MODELING DISPERSAL OF CLONING ECHINODERM LARVAE WITH A GAUSSIAN DISTRIBUTION: FOREVER YOUNG?

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ABSTRACT

Echinoderm larvae clone (reproduce asexually), but the implications of this remarkable life history trait for larval dispersal have not been explored. We develop a simple model of larval dispersal, in which cloning can be incorporated into the numerator of the Gaussian distribution:

$$P(x,t) = \frac{1}{2\sqrt{\pi D t}}\, e^{\frac{-x^2}{4Dt}} .$$

Each cloning event resets the time to final settlement. The timing of cloning and the number of sequential cloning events influence the dispersal distance, but neither the percent of larvae that clone nor larval mortality has an impact on distance traveled. The percent of larvae that clone and survive control the *number* (probability density) of larvae. The second moment (variance) in the model shows that the "spread" of the dispersion is linearly related to time ($2Dt$), where the constant D is the *diffusivity*. We discuss the implications of a few clones traveling long distances. This may effectively homogenize the population genetics and facilitate invasions but may not affect fishery management. The life history feature of larval cloning results in a limitless larval period (assuming they survive) and may act to promote long distance dispersal of a few larvae.

INTRODUCTION

Asexual reproduction in larval echinoderms was discovered recently (Bosch 1988; Bosch et al. 1989), yet its implications for larval dispersal has not been explored. Knowing how far larvae disperse (see review, Levin 2006) is critical in ecology and is fundamental to our understanding of population and community dynamics. The degree to which marine populations are open or closed (Cowen et al. 2000; Warner and Cowen 2002) is an important area of research. Larval dispersal distances, for example, can be estimated and used to design networks of marine protected areas (Roberts 1997) and to predict species invasions (Neubert and Caswell 2000). Gaussian distributions are often used to model animal dispersal (Okubo and Levin 2001) but have not been used, to our knowledge, to explore the consequences of cloning for dispersing larvae.

Cloning, or larval budding, by planktotrophic bipinnaria larvae of the sea star, *Luidia* spp., has been observed in field-caught specimens (Bosch 1988; Bosch et al. 1989). Larval cloning is quite common with 10%–90% of larvae in the field-caught samples having modified larval arms consistent with cloning (Bosch et al. 1989; Knott et al. 2003). High food concentrations and optimal temperatures appear to promote cloning in the laboratory (Vickery and McClintock 2000) as does the presence of predators (fish mucus) (Vaughn and Strathmann 2008). In addition, clones may themselves clone (Balser 1998; Vickery and McClintock 2000). Cloning asteroid larvae have been collected in several regions in the tropical and subtropical western Atlantic Ocean (Jaeckle 1994), the Sargasso Sea (Bosch et al. 1989), and the Bay of Bengal (Rao et al. 1993). The widespread distribution of sea star clones in the open waters of the oligotrophic western North Atlantic Ocean may be facilitated by the presence of symbiotic bacteria, a potential food source (Bosch 1992).

Purple sea urchins, *Strongylocentrotus purpuratus*, have been a model study organism in developmental biology for more than 100 years, however cloning has only recently been observed (Eaves and Palmer 2003). This oversight is even more egregious when we consider that Mortensen (1921) reported unusual looking brittle star larvae and suggested that they might be clones arising from asexual reproduction. His reports remained unexplored for the next 75 years (Mladenov and Burke 1994; Balser 1998). Cloning has now been observed in all echinoderm classes, with the possible exception of the crinoids (Eaves and Palmer 2003; Rogers-Bennett 2007). Cloning may therefore be an ancestral life history trait within the echinoderms. Lacalli (2000) and Eaves and Palmer (2003) suggest that this trait may be ancestral, possibly even within the deuterostomes which include echinoderms, acorn worms, sea squirts, and vertebrates.

Despite the potential disadvantages encountered with a longer larval period (Strathmann 1974), such as increased mortality by predation (Rumrill 1990) or starvation (Olson and Olson 1989), there are examples of successful long-lived marine invertebrate larvae (Scheltema 1971; Rice 1981). One mollusk, *Fusitriton oregonensis*, has been observed to settle successfully after 4.5 years in the larval planktonic stage (Strathmann and Strathmann 2007). Larvae can also delay metamorphosis (see review, Pechenik 1990). It has even been suggested that there may be an entirely pelagic bauplan (Eaves and Palmer 2003), although most animals metamorphose at some point. While we do not know the chances of survival of long-lived larvae and larvae that clone, they do have the potential to disperse long distances.

Here we model echinoderm larval dispersal using a Gaussian distribution and compare the dispersal distances in models with and without cloning. We incorporate cloning by having larvae clone at some time *t*, before settlement, in one pulse, essentially restarting the clock to settlement. The second cloned distribution is the same as the original dispersal pattern (of the *primary* larvae) but has wider dispersion than the original would have had. In this way, we explore the impacts of cloning on dispersal distances traveled by larvae in the model with effects of (1) the time that cloning occurs (early or late larval stage), (2) the percent of larvae that clone, and (3) the influence of multiple cloning events. We discuss the population implications of having a few clones successfully settle and eventually reproduce in distant regions far from the benthic populations where the primary larvae were produced.

THEORY

Suppose a particle (lattice point) moves in a one-dimensional space along the x axis with a most probable displacement Δx in time Δt, and that the particle is observed at regular intervals which are also Δt. If the particle is found at location x relative to an origin $x = 0$ at time t, + Δt, one does not know how it got there. It may have arrived at x by moving $-\Delta x$ toward the origin from a larger value of x or by moving Δx away from the origin. For random motion, the two probabilities are equal:

$$P(x_t + \Delta x \mid x_{t+\Delta t}) = P(x_t - \Delta x \mid x_{t+\Delta t}), \tag{1}$$

and

$$P_{total}(x,t) = P(x_t + \Delta x \mid x_{t+\Delta t}) + P(x_t - \Delta x \mid x_{t+\Delta t}). \tag{2}$$

The notation means that, having observed a particle at location x at time $t + \Delta t$, the probability that it was at $x + \Delta x$ is equal to the probability that it was at $x - \Delta x$ at time t. Since there are no other possible observations, the sum of these two probabilities is the total probability $P_{total}(x,t)$, which is usually normalized to 1.0.

The equation $y = f(x + at) + g(x - at)$ has a long history and a variety of names. In this restricted form, it is called the d'Alembert equation (Wylie and Barrett 1982). One way of treating it is through a Taylor expansion (Appendix) to arrive at:

$$\frac{\partial P(x,t)}{\partial t} = D\,\frac{\partial^2 P(x,t)}{\partial x^2}, \tag{3}$$

where the constant D is called the *diffusivity* (Okubo and Levin 2001). This is a *parabolic equation*, one of three classes of d'Alembert equations, and its solution is well known (Appendix):

$$P(x,t) = \frac{1}{2\sqrt{\pi D t}}\, e^{\frac{-x^2}{4Dt}} \;. \tag{4}$$

The function $P(x,t)$ is assumed to be separable and can be treated as $P(x)$ at fixed t over the range $[-\infty,\infty]$ of x. $P(x)$ at fixed t is used to generate Figures 1 and 2. $P(x)$ at fixed t is an even function over symmetrical intervals in x, so it has a first moment (mean) of zero. It is the second moment $M_2(t)$ that is of interest:

$$M_2(t) = \int_{-\infty}^{\infty} x^2 P(x,t)\,dx`. \tag{5}$$

This can be integrated by parts twice (Appendix) to give:

$$M_2(t) = 2D\int_{-\infty}^{\infty} P(x,t)\,dx, \tag{6}$$

but the integral of the probability over all event space $\int_{-\infty}^{\infty} P(x,t)dx$ is 1.0, so $M_2(t) = 2D$. Taking the second moment (variance) over the interval $[0,t]$ from a time defined as zero to a finite time t, gives:

$$M_2(t) = 2Dt. \tag{7}$$

Hence, the variance (spread of the probability density function) is *linear* with time. The lower limiting case is that of a particle observed at $t = 0$ which has not moved away from the origin. The upper limiting case is that of $M_2(t) \to \infty$ as $t \to \infty$. This is the case of complete uncertainty as to the location of the particle. The probability of finding a particle becomes very small at large x but it does not become zero.

A DISPERSION MODEL

A population P of echinoderm larvae diffuses away from a pulse at an origin $x = 0$ so as to give a Gaussian or some similar distribution. (The argument does not depend on the details of the dispersion model.) The distance away from the origin, $x = f(t)$ is determined by the diffusion speed v and the time in transit t. The larvae can move in two or three dimensions, so distance x and velocity v are vectors in x, y, z space. We consider only one dimension for simplicity.

Dispersion of larvae in the absence of cloning is modeled in Figure 1 as a Gaussian distribution. The horizontal axis represents the distance traveled by larvae in a specific time $x = vt$. For illustrative purposes, curves in

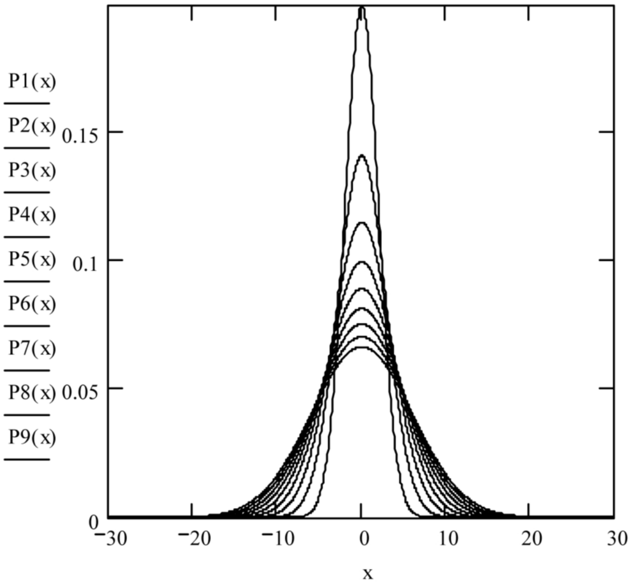

Figure 1. Larval Dispersion as a Function of Time. The horizontal axis is the linear distance away from an origin at $x = 0$. The vertical axis represents a set of number density curves $P_1 – P_8$ of larvae, and time is on the axis orthogonal to x and P. Eight curves are shown at times $t_1 – t_8$. The time axis is truncated at t_8 by settlement.*

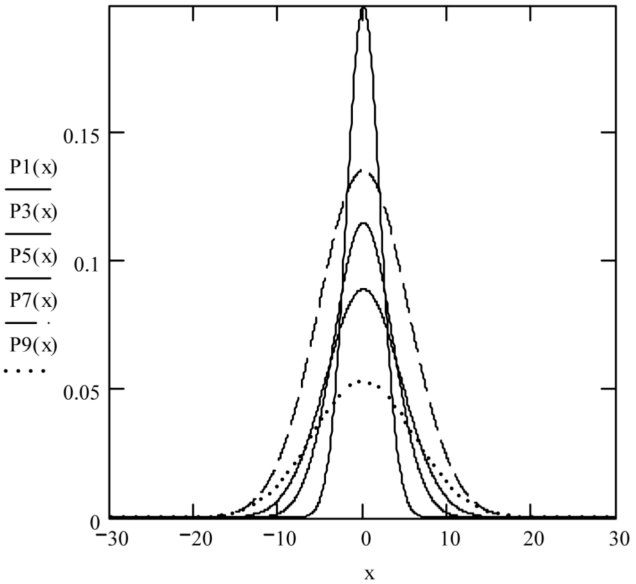

Figure 2. A Continuation of the Model in Figure 1. The curves show cloning at t_7 and settlement of the primary population at t_9. The red (dashed) curve is after 80% cloning but before settlement of the primary population. The blue (dotted) curve is after cloning and settlement. The curves show a decrease in the total number of larvae but an increase in dispersion.

Figure 1 are shown at a sequence of times t_1–t_8. The initial egg distribution t_0 has a high density and is represented by a narrow distribution, essentially a vertical plane of $x = 0$. Assuming 100% survival, the area under the curves is constant but the variance increases with time (as does distance traveled).

Dispersion Model with Cloning

Suppose a certain percent of the larvae cloned in a single pulse at some time t before settling at, say, t_7. The cloning event can be represented by multiplying Equation 4 by an appropriate constant, say, 1.8 for 80% of the larvae cloning. A new diffusion curve is produced with the characteristics of the old curve but with an area that is larger than the area before cloning. In addition to the population increment, the "clock" is reset (time to settlement is reset) for the new sample of larvae which diffuse until *they* settle, yielding a broader dispersion than the primary larvae would have attained. After settlement of the primary population (the original 100%), the area under the distribution curve is adjusted downward to reflect their loss from the plankton (post settlement). We make a few simplifying assumptions: (1) the absence of distance-dependent mortality, and (2) pulse cloning (no distribution of cloning over time).

Figure 2 shows the results of a cloning event at t_7. The area of the Gaussian is increased by an amount depending on the number of clones produced, say 80% of the original population. The new population, composed of cloned larvae, is distributed over the same standard deviation and variance as the initial population at the time of cloning, but the variance continues to increase as these larvae disperse. The density curve after cloning, but before settlement of the primary population, is shown as curve P_7 in Figure 2. The distance traveled by the clones increases in the model. Cloning occurring at times closer to settlement (late larvae) enhances dispersion relative to early cloning.

At some point the primary population settles and the area under the distribution curve drops to 80% (the percent of clones). The cloned population, however, continues to disperse and its variance, and thus its distribution, continues to increase.

Multiple Cloning Events

This argument can be continued *ad infinitum* since clones can continue to clone (Balser 1998), resulting in long distance dispersion of a few larvae. After four generations the gain in dispersal is substantial. The density of individuals reaching the fourth generation at 80% cloning is reduced to $0.8^4 = 0.41$ of the original population. Although the larval population (ignoring mortality) is reduced by more than half after four cloned generations, the original larval population may have been very large (e.g., one female laying several million eggs).

Mortality and Currents

In the ocean, additional factors influence dispersal, such as mortality and currents. These factors can be incorporated into the model in simple ways that will not

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*Online version of article has figures in color.

change the shape of the dispersal patterns or the general conclusions. Mortality will diminish the height of the curve (number density) and currents will shift the curve along the distance axis "downstream" or "upstream." Mortality can be incorporated into the model by simply multiplying the numerator by a mortality rate (either constant or variable). Similarly, currents can be included as a constant, either positive or negative, added to the right side of the equation.

DISCUSSION

Dispersal distances of larvae and their clones in simple Gaussian dispersal models increase linearly with time ($2Dt$) as seen in the second moment of the Gaussian model. Several variables influence the time larvae spend in the dispersal stage, including (1) the timing of cloning (early or late stage), and (2) the number of cloning events. Both increase dispersal, while the percent of clones does not. Cloning of late-stage larvae increases the time in the plankton more than cloning of early larvae does. Furthermore, if cloning increases developmental time for primary "parent" larvae and they metamorphose, as might occur when cloning occurs by fission, this too will increase the time in the plankton and therefore dispersal.

In our model, populations with multiple cloning events traveled the greatest distances since we assume each cloning event resets that population's larval dispersal clock. It is noteworthy that a linear combination of Gaussian, which enables us to extend our model for multiple cloning events and to construct a curve with a "fat tail" as in the Weibull equation (Weibull 1951; Greene 2004). In our model, any cloning mechanism which increases the developmental time of either the primary larvae or the clone will lead to further dispersal. This suggests that factors which increase time in the plankton warrant further research, specifically, (1) the timing of cloning (early or late larval stage), and (2) the number of times that an individual clones, both in the laboratory and in the field.

There are planktonic larvae that are long-lived and these larvae have been coined "teleplanic" larvae, or far wandering (Scheltema 1971). Sipunculid larvae, for example, have been found in the vast majority of open ocean plankton samples and it is estimated they may be planktonic for three to eight months, possibly traversing ocean basins (Rice 1981). Clearly, planktotrophic larvae, with the ability to clone, are capable of teleplanic dispersal. Cloning differs from delayed metamorphosis in that delays are for a limited time period and have negative consequences for some lecithotrophic larvae (Pechenik 1990; Pechenik et al. 1998). Cloning, on the other hand, does not appear to be inherently "bad" for larvae. Cloning might have negative consequences if clones result in a smaller initial size leading to a smaller size at metamorphosis, as has been shown for non-cloning larvae when initial egg size was experimentally reduced (Hart 1995).

Cloning, in addition to increasing the time spent in the dispersal stage, also increases the number of larvae. Increasing the number of larvae by cloning (which may increase the numbers surviving) simply increases the height of the dispersion curve but has no immediate impact on the distance traveled. The width of the curve "flattens out" over time *but the variance increases without limit*. Several factors that appear at first glance to conflict with this conclusion turn out to be unimportant; among them is larval mortality. Larval mortality does not influence the time-dependent variation of the dispersion though it does influence the *number* (probability density) measured near point x at some time t.

The ability of echinoderms to clone as larvae prior to settlement coupled with the production of tens of millions of eggs renders assumed limits of dispersion distances based on the time to settlement untenable. Even if some of the assumptions used in the present model, specifically the Gaussian dispersion curve, or pulse cloning, are not met, a limit on *dispersal distance by larval period* is incorrect. For echinoderms, larval "transport envelopes," regions within which they may disperse, as for coral reef fishes (Roberts 1997), either have leaky borders or can not be established. Similarly, species with secondary settlement, such as mussels (Bayne 1964), may not be retained locally since newly settled juveniles may disperse a "second" time, rendering the identification of dispersal windows (envelopes) challenging. The life history feature of cloning may act as an opposing force to factors which promote local retention (Swearer et al. 1999; Marko et al. 2007).

The ability of a few clones to travel long distances has implications for the population genetics of echinoderms. A few individuals traveling long distances may effectively homogenize the genetics at distant locations such that there is little or reduced differentiation in recruits relative to adults as has been observed (Flowers et al. 2002). In addition, cloning is a clear violation of Hardy-Weinberg assumptions of random mating (B. Swalla pers. comm.). A few individuals can serve as "founders," establishing new populations of invasive species far from the source (Carlton 1989), or can colonize empty patches. Dispersal of clones, however, may complicate the design of marine reserve networks (Shanks et al. 2003). While a few individuals may be capable of modifying the genetics and/or establishing new populations, we do not envision that a few clones may provide a "rescue effect" for fished areas or influence fishery management. Long distance "spillover" from marine protected areas is likely to be negligible from a fishery perspective. In the model, only a few clones traveled long distances as seen by the low profile and very long tail of the distribution curve.

The results of our model show that the addition of cloning greatly enhances long-distance dispersal. While modeling larval dispersal as a Gaussian distribution is not new (Okubo 1971; Possingham and Roughgarden 1990; Okubo and Levin 2001), the incorporation of asexual larval reproduction is. Theoretically, the distance traveled is unlimited if there are no limits to cloning events, rendering the larval period indefinite and making the larvae potentially immortal. However, dispersal would not be related to time in the plankton for demersal larvae (Gerrodette 1981).

In our Gaussian model, which assumes Fickian diffusion with a constant *D* diffusivity, dispersal distance is linearly related to time. In comparison with data on the dispersal of dye in the ocean, the variance (the second moment) was found to increase faster than linearly such that time was to the 2.34 power (Okubo 1971), suggesting that dispersal of surface currents in the ocean may be greater than our model depicts. Nevertheless, Gaussian curves are being used to track kelp spore dispersal patterns particularly for long-distance (3–12,000 m) dispersal incorporating current information (Gaylord et al. 2006). Dispersal models such as the ones presented here can help focus research questions on the dispersal biology of larval cloning which, in turn, influences population dynamics, population genetics, invasion biology, and marine protected area design.

ACKNOWLEDGMENTS

We thank those at Friday Harbor Laboratories, University of Washington, for discussions of larval echinoderm cloning, specifically R. Strathmann, A. Eaves, and D. Vaughn. DWR thanks the H. R. Whiteley Center for support. This work was supported by the California Department of Fish and Game. This is contribution number 2415 for Bodega Marine Laboratory.

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APPENDIX

S1. The Diffusion Equation

The *master equation* describing the one-dimensional random motion of lattice points (see text) situated at a distance Δx apart is:

$$P(x,t + \Delta t) = \frac{1}{2}\, P(x - \Delta x,t) + \frac{1}{2}\, P(x + \Delta x,t)\ . \qquad \text{(S.1)}$$

Taylor expansion (de Vries et al. 2006) of each term gives:

$$P(x,t) + \Delta t\, \frac{\partial P(x,t)}{\partial t} + \frac{(\Delta t)^2}{2}\, \frac{\partial^2 P(x,t)}{\partial t^2} + \ . \ . \ .$$

$$= \frac{1}{2}\left[P(x,t) - \Delta x\, \frac{\partial P(x,t)}{\partial x} + \frac{(\Delta x)^2}{2}\, \frac{\partial^2 P(x,t)}{\partial x^2} + \ . \ . \ . + P(x,t) + \Delta x\, \frac{\partial P(x,t)}{\partial x} + \frac{(\Delta x)^2}{2}\, \frac{\partial^2 P(x,t)}{\partial x^2} + \ . \ . \ . \right] .$$

We retain only the first three terms of each expansion. A good deal of cancellation takes place. The first term in each expansion $P(x,t)$ appears on both sides of the equation and drops out. The second terms of the expansions lead to:

$$\Delta t\, \frac{\partial P(x,t)}{\partial t} = \frac{1}{2}\left[-\Delta x\, \frac{\partial P(x,t)}{\partial x} + \Delta x\, \frac{\partial P(x,t)}{\partial x} \right],$$

where the terms on the right cancel. The third terms give:

$$\frac{\Delta t}{2}\, \frac{\partial^2 P(x,t)}{\partial t^2} = \frac{1}{2}\, \frac{(\Delta x)^2}{\Delta t}\, \frac{\partial^2 P(x,t)}{\partial x^2}\ ,$$

where both sides have been divided by Δt. Assembling all residual terms, we have:

$$\frac{\partial P(x,t)}{\partial t} + \frac{\Delta t}{2}\, \frac{\partial^2 P(x,t)}{\partial t^2} = \frac{(\Delta x)^2}{2\Delta t}\, \frac{\partial^2 P(x,t)}{\partial x^2}\ . \qquad \text{(S.2)}$$

The second term on the left drops out as $\Delta t \to 0$ and the pre-multiplier on the right

$$\frac{(\Delta x)^2}{2\Delta t}$$

in the limit of Δx, $\Delta t \to 0$ approaches a constant D which is called the *diffusion constant* D from Fick's second law (Crothers and Eisenberg 1979), or the *diffusivity*. This leaves:

$$\frac{\partial P(x,t)}{\partial t} = D\, \frac{\partial^2 P(x,t)}{\partial x^2}\ . \qquad \text{(S.3)}$$

S.2 Separation of the Partial Differential Diffusion Equation

The parabolic partial differential equation

$$\frac{\partial P(x,t)}{\partial t} = D\, \frac{\partial^2 P(x,t)}{\partial x^2}$$

can be reduced to two ordinary differential equations by making the simplifying assumption that the solution $P(x,t)$ is the product of a function in x only and a function in t only, $P(x,t) = p(x)p(t)$. This substitution gives:

$$\frac{\partial p(t)}{\partial t}\, p(x) = D\, \frac{\partial^2 p(x)}{\partial x^2}\, p(t), \qquad \text{(S.4)}$$

which, when divided by $p(x)p(t)$ gives:

$$\frac{1}{p(t)}\, \frac{\partial p(t)}{\partial t} = D\, \frac{1}{p(x)}\, \frac{\partial^2 p(x)}{\partial x^2}\ .$$

The left side of this equation is a function of the independent variable t and the right side is a function of the independent variable x. If we evaluate each side of the equation with arbitrary values of x or t, the two sides might be equal by luck, but they would not be *identically* equal. The only way for them to be identically equal is for each side to be equal to a constant. Call the constant $-\lambda$. Now:

$$\frac{1}{p(t)}\, \frac{dp(t)}{dt} = -\lambda\ , \qquad \text{(S.5a)}$$

and

$$D \frac{1}{p(x)} \frac{d^2p(x)}{dx^2} = -\lambda . \tag{S.5b}$$

S.3 Solution of the Time-Dependent Equation

Equation S.5a can be written:

$$\frac{dp(t)}{p(t)} = -\lambda\, dt . \tag{S.6}$$

When integrated, we get:

$$\ln p(t) = -\lambda t + C = -\lambda(t - t_0) = -\lambda t , \tag{S.7}$$

for $t_0 = 0$, or, equivalently:

$$p(t) = e^{-\lambda t} . \tag{S.8}$$

The logarithmic decrease in $p(t)$ in Eq. S.7 can be seen by following the peak probability from t_0 to t_8 in Figure 1. One can see from Eq. S.8 why the separation constant was chosen as $-\lambda$ rather than λ. Choosing λ leads to an exponential *increase* in $p(t)$, which is contrary to the physical reality of the problem.

S.4 The Second Moment

The diffusion equation:

$$\frac{\partial P(x,t)}{\partial t} = D \frac{\partial^2 P(x,t)}{\partial x^2} , \tag{S.3}$$

has a first moment (the limiting sum of deviations about an arithmetic mean):

$$M_1(t) = \int_{-\infty}^{\infty} xP(x,t)dx , \tag{S.9}$$

and a second moment (the variance about the mean):

$$M_2(t) = \int_{-\infty}^{\infty} x^2P(x,t)dx . \tag{S.10}$$

The left-hand side of the diffusion equation is a time derivative:

$$\dot{M}_2(t) = \int_{-\infty}^{\infty} x^2 \frac{\partial P(x,t)}{\partial t} dx , \tag{S.11}$$

thus it is also true that:

$$\dot{M}_2(t) = \int_{-\infty}^{\infty} x^2 D \frac{\partial^2 P(x,t)}{\partial x^2} dx , \tag{S.12}$$

which is a space derivative. Notice that we have gotten rid of ∂t in the integral. This is in effect, a separation of variables. The integral in x is vulnerable to the "integration by parts" technique. Since we are dealing with the space part of the equation, we can simplify the notation and let $P(x,t) = P$. Also a common notational simplification is to let

$$\frac{\partial P(x,t)}{\partial x} = P_x \text{ and } \frac{\partial^2 P(x,t)}{\partial x^2} = P_{xx} . \text{ Now:}$$

$$\dot{M}_2(t) = \int_{-\infty}^{\infty} x^2\, DP_{xx} dx . \tag{S.13}$$

S.5 Integration by Parts

The method has never been better or more succinctly stated than by J. W. Mellor in the early 20th century (Mellor 1929):

> *The differentiation of the product uv, furnishes*
>
> $d(uv) = vdu + udv$
>
> *By integrating both sides of this expression we obtain*
>
> $uv = \int vdu + \int udv$
>
> *Hence, by a transposition of terms, we have*
>
> $\int udv = uv - \int vdu + C$
>
> *that is to say, the integral of udv can be obtained provided vdu can be integrated.*

The constant of integration at the lower limit is subtracted from the constant of integration at the upper limit, so it vanishes.

S.6 Integrating the Space Part of the Moment

To integrate by parts, let $u = x^2$, hence $du = 2xdx$. Also let $v = P_x$ and $dv = P_{xx}dx$. Now $uv = x^2P_x$ and $vdu = P_x 2xdx$. The integral:

$$\int udv = uv - \int vdu + C$$

becomes

$$\int_{-\infty}^{\infty} x^2P_{xx}dx = x^2P_x \Big|_{-\infty}^{\infty} - \int_{-\infty}^{\infty} P_x 2xdx , \tag{S.14}$$

where we have set the limits $[-\infty,\infty]$ to cover the entire probability space. This also gets rid of the constant of integration. The interval is symmetrical about zero and P_x is an odd function over this interval, hence x^2P_x is also odd, $x^2P_x \big|_{-\infty}^{\infty}$ is zero and drops out. An odd function has opposite and equal values at the left and right of the symmetry. Symmetrical integrals of an odd function vanish. An example is $y = x$. The first derivative of the Gaussian is odd about the mean because it is positive to the peak and equal and opposite thereafter. We have reduced P_{xx} to P_x. For this reason Mellor (1929) refers to integration by parts as a *reduction equation.*

We now have the integral $-\int_{-\infty}^{\infty} P_x 2xdx$ to evaluate, but we can do this by repeating the method already used. Integrating by parts again, we get:

$$-\int_{-\infty}^{\infty} P_x 2x dx = -2xP\Big|_{-\infty}^{\infty} + \int_{-\infty}^{\infty} 2DPdx \,. \qquad \text{(S.15)}$$

Now x is odd so $-2xP\big|_{-\infty}^{\infty}$ drops out leaving $\int_{-\infty}^{\infty} 2DPdx$ but this is only $2D\int_{-\infty}^{\infty} Pdx$ where, restoring the original notation, the integral $\int_{-\infty}^{\infty} Pdx = \int_{-\infty}^{\infty} P(x,t)dx$ is defined as 1.0:

$$\dot{M}_2(t) = 2D\int_{-\infty}^{\infty} P(x,t)dx = 2D \,. \qquad \text{(S.16)}$$

We have the solution over the interval $[-\infty,\infty]$ but we are only interested in one half of it, the interval $[0,\infty]$. Over this interval, the time part of the equation gives:

$$\dot{M}_2(t) = \frac{dM_2}{dt} = 2D \,, \qquad \text{(S.17)}$$

so that $\int_0^t dM_2(t) = 2D\int_0^t dt$, and

$$M_2(t) = 2Dt \,. \qquad \text{(S.18)}$$

That is, the position uncertainty or probability dispersion is *linear* with time.

S.7 Solution to the Space-Dependent Part

For the space part of the original equation, Jordan and Smith (1997) define the *variance* as:

$$\sigma^2 = \int_{-\infty}^{\infty} (x-\mu)^2 f(x)dx \,, \qquad \text{(S.19)}$$

where μ is the arithmetic mean and $f(x)$ is some distribution function (see also Eq. S.10). In the *normal distribution* about a mean, $\mu = 0$, and

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{x^2}{2\sigma^2}} \,. \qquad \text{(S.20)}$$

The *coefficient of variation* (de Vries et al. 2006) of a one-step random walk is

$$\sigma = \sqrt{\sigma^2} = \sqrt{2Dt}$$

by Eq. S. 18. Substituting for σ yields the desired spatial probability function:

$$f(x) = P(x,t) = p(x)p(t) = \frac{1}{2\sqrt{D\pi t}} e^{\frac{-x^2}{4Dt}} \,, \qquad \text{(S.21)}$$

which is the function plotted in Figs. 1 and 2 at sequential fixed values of t (see also Eq. S.7).

S.8 Mathcad Input

One can demonstrate by Mathcad© that all Gaussians in Figure 1

$$P(x) := \frac{1}{2\sqrt{\pi Dt}} e^{\frac{-x^2}{4\cdot Dt}}$$

are normalized to 1.0. For example, at t held constant at 6 time units, the integral over the interval $[-\infty,\infty]$ is:

$$D := 2 \quad t := 6$$

$$\int_{-\infty}^{\infty} \left(\frac{1}{2\sqrt{\pi Dt}} e^{\frac{-x^2}{4\cdot Dt}} \right)$$

Typical input expressions for Mathcad© are given below. In each case, the time is inserted into the equation as a constant 1, 2, . . . , 9, and the constant D is initially defined as 2 for all.

TABLE S.1
Input Equations for the Mathcad© Two-Dimensional Graphing Function.

$$D := 2$$

$$P1(x) := \frac{1}{2\sqrt{D\pi}} e^{\frac{-x^2}{4D}} \qquad P2(x) := \frac{1}{2\sqrt{2D\pi}} e^{\frac{-x^2}{4D\cdot 2}} \qquad P3(x) := \frac{1}{2\sqrt{3D\pi}} e^{\frac{-x^2}{4D\cdot 3}}$$

$$P4(x) := \frac{1}{2\sqrt{4D\pi}} e^{\frac{-x^2}{4D\cdot 4}} \qquad P5(x) := \frac{1}{2\sqrt{5D\pi}} e^{\frac{-x^2}{4\cdot D\cdot 5}} \qquad P6(x) := \frac{1}{2\sqrt{6D\pi}} e^{\frac{-x^2}{4\cdot D\cdot 6}}$$

$$P7(x) := \frac{1.8}{2\sqrt{7D\pi}} e^{\frac{-x^2}{4\cdot D\cdot 7}} \qquad P8(x) := \frac{1.8}{2\sqrt{8D\pi}} e^{\frac{-x^2}{4\cdot D\cdot 8}} \qquad P9(x) := \frac{.8}{2\sqrt{9D\pi}} e^{\frac{-x^2}{4\cdot D\cdot 9}}$$

Simple variations on these input files include addition of a constant or simple function on the right to represent current, plus or minus for the augmenting or retarding case. Multiplication of the numerator of the premultiplying factor on the right by 1.8 has been used to represent 80% cloning before settlement of the primary population (red curve) and 0.8 has been used to represent the population after 80% cloning and after settlement (blue curve). This numerator could have been multiplied by a function linear with time or a more complicated function of time to represent mortality.

S.9 References

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