The fine art of surfacing: Its efficacy in broadcast spawning

Jan Moláček a,1, Mark Denny b,2, John W.M. Bush a,1,n

a Department of Mathematics, Massachusetts Institute of Technology, 77 Massachusetts Avenue, Cambridge, MA 02139, USA
b Hopkins Marine Station of Stanford University, Pacific Grove, CA 93950, USA

1. Introduction

Sexual reproduction in both plants and animals often involves broadcasting gametes into a fluid environment, either air or water. In some such broadcast spawners (notably, red algae, terrestrial plants, and a wide sampling of marine invertebrates) male propagules (either pollen or sperm) are released into the fluid and make their way to the eggs retained by females. More commonly, both sperm and eggs are released, and fertilization occurs in the fluid. Unlike animals that copulate – for whom the motility of the adult is used to ensure that sperm meets egg – few reproductive propagules of broadcast spawners are sufficiently motile to control their position in the environment. Instead, they move at the whim of wind or currents. The resulting random transport can be advantageous – it allows for mating among widely dispersed or sedentary individuals – but it also poses a serious challenge. Because random mixing causes dilution of propagules, through time the likelihood decreases that sperm and egg will meet (Denny, 1988; Denny and Shibata, 1989). Even in still water, the effective rotational diffusion of small motile gametes causes them to move randomly (Berg, 1993).

At least two obvious strategies are available to broadcast spawners to maximize their probability of fertilization in the presence of random mixing. First, species that release both male and female propagules should spawn synchronously in response to either chemical or environmental cues, thereby increasing the initial concentration of gametes. This strategy is commonplace among marine invertebrates and seaweeds (e.g. Pearse et al., 1988; Levitan and Petersen, 1995; Togashi and Cox, 2001; Santelices, 2002). Second, organisms should minimize the spatial domain in which gametes move, thereby increasing their encounter rates. For example, some seaweeds living in tide pools release gametes only at low tide when the pool is isolated from the sea (Pearson and Brawley, 1996). Other broadcast spawners take advantage of the coherent structures in the turbulent field, which confine their gametes to relatively thin filament sheets (Crimaldi and Browning, 2004). A more general implementation of this second strategy (“surfacing”) constrains propagules to a surface rather than allowing them to mix through a volume. Gametes in water could be positively buoyant, for example, leading to confinement at the water’s surface. Alternatively, negative buoyancy in water leads to confinement near the seafloor or lake bed. In air, the negative buoyancy of pollen grains tends to concentrate them near the ground (Denny, 1994).

While it would seem intuitively obvious that confining the search for a mate to a plane provides an advantage, there are several complications to consider. First, the risk of death might be higher near the surface than in the fluid bulk. The seafloor, for example, is densely covered with a variety of suspension feeders all too willing to consume reproductive propagules, and rainfall and the resulting decrease in sea-surface salinity can kill buoyant gametes of corals (Harrison et al., 1984). Moreover, the delay and perils associated with traveling to a surface might conceivably make it faster and safer to remain in the bulk fluid. Under what
circumstances is surfacing a viable reproductive strategy? We here provide a quantitative comparison between encounter rates at surfaces and in the bulk, and so rationalize and quantify the evolutionary advantage of surfacing.

The results are applicable to numerous scenarios covering a wide range of scales, including biofilms, puddles, ponds, lakes, oceans, and the atmosphere. Examples abound. A thin liquid film is required for sexual reproduction of liverworts, hornworts, mosses and ferns, in order for the antherozoids (the equivalent of sperm) to be able to reach neighbouring egg cells. In red algae (genus 
*Vallisneria*), male flowers detach from the plant and float up to the surface while the female flowers rise to the surface by straightening their coiled stalks. After successful pollination, the stalks coil down again and the fruit develops underwater. Aquatic plants of genera *Lepilaena*, *Ruppia*, *Haloidele* and others (*Cox and Knox, 1988*) live in coastal waters or brackish lakes and release flowers that float to the water surface, where they rupture and expel pollen which then floats on the surface until colliding with a stigma. Several species of corals on the Great Barrier Reef release buoyant gamete bundles that float to the surface and then break apart, releasing eggs and sperm (*Harrison et al., 1984*).

We will model the movement of all such gametes as a random walk (*Cox, 1983*). By that we specifically mean movement consisting of discrete steps of constant length \( \delta \) in a random direction happening over a constant timescale \( \tau \), resulting in an effective diffusivity \( D = \delta^2/\tau \). This provides a good model of particle motion in many biological settings. Small passive particles, like the gametes of red algae in calm water, may be moved about by the random motion of surrounding molecules and the resulting Brownian motion is a quintessential example of a random walk. Motile small cells, i.e. flagellated sperm or their equivalent, can be separated into two types according to their mode of propulsion. Cells of the first type “run and tumble”, abruptly changing direction after some approximately constant time interval within which they swim along straight lines, hence the relevance of the random walk model. Cells of the second type do not run and tumble, but the direction of their movement changes frequently due to random impacts with surrounding molecules. The impact rate gives us the typical timescale over which the direction of movement is constant, beyond which velocities are uncorrelated.

The random walk also provides a simple model for particles being advected and dispersed by ambient turbulence. The characteristic movement is constant, beyond which velocities are uncorrelated.

In Section 3, we compare the encounter probabilities in the two scenarios. We first consider the case in which the environmental conditions are the same on the surface and in the bulk, and then the more general case, in which there may be a larger loss rate or more vigorous turbulent mixing near the surface. We deduce the critical water depth at which the surface search become advantageous relative to the bulk search. Furthermore, we consider the influence of anisotropic diffusion on the advantage gained by surfacing. Finally, in Section 4 we apply the results to three typical real-world scenarios, and discuss the implications of our results and the limitations of our approach.

2. The model

Consider an organism living in a body of water of constant finite depth \( H \) and infinite horizontal extent. We suppose that its sexual reproduction involves encounters between male gametes and female gametes, where at least one of the gametes is moving, either passively or actively. If the sum of typical radii of the male and female gametes is \( r_T \), we can model the male gametes as point particles while the female gametes can be represented by a sphere (or, in 2D, a circle) of radius \( r_T \). Henceforth, we shall refer to the male gametes as “particles” and the female gametes as “targets”. Successful encounter occurs when the particle touches the surface of the target. We assume that the organisms are distributed uniformly across the bottom surface of the water body and that each organism releases the same number of targets (female gametes). The number of particles (male gametes) released by each organism does not impact the differential encounter probability of surface and bulk searches; therefore we consider the encounter probability of a single particle. Note that our model is not restricted to the case of a female gamete being much larger than the male, as \( r_T \) represents the sum of the gamete radii and so applies equally well to the case of isogamy.

To model the loss of viable gametes due to predation, energy depletion, senility or other causes, we introduce the loss rate \( \lambda \). We assume that \( \lambda \) is constant, that is, the probability of a given gamete dying during a small time interval \( \delta t \) is \( \lambda \delta t \). Such an approximation is appropriate when predation is the primary cause of gamete mortality, and adopted here in general for the sake of mathematical simplicity. Since the gametes are generally different in size and motility, we expect the loss rates to be different for different sexes. Therefore we denote by \( \lambda_1 \) and \( \lambda_2 \) the target and particle loss rates, respectively. As we shall demonstrate below in Section 2.1, only the total loss rate \( \lambda = \lambda_1 + \lambda_2 \) will enter into our calculations. We assume the gametes are released simultaneously from multiple points distributed uniformly long the water’s lower or upper surface. This corresponds to the simultaneous gamete release by bottom-dwelling or surface-dwelling organisms, respectively.

There are two reproductive strategies available to the organisms: either they can release their gametes onto a surface (the water surface or the bottom) or into the water bulk. We will compare the two reproductive strategies using the gamete encounter probability. The encounter probability \( P_{\text{enc}} \) will be the probability that a particle (male gamete) introduced randomly onto a plane uniformly filled with points simultaneously releasing \( N \) targets (female gametes) each, will be successful in encountering at least one target before it dies. Similarly, \( P_{\text{bulk}} \) will be the encounter probability for a particle introduced into the water bulk of constant depth \( H \), whose bottom surface is again uniformly filled with target-releasing points. If the average density of the organisms per unit area is \( N_0 \),  then \( P_{\text{enc}} = N_0 P_{\text{enc}} \) and each organism releases \( N \) targets, then if the targets are released onto the surface, their surface density will be \( P_{\text{enc}} = N_0 P_{\text{enc}} \).
2.1. Encounter probability

It is our aim to determine the encounter probabilities \( P_S \) and \( P_B \) of a single particle with targets released from uniform planar distribution of points, on the surface and in the bulk, respectively. A good starting point is to consider a simpler scenario – the case of one particle and one target, in a one-dimensional space (so that no boundaries need to be considered). Suppose that the target has size \( r_T \) and is originally a distance \( R \) from the particle. Then the encounter probability \( P_d \) will be a function of \( r_T \), the loss rates \( \lambda_1, \lambda_2 \) and distance \( R \) only. For \( d=2.3 \), that is for search on a surface or in an infinite fluid bulk, we can find \( P_d \) exactly. In Appendix A we derive the following formulæ:

\[
P_d(R,r_T,\kappa_S) = \frac{K_0(R/\kappa_S)}{K_0(r_T/\kappa_S)},
\]

\( d=1 \) (1)

\[
P_f(R,r_T,\kappa_S) = \frac{r_T}{R} \exp \left[ \frac{r_T}{\kappa_S} \right] \frac{1}{R} \exp \left[ \frac{K_0(R/\kappa_S)}{K_0(r_T/\kappa_S)} \right].
\]

(2)

where \( K_0(s) \) is the modified Bessel function of the second kind of order \( 0 \), \( \kappa_S = \sqrt{D_S/\lambda_S} \) and \( \kappa_B = \sqrt{D_B/\lambda_B} \). Here \( \lambda_S, \lambda_B \) and \( D_S, D_B \) are the total loss rates and diffusivities on the surface and in the bulk, respectively. \( \lambda_S, \lambda_B \) are considered as the typical distances a gamete travels before dying, on the surface and in the bulk, respectively, and will be henceforth referred to as the gamete’s range. In each region the total loss rate is \( \lambda_1 + \lambda_2 \) and the diffusivity \( D = (\delta_1^2 + \delta_2^2)/(2\text{d}t) \) is a constant associated with the gamete random walk with steplengths \( \delta_1, \delta_2 \) for each gamete and common time-step \( \tau \). By definition, \( P_d \) and \( P_f \) are equal to 1 for \( R = r_T \), and then rapidly decrease. For large \( R \) they decrease roughly exponentially.

Fig. 2 illustrates the dependence of \( P_S \) and \( P_f \) on the nondimensional distance \( R/\kappa \) for two values of \( r_T/\kappa \), when \( \kappa_S = \kappa_B = \kappa \). We observe that \( P_S > P_f \) for \( R > r_T \), \( P_f \) decreases faster than \( P_S \) with the initial gamete distance \( R/\kappa \), and the difference between the two probabilities increases with decreasing \( r_T/\kappa \), so smaller target size makes surface search more advantageous compared to fluid bulk search.

Since in our 3D scenario we work with a body of finite depth only, we now consider the case of one particle and one target originally a distance \( R \) apart on the bottom surface, in a body of water of constant depth \( H \) (see Fig. 1 with \( h=0 \)). Denote the encounter probability in this scenario by \( P_{3f} \). In Appendix B we derive the formula

\[
P_{3f}(R,r_T,\kappa_S) = \frac{A(R/\kappa_S,H/\kappa_S),}{\bar{A}(R/\kappa_S,H/\kappa_S),}
\]

(3)

where

\[
A(x,y) = \sum_{n=1}^\infty \frac{\exp(-x\sqrt{2 + 4\pi^2y^2})}{\sqrt{x + 4\pi^2y^2}}.
\]

(4)

Now that we know \( P_S \) and \( P_{3f} \) – the single-particle, single-target encounter rates – it is straightforward to derive \( P_B \) and \( P_{3F} \), the single-particle, multiple-target encounter rates, since we know the original target density \( \rho_S \) and hence also the probability of finding a target release point at a distance \( R \) (Table 1). Integrating over all possible distances \( R \) we obtain (see Appendix C)

\[
P_S(\rho_S,r_T,\kappa_S) = 1 - \exp \left[ -\rho_S \int_0^\infty 2\pi R \bar{P}_S(R) dR \right],
\]

(5)

\[
P_B(\rho_B,r_T,\kappa_S) = 1 - \exp \left[ -\rho_B \int_0^\infty 2\pi R \bar{P}_B(R) dR \right],
\]

where \( \bar{P}_S \) and \( \bar{P}_{3f} \) are defined by Eqs. (1) and (3), respectively. Evaluating the integrals in Eqs. (4) and (5) yields

\[
P_S(\rho_S,r_T,\kappa_S) = \int_0^\infty \exp(-\rho_S \bar{P}_S(R)),
\]

(6)

\[
P_B(\rho_B,r_T,\kappa_S) = \int_0^\infty \exp(-\rho_B \bar{P}_B(R)),
\]

where \( \bar{P}_S(R) = 2\pi R K_0(S) \int_0^\infty xK_0(x) dx \), and \( \bar{P}_{3f}(R) = 2\pi R A(S,T) \int_0^\infty xA(x,t) dx \). The encounter probabilities \( P_B \), \( P_{3f} \) are proportional to target density \( \rho_B \) when \( \rho_B \) is small. With increasing target density they converge exponentially to 1. \( P_B \) is proportional to \( r_T \) for small target size \( r_T \), whereas \( P_{3f} \) is proportional to \( 1/\ln(1/r_T) \), so target size plays a smaller role in the surface than the bulk searches.

3. Comparison of surface and bulk encounter probabilities

We proceed by comparing encounter probabilities on the surface and in the bulk. In Section 3.1, we consider the case in which the conditions on the surface and in the bulk are equally favourable, that is, the loss rates and gamete motilities are equal. In Section 3.2, we consider the more general case of unequal loss rates and motilities, and derive an expression for the critical water depth at which the surface and fluid bulk searches are
equally advantageous. Finally, in Section 3.3, we consider the case of anisotropic diffusion and show that it can be included in our model by suitable rescaling of parameters.

3.1. Equal loss rates and motilities at the surface and in the bulk

Suppose that both the loss rate and the gamete motility are the same on the surface and in the bulk. Then \( k_S = \sqrt{D/\lambda} = (\sqrt{\lambda} + \sqrt{\kappa})/2\lambda \) while \( k_B = \sqrt{D/\lambda} = \sqrt{4/\sqrt{\lambda} k_S} \).\footnote{Note: The values of \( \lambda \) and \( \kappa \) are not specified in the text.} From the definition of diffusivity \( D \) (see Appendix A), where \( \lambda \) and \( \kappa \) are the length scales associated with the random walk of each type of gamete, and \( \tau \) is the associated time-step. Let us write \( k = k_S = k_B \), so \( k_S = k/\sqrt{\sqrt{\lambda}} \).

By writing \( P = p_k \kappa^2, r = r_\tau/k \) and \( \Pi = H/\kappa \) for the nondimensional target density, target size and water depth, respectively, Eqs. (6) and (7) transform to

\[
P_S(\Pi, r) = 1 - \exp(-\Pi_1(r)),
\]

\[
P_B(\Pi, r, \Pi) = 1 - \exp\left(-\frac{2}{\kappa} I_2(\sqrt{1.5r}, \sqrt{1.5\Pi})\right).
\]

Since \( r = r_\tau/k \) is the ratio of target radius to the gamete’s range, we expect this to be a small parameter, \( r \ll 1 \). When the loss rate and gamete motility are the same for the surface and bulk searches, the only reason that \( P_S \) and \( P_B \) differ is that the bulk provides a larger region for the gametes; equivalently, the average spacing between male and female gametes is less at the surface. Therefore we must have \( P_S > P_B \) for all \( \Pi > 0 \).

Now we can visualize the advantage of the surface search by plotting the ratio of \( P_S/P_B \) as a function of \( \Pi \) for various values of \( r \) and \( \Pi \). The results are shown in Fig. 3. For large target densities, the ratio \( P_S/P_B \) tends to 1, since with increasing target density, both \( P_S \) and \( P_B \) must tend to 1 separately: the particle is bound to encounter a target for sufficiently high target density. We also observe that the convergence of \( P_S/P_B \) to 1 happens for increasingly large target densities \( \Pi \) as we increase the relative depth \( \Pi \), because a larger total number of targets is required to fill a larger volume with sufficiently high density. Conversely, for small target densities \( \Pi \), the ratio \( P_S/P_B \) is independent of target density and proportional to \( \Pi \).

3.2. Unequal loss rates and motilities at the surface and in the bulk

We now determine the conditions under which \( P_S > P_B \). Combining Eqs. (6) and (7), we see that \( P_S > P_B \) requires that

\[
\rho_S k_S^2 I_1(r_\tau/k_S) > \rho_S k_S^2 I_2(r_\tau/k_S, H/k_S) = \frac{k_S^2}{\kappa_S^2} \frac{I_2(r_\tau/k_S, H/k_S)}{I_1(r_\tau/k_S)}.
\]

We now nondimensionalize as in the previous case, setting \( r = r_\tau/k_S, \Pi = H/k_S \) and \( \mu = k_S/k_B \). Thus \( \mu \) is the ratio of the gamete ranges on the surface and in the bulk, and hence indicates how favourable the conditions are for random walk encounters on the surface relative to the bulk. As we might expect the conditions to be more favourable in the bulk due to lower predation, one might expect \( k_S > k_B \) so \( \mu = k_S/k_B < 1 \). The criterion (10) then transforms to

\[
P_S > P_B \quad \text{if} \quad I_1(r) > I_2(\mu, \mu \Pi)
\]

with \( I_1(r) = 2\pi K_0(r) \int_0^\infty nK_0(\kappa) \, d\kappa \) and \( I_2(r,s) = 2\pi K_0(r, s) \int_0^\infty xA(\kappa, s) \, d\kappa \).

The curves of \( P_S = P_B \) are shown graphically in Fig. 4 for three typical values of \( r \) and a range of \( \mu \) and \( \Pi \). We observe that for smaller relative target size \( r \) the surface search becomes more advantageous. For small values of \( \Pi \), the critical value of \( \mu \), for which \( P_S = P_B \), is close to 1, whereas for large \( \Pi \) the critical value of \( \mu \) converges to a constant that decreases linearly with \( r \).

3.3. Anisotropic diffusion

So far, we have compared the cases of search in the fluid bulk and on the surface. However, in many cases the particles are not strictly constrained to the surface but rather to a region just beneath it. This is the case, for example, for light-sensitive motile gametes or for buoyant particles in turbulent waters. Since we have shown that \( P_S = P_B \) when \( H \rightarrow r_\tau \), if the depth of this region is

![Fig. 3. The dependence of the ratio of surface and bulk encounter probabilities, \( P_S/P_B \), on the nondimensional target density, \( \Pi \), for relative target size (a) \( r = 10^{-3} \) and (b) \( r = 10^{-4} \), and various relative water depths \( \Pi \). Here \( r = r_\tau/k_S, \Pi = H/k_S \) and \( \Pi = k_S^2/\kappa_S^2 \).](image)

![Fig. 4. Log–log graph of the critical relative water depth \( \Pi = H/k_S \) at which surface and bulk searches are equally advantageous (\( P_S = P_B \)) as a function of \( \mu = \sqrt{\kappa_S/k_B} D_S/\kappa_B \).](image)
It is apparent that when anisotropic diffusion with horizontal and vertical diffusivities allows our model to capture the influence of anisotropic diffusion.

Table 2. Values of relevant parameters for three types of water-dwelling organisms. The values of relevant parameters for three types of water-dwelling organisms. The reason why we do not get exactly the familiar scenario is the large size of the annelid gametes relative to their range, which accounts for their use of the bulk search. Hence, surface search is again advantageous. Third, we consider the case of a polychaete annelid worm Phragmatopoma californica, which does not employ surface search. We obtain a critical value of \( \mu \approx 0.3 \), so indeed, in this scenario the advantage predicted by our model.

4. Discussion

We proceed by applying our results to three specific biological systems. Relevant parameters for each system are listed in Table 2. First, for a typical coral we assume the gamete diffusion to be mainly due to the fluid motion. Both the surface turbulence and currents near the bottom have typical speed \( U = 0.1 \) m/s and scale \( L = 0.1 \) m, giving a diffusivity \( D \approx 10^{-5} \) m\(^2\)/s. As the gametes survive for many hours after release, the loss rate \( \lambda < 10^{-4} \) s\(^{-1}\). We here consider the worst case scenario \( \lambda = 10^{-5} \) s\(^{-1}\). Referring to Table 2 and Fig. 6, we see that bulk search would be advantageous for \( \mu < 0.03 \), which corresponds to the loss rate being 1000 times larger on the surface than in the bulk. Hence, we expect the surface search to be advantageous for all realistic values of loss rates and diffusivities, an inference consistent with the fact that many coral species do employ the water surface for their reproduction (Oliver and Babcock, 1992). We discuss below why some species do not use this strategy despite the robust advantage predicted by our model.

Second, marine green alga Monostroma angicava has phototactic gametes that concentrate near the water surface. Their typical gamete speed is \( 2 \times 10^{-4} \) m/s and tumbling timescale \( 5 \times 10^{-2} \) s, giving a diffusivity \( D = 2 \times 10^{-6} \) m\(^2\)/s. We estimate the dimensional loss rate to be on the order of \( 2 \times 10^{-4} \) s\(^{-1}\) (i.e. more than half of the gametes will be dead after 2 h, see Grave and Oliphant, 1930). From Table 2 and Fig. 6, we infer that a surface to bulk loss rate ratio of at least 5000 is required to favour the bulk search. Hence, surface search is again favourable.

Third, we consider the case of a polychaete annelid worm Phragmatopoma californica, which does not employ surface search. We obtain a critical value of \( \mu \approx 0.3 \), so indeed, in this scenario the advantage of surfacing can be easily outweighed by relatively hostile surface conditions. The main difference between this and the previous two examples is the large size of the annelid gametes relative to their range, which accounts for their use of the bulk search. The results of our analysis suggest that surface search is advantageous in a variety of situations spanning a broad range of scales. However, we have thus far tacitly assumed that organisms release their gametes onto the same surface on which they themselves live. Many bottom-dwelling organisms nevertheless release positively buoyant gametes, which float to the surface.
water surface. Getting to the surface might be a long and dangerous process, especially in deep water. If the male gametes have any means of detecting the location of female gamete (e.g. chemotaxis), this may also negate the disadvantage of the 3D random walk. There are many other ways in which organisms can tweak the encounter probability in the right direction; however, as this can be typically be done both on the surface and in the bulk, this introduces complications beyond the scope of our model. For example, deep dwelling organisms release their gametes with significant initial velocity, which hastens their spread. Flowers on the water surface use surface tension to distort the neighbouring free surface and thus increase their effective target size. The maximum increase in the target radius attainable by this method is twice the capillary length effective target size. The maximum increase in the target radius as this can be typically be done both on the surface and in the water surface. Getting to the surface might be a long and dangerous process, especially in deep water. If the male gametes were possibly further concentrated near the water surface. Finally, our model points in the direction of novel models of predator–prey dynamics. Predatory habits will generally depend that operating when antherozoids are dispersed into a lake or increase the probability of antherozoid–egg encounter relative to that that would have been accelerated had it arisen on the water surface.

Under most conditions, the encounter rates between passive particles are higher on or near the surface than within the bulk. This geometric consequence may have some bearing on models of the creation of early terrestrial life. According to most current theories, the simple organic molecules created by natural processes in the atmosphere and oceans (Miller, 1953) accumulated on the water surface, and were possibly further concentrated near the shores by wind (Panno, 2004), there combining to form macromolecules capable of replication and metabolism. Although the mechanism responsible remains a point of contention, it is clear that constraining the basic molecules to lie on a surface would significantly increase the encounter rate, thus accelerating the process. We note that other factors might have further concentrated these molecules, for example containment within bubbles or drops created by breaking waves or hydrothermal vents. In any case, our study suggests that the evolution of early life would have been accelerated had it arisen on the water surface.

Increased encounter rates near surfaces can also affect how we interpret reproduction in liverworts and hornworts, “lower” plants thought to be similar to those that first invaded the terrestrial environment. Because liverworts and hornworts require a film of liquid water as a pathway by which antherozoids are delivered to eggs, reproduction in the terrestrial environment is considered to be at a disadvantage relative to that in water. However, confinement to a thin film of water might actually increase the probability of antherozoid–egg encounter relative to that operating when antherozoids are dispersed into a lake or stream.

Finally, our model points in the direction of novel models of predator–prey dynamics. Predatory habits will generally depend on the type of region to which movement is confined. Presumably different strategies will be required for catchment of prey moving on a surface than in the bulk. While predators and prey are often confined to the same fluid domain, such is not always the case; for example, some birds prey on fish only at or near the water surface. The role of geometry on predator–prey dynamics is left as a subject for future research.

Appendix A. Exact solutions for $P_d$ in infinite geometries

Consider two motile gametes (point particles) performing random walks in $d$-dimensional space. Let the lengthscales of the random walk steps be $\delta_1$ and $\delta_2$ for the first and second gamete, respectively, and the timescale of the step be $\tau$, common for both. Also let the loss rates for each gamete be $\lambda_1$, $\lambda_2$, respectively. Now let $P_d$ be the probability that the gametes will ever encounter each other, that is, that they will get within a distance $r_T$ of each other before expiring. Only the distance between the gametes and the loss rates $\lambda_1$, $\lambda_2$ play a role in this probability, so $P_d = P_d(R, \lambda_1, \lambda_2)$ where $R = |\mathbf{x}_1 - \mathbf{x}_2|$. We can choose the coordinates so that at time $t=0$ one gamete is at the origin and the other one is at $R \mathbf{e}_c$. Considering the encounter probability at time $t = \tau$, we arrive at

$$P_d(R) = (1 - \lambda_1 \tau)(1 - \lambda_2 \tau) \left[ \int d\mathbf{m} P_d(R, \delta_1 - \delta_c \mathbf{m}, -\delta_c \mathbf{n}) \right]$$

$$+ \frac{\delta_1^2 + \delta_2^2}{2d} P_d(R) + O \left( \frac{\tau^2}{\mathbf{r}^2} \right).$$

Writing $D = (\delta_1^2 + \delta_2^2)/2d \tau$, $\lambda = \lambda_1 + \lambda_2$, and setting $\delta_1 \to 0$, $\delta_2 \to 0$ and $\tau \to 0$ while keeping $D$ and $\lambda$ constant simplifies Eq. (A.2) to

$$P_d(R) = k_2 \frac{|d-1|}{R} P_d(R) + P_d(R).$$

Appendix B. Encounter probability in finite-depth 3D scenario

When the body of water has a finite depth $H$, we cannot use the spherical symmetry which allowed us to treat the encounter probability as a function of the initial gamete distance only. We will use a less direct method based on manipulations of the probability density function $f(x,t)$ describing the location of a gamete. For simplicity, we will assume one gamete (the target) to be non-motile and place it at the origin of our coordinate system. The integral of $f(x,t)$ over the whole space gives us the probability that the motile gamete is still alive at time $t$. Introduction of an absorbing boundary condition at the encounter distance from the target (i.e. distance $r_T$ from the origin) further reduces the total integral of $f(x,t)$, by an amount which must be equal to the encounter probability between the two gametes. We proceed by deriving the evolution equation for $f(x,t)$ and then solving it under the initial and boundary conditions of the two- and three-dimensional scenarios.

B.1. Evolution of $f(x,t)$

Consider the evolution of the PDF $f(x,t)$ for a particle performing a random walk in $d$-dimensional space. We assume that the particle moves in discrete steps of length $\delta$, each step takes time $\tau$ and the loss rate is $\lambda$, i.e. over a timestep $\tau$, $f$ is reduced by an amount $\lambda \tau f$. The direction of each step is random and every direction is equally
likely, if the particle is at \( \mathbf{x} \) at time \( t \), at time \( t-\tau \) it must have been at a point \( \hat{\mathbf{x}} \) with \( |\mathbf{x} - \hat{\mathbf{x}}| = \delta \). Hence if we average the PDF at all such points, we will get the PDF at \( \mathbf{x} \) and \( t \). In \( d \) dimensions (\( S_d \) is the surface of the \( d \)-dimensional unit sphere)

\[
f(\mathbf{x},t) = \frac{1-\delta^2}{2\delta} \int_{S_d} f(\mathbf{x}+\delta\mathbf{n},t-\tau) \, ds_d. \tag{B.1}
\]

Assuming \( \delta \) small and using the symmetry of \( S_d \), Taylor expansion of the right-hand side of \( \text{(B.1)} \) yields

\[
f(\mathbf{x},t) = (1-\frac{\delta^2}{2\tau}) \left[ f(\mathbf{x},t-\tau) + \frac{\delta^2}{2\tau^2} \nabla^2 f(\mathbf{x},t-\tau) + O(\delta^3) \right]. \tag{B.2}
\]

Writing \( D = \delta^2/2\tau \) and letting \( \tau \rightarrow 0 \) and \( \delta \rightarrow 0 \) while keeping \( D \) fixed yields

\[
\frac{df}{dt} = D\nabla^2 f - \frac{df}{\tau}. \tag{B.3}
\]

### B.2. 2D absorption

We want to solve the evolution Eq. \( \text{(B.3)} \) subject to the initial condition \( f(\mathbf{x},0) = \delta(\mathbf{x}-\mathbf{x}_0) \) and the absorbing boundary condition \( f(\mathbf{x},t) = 0 \) on \( |\mathbf{x}| = \tau/\lambda \). Letting \( R = |\mathbf{x}_0| \) and nondimensionalizing using

\[
\mathbf{x} = R\mathbf{x}, \quad t = \frac{R^2}{D} \tau, \quad \tau = R t, \quad \lambda = \frac{2D}{R}, \tag{B.4}
\]

we transform the system into

\[
\frac{df}{d\tau} = \nabla^2 f - \frac{df}{\tau} \quad \text{for} \quad \tau \geq 0,
\]

\[
f(\mathbf{x},0) = \delta(\mathbf{x}-\mathbf{x}_0),
\]

\[
f(\mathbf{x},\tau) = 0 \quad \text{for} \quad |\mathbf{x}| = \tau.
\]

Without the absorbing boundary condition and with \( \lambda = 0 \), \( f \) would be given simply by

\[
f(\mathbf{x},\tau) = \frac{1}{4\pi\tau} e^{-|\mathbf{x}-\mathbf{x}_0|^2/4\tau}.
\]

Now since the governing equation in \( \text{(B.5)} \) is linear, the solution to the full system will be given by the sum of \( \text{(B.6)} \) and a corrector function \( f_c(\mathbf{x},\tau) \), whose value at \( |\mathbf{x}| = \epsilon \) will be exactly the opposite of the value of \( \text{(B.6)} \) there, so together they satisfy the boundary condition. Assuming \( \epsilon < 1 \), the variation of Eq. \( \text{(B.6)} \) over the circle \( |\mathbf{x}| = \epsilon \) will be always small relative to its value, so we can approximate it by its value at the origin. This means that our approximation to \( f_c \) (call it \( f_c \)) has to satisfy radially symmetric boundary condition \( f_c(\mathbf{x},\tau) = -f_c(0,\tau) \) at \( |\mathbf{x}| = \epsilon \). Therefore \( f_c \) will be radially symmetric; \( f_c(\mathbf{x},\tau) = f_c(r,\tau) \). We can thus write the general form of \( f_c(r,\tau) \) satisfying I.C.

\[
f_c(\tau,0) = 0
\]

\[
f_c(\mathbf{x},\tau) = -\int_0^\tau A_2(u) \frac{e^{-r^2/(4\tau-u)}}{4\pi(t-u)} \, du \tag{B.7}
\]

and it must satisfy the boundary condition at \( |\mathbf{x}| = \epsilon \)

\[
-f_c(0,\tau) = f(0,0) = \frac{e^{-|\mathbf{x}_0|^2/4\tau}}{4\pi\tau} = \frac{e^{-1/4\tau}}{4\pi}. \tag{B.8}
\]

We can visualize \( f_c \) as continually releasing "particles" at the origin. From now on we will drop the hats on the nondimensionalized time.

Hence our approximate solution to \( \text{(B.5)} \) is

\[
f(\mathbf{x},t) = \frac{e^{-|\mathbf{x}-\mathbf{x}_0|^2/4\tau}}{4\pi\tau} - \int_0^t A_2(u) \frac{e^{-r^2/(4\tau-u)}}{4\pi(t-u)} \, du. \tag{B.9}
\]

In order for Eq. \( \text{(B.9)} \) to satisfy Eq. \( \text{(B.8)} \), we must have

\[
\int_0^\tau A_2(u) \frac{e^{-r^2/(4\tau-u)}}{4\pi(t-u)} \, du = e^{-1/4\tau}, \quad \forall t \geq 0.
\]

The total encounter (absorption) probability is given by

\[
\mathcal{P}_2 = \int_0^\infty A_2(u) \, du, \tag{B.11}
\]

where \( A_2(x) \) is determined for all \( x \geq 0 \) by the relation \( \text{(B.10)} \). If we now have non-zero \( \hat{l} \) in Eq. \( \text{(B.5)} \), we can proceed in a similar manner as above, inserting factors of \( e^{-\hat{l}t} \) where necessary to finally arrive at Eq. \( \text{(B.11)} \) again, but this time with \( A_2(x) \) determined by

\[
\int_0^\infty A_2(u) K_2(t-u,\hat{l},\hat{c}) \, du = K_2(t,\hat{l},1) \quad \text{for} \quad \forall t \geq 0,
\]

where \( K_2(x,\hat{l},\hat{c}) = 1/(xe^{-\hat{l}x^2/4c}) \).

We can compute \( \mathcal{P}_2 \) by integrating Eq. \( \text{(B.12)} \) from \( 0 \) to \( \infty \) with respect to \( \hat{l} \) and using Eq. \( \text{(B.11)} \) to obtain

\[
\mathcal{P}_2(\hat{l},\hat{c}) = \int_0^\infty \int_0^\infty K_2(u,\hat{l},1) \, du \, d\hat{l} = \int_0^\infty \frac{1}{u} \frac{e^{-u-1/4u}}{\int_0^\infty e^{-2u-1/4u} \, du} \, du. \tag{B.13}
\]

### B.3. 3D absorption

We proceed just as in the 2D case, starting from the system (dropping the hats and writing \( x = H/R \))

\[
\frac{df}{dt} = \nabla^2 f - \frac{df}{\tau} \quad \text{for} \quad t \geq 0, \quad f(\mathbf{x},0) = \delta(\mathbf{x}-\mathbf{x}_0), \quad f(\mathbf{x},t) = 0 \quad \text{for} \quad |\mathbf{x}| = \epsilon, \tag{B.14}
\]

\[
\frac{df}{dt} = 0 \quad \text{at} \quad z = 0 \quad \text{and} \quad z = z, \tag{B.15}
\]

only this time, the solution with \( \hat{l} = 0 \), without absorbing boundary condition and without the reflecting surfaces at \( z = 0 \) and \( z = z \) would be given by

\[
f(\mathbf{x},t) = \frac{e^{-|\mathbf{x}-\mathbf{x}_0|^2/4\tau}}{(4\pi\tau)^{3/2}}. \tag{B.16}
\]

where \( \mathbf{x}_0 = (1,0,0) \).

In order to get rid of the boundary conditions at \( z = 0 \) and \( z = z \), we reflect the point \( \mathbf{x}_0 \) and the absorbing surface in both planes infinitely many times (see Fig. 7), so that they are satisfied.
automatically by symmetry

\[
 f(x,t) = \frac{1}{(4\pi)^{3/2} t^{3/2}} \left[ \sum_{n=0}^{\infty} e^{-|x|^{2}/4t} \right],
\]

(B.17)

where \( x_0 = (1,0,z_0) \) with \( z_0 = 2nx \). Again the situation is symmetrical about both \( z=0 \) and \( x=x_0 \) so the reflecting boundary conditions are met. Now we consider the absorbing boundary at the origin and all its reflections (centered at \( 0,0,z_0 \)). Since \( \epsilon \leq 1 \), just as previously we can introduce a correcfion factor \( f_c \), which is now a superposition of a spherically symmetric function about the origin and all its planes in the reflection. Due to the symmetry of the situation, if we satisfy the boundary condition on one of the absorbing surfaces (say the one around the origin) then we will automatically satisfy the boundary condition on all of its reflections too. Hence our approximate solution to the whole system (B.14) and (B.15) is given by

\[
 f(x,t) = \frac{1}{(4\pi)^{3/2} t^{3/2}} \left[ \sum_{n=0}^{\infty} e^{-|x_0|^{2}/4t} - \sum_{n=-\infty}^{\infty} \int_{0}^{t} A_3(u) e^{-|x_0|^{2}/4t} (t-u)^{3/2} du \right],
\]

(B.18)

where \( x_0 = (0,0,z_0) \), subject to \( f(x,0,t) = 0 \), i.e.

\[
 \sum_{n=0}^{\infty} \int_{0}^{t} A_3(u) e^{-|x_0|^{2}/4t} (t-u)^{3/2} du = \frac{1}{t^{3/2}} \sum_{n=0}^{\infty} e^{-(1+1)|x_0|^{2}/4t}.
\]

(B.19)

Then our encounter (absorption) probability function is \( P_{3f} = \int_{0}^{s} A_3(u) du \). If we denote \( S(x) = \sum_{n=0}^{\infty} e^{-|x_0|^{2}/4t} \), then \( S(x) = e^{-|x|^{2}/4t} \). Taking the limit of both sides yields \( \ln(1-P_f) = \sum_{n=0}^{\infty} \ln(1-(2\pi|n|\delta r) P_{3f}(\delta r)) \). Hence the total probability of the male gamete not encountering any female gamete is then \( 1-P_f = \prod_{n=0}^{\infty} [1-(2\pi|n|\delta r) P_{3f}(\delta r)] \). Taking the logarithm of both sides yields \( \ln(1-P_f) = \sum_{n=0}^{\infty} \ln[1-(2\pi|n|\delta r) P_{3f}(\delta r)] \) and taking the limit \( \delta r \to 0 \) gives \( \int_{0}^{s} \ln[1-(2\pi|n|\delta r) P_{3f}(\delta r)] d\delta r = -\frac{1}{2} \ln(1-2\pi|n|\delta r) P_{3f}(\delta r) \).

(C.1)

Similarly, in 3D we find

\[
 P_b = 1 - \exp \left\{ -\rho_3 \int_{r_1}^{r_2} 2\pi r P_{3f}(r) dr \right\},
\]

(C.2)

References


