|\nabla\Delta^{-1}f\|_{L^\infty} + \|g\|_{M_n}\|\nabla\Delta^{-1}(f - g)\|_{L^\infty} \leq C(\|f\|_{H^s} + \|g\|_{H^s})(\|f - g\|_{M_n} + \|f - g\|_{H^s}).$$

For the case of the gradient, observe that

$$\nabla \cdot (f\nabla\Delta^{-1}f - g\nabla\Delta^{-1}g) = (\nabla f \cdot \nabla\Delta^{-1}f - \nabla g \cdot \nabla\Delta^{-1}g) + (f^2 - g^2).$$

The first two terms are then controlled similarly to the previous estimate, while the last two terms are easy to handle. \square

Now we can prove a key Lemma setting up contraction mapping.

Lemma 5.3. *Suppose that $u \in C^\infty(\mathbb{R}^d \times [0, \infty))$ and $\nabla \cdot u = 0$. Let s, q and n be positive integers, $s > \frac{d}{2} + 1$. Let $f, g \in X_{s,n}^T$. Then*

$$\|B_T(f) - B_T(g)\|_{X_{s,n}^T} \leq \alpha\|f - g\|_{X_{s,n}^T}, \quad (5.9)$$

where for $T \leq 1$, we have

$$\alpha \leq C(d, q, n) \max_{0 \leq t \leq T} (\|u(\cdot, t)\|_{C^s} + \|f(\cdot, t)\|_{H^s}^{q-1} + \|g(\cdot, t)\|_{H^s}^{q-1} + \|f(\cdot, t)\|_{H^s} + \|g(\cdot, t)\|_{H^s}) T^{1/2}. \quad (5.10)$$

Proof. Consider

$$B_t(f) - B_t(g) = \int_0^t e^{\Delta(t-r)} (\nabla(u(f - g)) - (f^q - g^q) + \nabla(f\nabla\Delta^{-1}f - g\nabla\Delta^{-1}g)) dr.$$

Using Lemmas 5.1 and 5.2, we find

$$\begin{aligned} \|B_t(f) - B_t(g)\|_{K_{s,n}} &\leq C \int_0^t [((t-r)^{-1/2} + (t-r)^{(n-1)/2}) (\|u\|_{C^s} + \|f\|_{H^s} + \|g\|_{H^s}) \\ &\quad + (1 + (t-r)^{n/2}) (\|f\|_{H^s}^{q-1} + \|g\|_{H^s}^{q-1})] \|f - g\|_{K_{s,n}} dr \\ &\leq C [(t^{1/2} + t^{(n+1)/2}) \max_{0 \leq r \leq t} (\|u\|_{C^s} + \|f\|_{H^s} + \|g\|_{H^s}) \\ &\quad + (t + t^{(n+2)/2}) \max_{0 \leq r \leq t} (\|f\|_{H^s}^{q-1} + \|g\|_{H^s}^{q-1})] \max_{0 \leq r \leq t} \|f - g\|_{K_{s,n}}. \end{aligned} \quad (5.11)$$

Therefore, we obtain (5.9). For $T \leq 1$ we can ignore the higher powers of T and the estimate (5.10) for α follows from (5.11). \square

In a standard way, Lemma 5.3 implies existence of local solution via the contraction mapping principle.

Theorem 5.4. *Assume q, s, n are positive integers and $s > \frac{d}{2} + 1$, $u \in C^\infty(\mathbb{R}^d \times [0, \infty))$, $\nabla \cdot u = 0$. Suppose $\rho_0 \in K_{s,n}$. Then there exists $T = T(q, d, u, s, \|\rho_0\|_{H^s})$ such that there exists a unique solution $\rho(x, t) \in X_{s,n}^T$ of the equation (5.4) satisfying $\rho(x, 0) = \rho_0(x)$.*

Remark. Higher regularity of the solution in space and time (in particular implying $\rho(x, t) \in C(H^m, (0, T])$ for every $m > 0$) follows from Theorem 5.4 and standard parabolic regularity estimates applied iteratively.

Proof. The only feature of the theorem that is not completely standard is the fact that T depends only on $\|\rho_0\|_{H^s}$ and not on $\|\rho_0\|_{K_{n,s}}$. This is a consequence the fact that only H^s norms of f and g enter in the estimate (5.10) for the contraction constant α , and only H^s norms appear on the right hand side of (5.6), (5.5). Then the statement can be checked by tracing through the standard proof of the solution existence via contraction mapping principle. \square

Corollary 5.5. *If under conditions of Theorem 5.4 we prove a uniform in time estimate on $\|\rho(\cdot, t)\|_{H^s}$, then the local solution can be extended globally to $X_{n,s}^T$ with arbitrary T .*

Indeed, if the H^s norm of the solution does not grow, we can just extend it by uniform time steps as far as we want. To prove uniform in time bound for the H^s norm of solution, we first establish control of the L^∞ norm.

Lemma 5.6. *Assume that $\rho(x, t)$ is the local solution guaranteed by Theorem 5.4. Then*

$$\|\rho(\cdot, t)\|_{L^\infty} \leq N_0 \equiv \max\left(\chi^{\frac{1}{q-2}}, \|\rho_0\|_{L^\infty}\right) \quad (5.12)$$

for all $0 \leq t \leq T$.

Proof. Assume this is false, and there exists $N_1 > N_0$ and $0 < t_1 \leq T$ such that we have $\|\rho(x, t_1)\|_{L^\infty} = N_1$ for the first time (that is, for all x and $0 \leq t \leq t_1$, $|\rho(x, t)| \leq N_1$). We claim that in this case there exists x_0 such that $\rho(x_0, t_1) = N_1$. Indeed, the only alternative is that there exists a sequence x_k such that $\rho(x_k, t_1) \rightarrow N_1$ as $k \rightarrow \infty$. If x_k has finite accumulation points, set one of them as x_0 . By continuity $\rho(x_0, t_1)$ will be equal to N_1 . Thus it remains to consider the case where $x_k \rightarrow \infty$ and passing to a subsequence if necessary we can assume that unit balls around x_k , $B_1(x_k)$, are disjoint. By a version of Poincare inequality (see e.g. [29]), we have $\|\rho - \bar{\rho}\|_{L^\infty(B_1(x_k))}^2 \leq C\|\rho\|_{H^s(B_1(x_k))}^2$. Since $\sum_k \|\rho\|_{H^s(B_1(x_k))}^2 \leq C(t_1) < \infty$, we get that

$$\bar{\rho}_k \equiv \frac{1}{|B_1(x_k)|} \int_{B_1(x_k)} \rho dx \xrightarrow{k \rightarrow \infty} N_1.$$

But this is a contradiction with $\int_{\mathbb{R}^d} |\rho(x)|(1 + |x|^n) dx \leq C(t_1)$.

Therefore, there exists x_0 such that $\rho(x_0, t_1) = N_1$ (we consider the case of a maximum; the case of minimum equal to $-N_1$ is considered similarly). Then

$$\begin{aligned} \partial_t \rho(x_0, t)|_{t=t_1} &= (u \cdot \nabla)\rho(x_0, t_1) + \Delta \rho(x_0, t_1) + \chi \nabla \rho(x_0, t_1) \cdot \nabla \Delta^{-1} \rho(x_0, t_1) \\ &+ \chi \rho(x_0, t_1)^2 - \rho(x_0, t_1)^q \leq \rho(x_0, t_1)^2 (\chi - \rho(x_0, t_1)^{q-2}). \end{aligned}$$

By assumption on N_1 , we see that $\partial_t \rho(x_0, t_1) < 0$, contradiction with our choice of t_1 . \square

Now we are ready to prove uniform in time bounds on the H^s norm of the solution.

Lemma 5.7. *Let $\rho(x, t)$ be the local solution whose existence is guaranteed by Theorem 5.4. Suppose that $\|\rho(\cdot, t)\|_{L^\infty}$ does not exceed N_0 for all $0 \leq t \leq T$. Then*

$$\|\rho(\cdot, t)\|_{H^s} \leq \max(\|\rho_0\|_{H^s}, C(u, d, q, s, N_0)). \quad (5.13)$$

Proof. Consider for simplicity the case where s is even (the odd case is very similar). Apply $\Delta^{s/2}$ to (4.1), multiply by $\Delta^{s/2}\rho(x, t)$ and integrate. We obtain

$$\begin{aligned} \frac{1}{2}\partial_t\|\rho\|_{H^s}^2 &= \int_{\mathbb{R}^d} [\Delta^{s/2}(u \cdot \nabla)\rho](\Delta^{s/2}\rho) dx - \int_{\mathbb{R}^d} (\Delta^{s/2}\rho^q)(\Delta^{s/2}\rho) dx - \|\rho\|_{H^{s+1}}^2 \\ &+ \int_{\mathbb{R}^d} [\nabla \cdot \Delta^{s/2}(\rho\nabla\Delta^{-1}\rho)](\Delta^{s/2}\rho) dx. \end{aligned} \quad (5.14)$$

Using $\nabla \cdot u = 0$, we obtain

$$\left| \int_{\mathbb{R}^d} [\Delta^{s/2}((u \cdot \nabla)\rho)](\Delta^{s/2}\rho) dx \right| \leq C\|u\|_{C^s}\|\rho\|_{H^s}^2.$$

Next, the second integral on the right hand side of (5.14) can be written as a sum of a finite number of terms of the form $\int_{\mathbb{R}^d} D^s\rho \prod_{i=1}^q D^{s_i}\rho dx$, $s_1 + \dots + s_q = s$, $s_i \geq 0$. Here D^l denotes any partial derivative operator of the l th order. By Hölder's inequality, we have

$$\left| \int_{\mathbb{R}^d} D^s\rho \prod_{i=1}^q D^{s_i}\rho dx \right| \leq \|D^s\rho\|_{L^2} \prod_{i=1}^q \|D^{s_i}\rho\|_{p_i},$$

$\sum_{i=1}^q p_i^{-1} = 1/2$. Take $p_i = 2s/s_i$, and recall the Gagliardo-Nirenberg inequality ([10, 21, 17])

$$\|D^{s_i}\rho\|_{L^{2s/s_i}} \leq C\|\rho\|_{L^\infty}^{1-\frac{s_i}{s}} \|D^s\rho\|_{L^2}^{\frac{s_i}{s}}. \quad (5.15)$$

Then we get

$$\left| \int_{\mathbb{R}^d} \Delta^{s/2}\rho^q \Delta^{s/2}\rho dx \right| \leq C\|\rho\|_{L^\infty}^{q-1}\|\rho\|_{H^s}^2.$$

Finally, we claim that the third integral on the right hand side of (5.14) can be written as a sum of a finite number of terms of the form $\int_{\mathbb{R}^d} D^s\rho D^k\rho D^{s+2-k}\Delta^{-1}\rho dx$, where $k = 0, \dots, s$. The only term one gets from the direct differentiation that does not appear to be of this form is $\int_{\mathbb{R}^d} \Delta^{s/2}\rho \nabla \Delta^{s/2}\rho \nabla \Delta^{-1}\rho dx$. However, integrating by parts, we find that this term is equal to $-\frac{1}{2} \int_{\mathbb{R}^d} |\Delta^{s/2}\rho|^2 dx$. Now

$$\left| \int_{\mathbb{R}^d} D^s\rho D^k\rho D^{s+2-k}\Delta^{-1}\rho dx \right| \leq C\|D^s\rho\|_{L^2}\|D^k\rho\|_{L^{p_1}}\|D^{s-k}\rho\|_{L^{p_2}},$$

$p_1^{-1} + p_2^{-1} = 1/2$, $p_2 < \infty$. Here we used boundedness of Riesz transforms on L^{p_2} , $p_2 < \infty$. Set $p_1 = \frac{2s}{k}$, $p_2 = \frac{2s}{s-k}$. By Gagliardo-Nirenberg inequality (5.15) with $s_i = k, s - k$, we get

$$\left| \int_{\mathbb{R}^d} D^s\rho D^k\rho D^{s+2-k}\Delta^{-1}\rho dx \right| \leq C\|\rho\|_{L^\infty}\|\rho\|_{H^s}^2.$$

Putting all the estimates into (5.14), we find that

$$\frac{1}{2}\partial_t\|\rho\|_{H^s}^2 \leq C\|\rho\|_{L^\infty}\|\rho\|_{H^s}^2 - \|\rho\|_{H^{s+1}}^2 \leq C\|\rho\|_{L^\infty}\|\rho\|_{H^s}^2 - \|\rho\|_{H^s}^{2+\frac{2}{s-d/2}}\|\rho\|_{L^\infty}^{-\frac{2}{s-d/2}}. \quad (5.16)$$

We used another Gagliardo-Nirenberg inequality in the last step. The differential inequality (5.16) implies the result of the lemma. \square

6. APPENDIX II: THE GAGLIARDO-NIRENBERG INEQUALITY WITH $p < 1$

Twice in the paper, we needed to apply Gagliardo-Nirenberg inequalities with one of the summation exponents less than one (see (4.11), (4.13)). Such inequalities are certainly known and can be found in mathematical literature (see e.g. encyclopedic [17]). However, it was not easy for us to find a reference with a transparent self-contained proof, and for the sake of completeness we provide a sketch of an elegant and simple proof here. The idea of this argument has been communicated to us by Fedor Nazarov. We will prove a slightly more general inequality containing both (4.11) and (4.13).

Theorem 6.1. *Let $v \in C_0^\infty(\mathbb{R}^d)$, $d \geq 2$. Then*

$$\|v\|_{L^q} \leq C(q, d)\|\nabla v\|_{L^2}^a\|v\|_{L^r}^{1-a}, \quad a = \frac{\frac{1}{r} - \frac{1}{q}}{\frac{1}{d} - \frac{1}{2} + \frac{1}{r}}. \quad (6.1)$$

The inequality holds for all $q, r > 0$ such that $q > r$ and $\frac{1}{d} - \frac{1}{2} + \frac{1}{r} > 0$.

Proof. Let A_k denote regions in \mathbb{R}^d such that $|A_k| = 2^{kd}$, $k \in \mathbb{Z}$, the boundary of A_k coincides with a level set of $|v(x)| \equiv v_{k+1}$, and $|v(x)| \geq v_{k+1}$ inside A_k . Then

$$\|v\|_{L^q}^q \leq \sum_{k \in \mathbb{Z}} |A_k| v_k^q.$$

Fix a small $\epsilon > 0$. Let us call k "important" if $v_{k+1} < (1 - \epsilon)v_k$. Denote the set of all important k by I . Observe that

$$\sum_{k \in \mathbb{Z}} |A_k| v_k^q \leq C(\epsilon) \sum_{k \in I} |A_k| v_k^q.$$

Indeed, a sequence of not important consequent k contributes at most $\sum_{l>0} 2^{-dl}(1-\epsilon)^{-ql}|A_{k+1}|v_{k+1}^q$ compared to the contribution $|A_{k+1}|v_{k+1}^q$ of the single next term.

For the L^r norm, we have the estimate

$$\|v\|_{L^r}^{(1-a)q} \geq C \left(\sum_{k \in \mathbb{Z}} |A_k| v_k^r \right)^{(1-a)q/r}.$$

For the gradient term, by the co-area formula (see e.g. [5]) we have

$$\int_{v_{k+1} \leq v(x) \leq v_k} |\nabla v| dx = \int_{v_k}^{v_{k+1}} \mathcal{H}^{d-1}(x : |v(x)| = s) ds,$$

where \mathcal{H}^{d-1} is the $d - 1$ -dimensional Hausdorff measure. By the isoperimetric inequality,

$$\mathcal{H}^{d-1}(x : |v(x)| = s) \geq C|A_k|^{1-\frac{1}{d}}$$

if $s \geq v_{k+1}$ (see e.g. [5]). Therefore,

$$\int_{v_{k+1} \leq v(x) \leq v_k} |\nabla v| dx \geq C |A_k|^{1-\frac{1}{d}} (v_k - v_{k+1}).$$

By Cauchy-Schwartz,

$$\int_{v_{k+1} \leq v(x) \leq v_k} |\nabla v|^2 dx \geq \frac{1}{|A_k|} \left(\int_{v_{k+1} \leq v(x) \leq v_k} |\nabla v| dx \right)^2 \geq C |A_k|^{1-\frac{2}{d}} (v_k - v_{k+1})^2.$$

Therefore,

$$\int_{\mathbb{R}^d} |\nabla v|^2 dx \geq C \sum_{k \in \mathbb{Z}} (v_k - v_{k+1})^2 |A_k|^{1-\frac{2}{d}} \geq C \epsilon^2 \sum_{k \in I} v_k^2 |A_k|^{1-\frac{2}{d}}.$$

Thus, it remains to prove that

$$\sum_{k \in I} |A_k| v_k^q \leq C \left(\sum_{k \in \mathbb{Z}} |A_k| v_k^r \right)^{(1-a)q/r} \left(\sum_{k \in I} v_k^2 |A_k|^{1-\frac{2}{d}} \right)^{aq/2}. \quad (6.2)$$

Observe that, if $d \geq 3$, then we have

$$\left(\sum_{k \in I} v_k^2 |A_k|^{1-\frac{2}{d}} \right)^{aq/2} \geq \left(\sum_{k \in I} v_k^{\frac{2d}{d-2}} |A_k| \right)^{\frac{aq(d-2)}{2d}}$$

(since $\sum_k b_k^s \geq (\sum_k b_k)^s$ for $b_k \geq 0$, $0 < s \leq 1$). Write

$$|A_k| v_k^q = \left[|A_k|^{(1-a)q/r} v_k^{(1-a)q} \right] \left[v_k^{aq} |A_k|^{\frac{aq(d-2)}{2d}} \right]. \quad (6.3)$$

Apply Hölder inequality on the left hand side of (6.2), raising the first term in (6.3) to the power $\frac{r}{q(1-a)}$, and the second term to the power $\frac{2d}{aq(d-2)}$. Notice that the inverses of these powers sum to one due to the definition of a in (6.1). The resulting inequality coincides with (6.2). Finally, when $d = 2$, we have $a = 1 - q/r$, and (6.2) follows from a more elementary consideration. \square

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REFERENCES

- [1] J.C. Coll et al, *Chemical aspects of mass spawning in corals. I. Sperm-attractant molecules in the eggs of the scleractinian coral Montipora digitata*, Mar. Biol. **118**, 177-182
- [2] J.C. Coll et al, *Chemical aspects of mass spawning in corals. II. (-)-Epi-thunbergol, the sperm attractant in the eggs of the soft coral Lobophytum crassum (Cnidaria: Octocorallia)*, Mar. Biol. **123** (1995), 137-143
- [3] P. Constantin, A. Kiselev, A. Oberman and L. Ryzhik, *Bulk burning rate in passive-reactive diffusion*, Arch. Ration. Mech. Anal. **154** (2000), 53-91

- [4] M.W. Denny and M.F. Shibata, *Consequences of surf-zone turbulence for settlement and external fertilization*, Am. Nat. **134** (1989), 859–889
- [5] L.C. Evans and R.F. Gariepy, *Measure Theory and Fine Properties of Functions*, CRC Press, 1992
- [6] J.P. Crimaldi, J.R. Hartford, and J.B. Weiss, *Reaction enhancement of point sources due to vortex stirring*, Phys. Rev. E **74** (2006), 016307
- [7] J.P. Crimaldi, J.R. Cadwell, and J.B. Weiss, *Reaction enhancement by isolated scalars by vortex stirring*, Physics of Fluids **20** (2008), 073605
- [8] J.E. Eckman, *Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates*, J. Exp. Mar. Biol. Ecol. **200** (1996), 207
- [9] A. Fannjiang, A. Kiselev and L. Ryzhik, *Quenching of reaction by cellular flows*, GAFA **16** (2006), 40–65
- [10] E. Gagliardo, *Ulteriori proprietà di alcune classi di funzioni on più variabili*, Ric. Math. **8** (1959), 24–51
- [11] E.F. Keller and L.A. Segel, *Initiation of slide mold aggregation viewed as an instability*, J. Theor. Biol. **26** (1970), 399–415
- [12] E.F. Keller and L.A. Segel, *Model for chemotaxis*, J. Theor. Biol. **30** (1971), 225–234
- [13] A. Kiselev and L. Ryzhik, *Enhancement of the traveling front speeds in reaction-diffusion equations with advection*, Ann. Inst. H. Poincaré Anal. Non Linéaire **18** (2001), 309–358
- [14] A. Kiselev and A. Zlatos, *Quenching of combustion by shear flows*, Duke Math. J. **132** (2006), 49–72
- [15] H. Lasker, *High fertilization success in a surface-brooding Caribbean Gorgonian*, Biol. Bull. **210** (2006), 10–17
- [16] A. Majda and P. Souganidis, *Large scale front dynamics for turbulent reaction-diffusion equations with separated velocity scales*, Nonlinearity, **7**, 1994, 1–30
- [17] V. Maz'ja, *Sobolev Spaces*, Springer-Verlag, Berlin Heidelberg, 1985
- [18] R.L. Miller, *Sperm chemotaxis in hydromedusae. I. Species specificity and sperm behavior*, Mar. Biol **53** (1979), 99–114
- [19] R.L. Miller, *Demonstration of sperm chemotaxis in Echinodermata: Asteroidea, Holothuroidea, Ophiuroidea*, J. Exp. Zool. **234** (1985), 383–414
- [20] J. Nash, *Continuity of solutions of parabolic and elliptic equations*, Amer. Jour. Math., **80**, 1958, 931–954
- [21] L. Nirenberg, *On elliptic partial differential equations: Lecture II*, Ann. Sc. Norm. Super. Pisa, S. 3, **13** (1959), 115–162
- [22] J.M. Ottino, *Mixing and Chemical Reactions: A Tutorial*, Chem. Eng. Soc. **49** (1994), 4005–4027
- [23] C.S. Patlak, *Random walk with persistence and external bias*, Bull. Math. Biol. Biophys. **15** (1953), 311–338
- [24] J. Pennington, *The ecology of fertilization of echinoid eggs: The consequences of sperm dilution, adult aggregation and synchronous spawning*, Biol. Bull. **169** (1985), 417–430
- [25] B. Perthame, *Transport equations in biology*, Birkhäuser Verlag, Basel, 2007
- [26] P. Ronney, *Some open issues in premixed turbulent combustion*, in Modeling in Combustion Science, J.Buckmister and T.Takeno, eds., Springer-Verlag, Berlin, 1995
- [27] V. Yakhot, *Propagation velocity of premixed turbulent flames*, Combust. Sci. and Tech., **60**, 191-214
- [28] P. Yund, *How severe is sperm limitation in natural populations of marine free-spawners?* Trends Ecol. Evol. **15** (2000), 10–14
- [29] W.P. Ziemer, *Weakly Differentiable Functions*, Springer-Verlag, New York