Chapter 3

Age-structured models

The simplest models of population dynamics treat all individuals as identical. Consider, for example, the logistic growth law. More sophisticated models decompose the population into distinct subgroups. For example, SIR models of diseases such as measles, chicken pox and HIV/AIDS typically decompose the population into three subgroups (susceptibles, infectives and recovereds), and time-dependent ordinary differential equations describe their evolution. In practice, however, many processes involved in population growth and/or disease spread depend on age: young and old individuals may have higher mortality rates and be more susceptible to a disease; only individuals of a certain age may be able to produce offspring; school children who frequently come into contact with each other may play a stronger role in disease transmission than other age-groups. Figure 3.1 shows examples of the population age distribution for Germany, Mexico and Uganda, and illustrates how they are likely to change by 2050.

In this chapter we will develop and analyse age-structured population models and show how they can be used to study population dynamics, epidemics and cell-cycle dynamics.

3.1 Simple birth-death population models with age structure

We denote by $n(t, a)$ the number of individuals of age a at time t, and suppose that the population changes only through births and deaths. We introduce $b = b(a)$ as the birth rate of individuals of age a, and $\mu = \mu(a)$ as the death rate of individuals of age a.

Possible functional forms for the birth and death rates $b(a)$ and $\mu(a)$ are

$$\mu(a) = \mu_{\max}\left(1 - \frac{A_{\min} a}{A_{\min}^2 + a^2}\right) \quad \text{and} \quad b(a) = \begin{cases} b & \text{for } a_L < a < a_R, \\ 0 & \text{otherwise.} \end{cases} \tag{3.1}$$

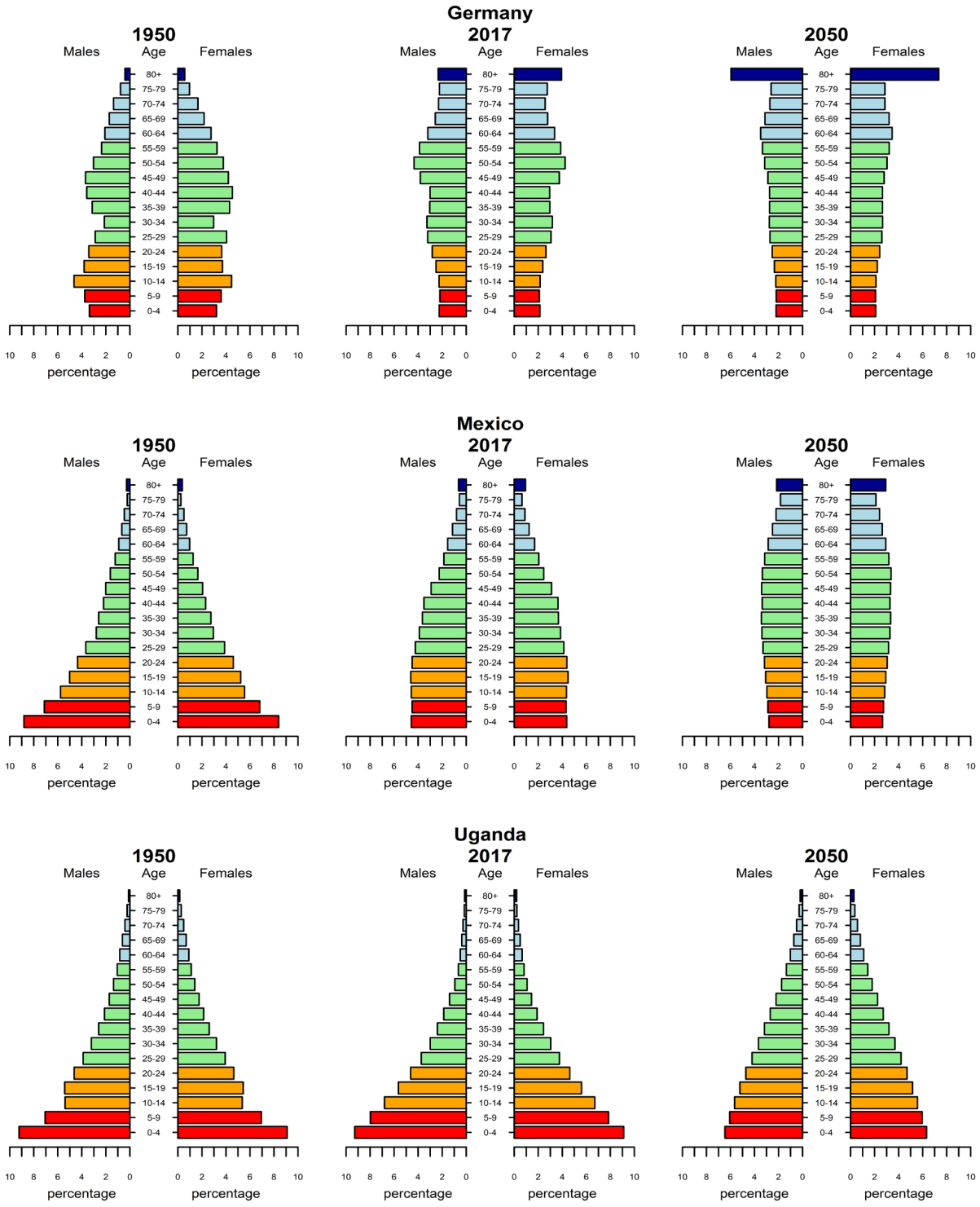

Figure 3.1: Histograms highlighting differences in the age distribution of males and females in Germany, Mexico and Uganda, and how they are likely to change by 2050 [15].

3.1.1 Von Foerster's equation

To build a model of how the population evolves in time we use the principle of mass conservation. First, we note that the birth rate contributes only to the number of newborns, $n(t, a = 0)$. In addition, over a given period of time only death and ageing will alter the number of individuals of a given age $a > 0$. We deduce that, over the short interval of time δt,

$$\mathrm{d}n(t,a) = \frac{\partial n}{\partial t}\delta t + \frac{\partial n}{\partial a}\delta a = -\mu(a)n(t,a)\delta t. \tag{3.2}$$

Dividing through by δt and noting that, since a is chronological age,

$$\lim_{\delta t \to 0} \frac{\delta a}{\delta t} = \frac{\mathrm{d}a}{\mathrm{d}t} = 1, \tag{3.3}$$

we deduce that $n(t, a)$ satisfies the following linear partial differential equation:

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n, \tag{3.4}$$

which is known as **von Foerster's equation**.

To solve Equation (3.4), we impose the following initial and boundary conditions:

$$n(0,a) = f(a), \quad \text{initial age-distribution of population;} \tag{3.5}$$

$$n(t,0) = \int_0^\infty b(a)n(t,a)\mathrm{d}a, \quad \text{birth rate of population.} \tag{3.6}$$

We use the method of characteristics to solve Equations (3.4)–(3.6). The characteristic curves satisfy

$$\frac{\mathrm{d}a}{\mathrm{d}t} = 1 \qquad \text{on which} \qquad \frac{\mathrm{d}n}{\mathrm{d}t} = -\mu n. \tag{3.7}$$

From Figure 3.2 it is clear that:

- characteristic curves for which $0 < t < a$ emanate from the initial data (where $t = 0$);
- characteristics for which $0 < a < t$ emanate from the boundary conditions (at $a = 0$).

Since information from the boundary and initial conditions propagates along characteristics, we deduce that the solution will have different forms in $0 < t < a$ and $0 < a < t$. We construct these solutions below.

Using Figure 3.2, we see that the characteristic curves are given by

$$a = \begin{cases} t + a_0 & \text{for } a > t, \\ t - t_0 & \text{for } a < t, \end{cases} \tag{3.8}$$

where a_0 represents the initial age of an individual who has age $a > t$ at time t, and t_0 represents the time at which an individual of age $0 < a < t$ was born.

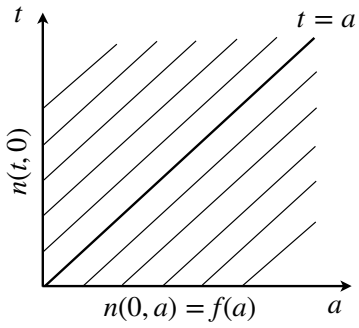

Figure 3.2: The characteristic curves associated with von Foerster's equation.

Region 1. In this region $0 < t < a$ and so we have

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n, \qquad n(0, a) = f(a), \tag{3.9}$$

Hence

$$\begin{aligned} a &= t + a_0, & (3.10)\\ \frac{\mathrm{d}n}{\mathrm{d}t} &= -\mu n, & (3.11)\\ n(0, a_0) &= f(a_0). & (3.12) \end{aligned}$$

so that

$$n(t, a) = n(0, a_0) \exp\left\{ -\int_{a_0}^{a} \mu(\theta)\mathrm{d}\theta \right\}. \tag{3.13}$$

Since $a_0 = a - t$ along characteristic curves, we have

$$n(t, a) = f(a - t) \exp\left\{ -\int_{a-t}^{a} \mu(\theta)\mathrm{d}\theta \right\}. \tag{3.14}$$

Region 2. In this region $0 < a < t$ and so we have

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n, \qquad n(t, 0) = \int_0^\infty b(a)n(t, a)\mathrm{d}a. \tag{3.15}$$

Hence

$$\begin{aligned} a &= t - t_0, & (3.16)\\ \frac{\mathrm{d}n}{\mathrm{d}t} &= -\mu n, & (3.17)\\ n(t_0, 0) &= \int_0^\infty b(a)n(t_0, a)\mathrm{d}a. & (3.18) \end{aligned}$$

so that

$$n(t,a) = n(t_0,0)\exp\left\{-\int_0^a \mu(\theta)\mathrm{d}\theta\right\} \tag{3.19}$$

$$= n(t-a,0)\exp\left\{-\int_0^a \mu(\theta)\mathrm{d}\theta\right\}. \tag{3.20}$$

We can write down an expression for $n(t-a,0)$ using Equation (3.6) together with Equations (3.14) and (3.20)

$$n(t,0) = \int_0^\infty b(a)n(t,a)\mathrm{d}a = \underbrace{\int_0^t b(a)n(t,a)\mathrm{d}a}_{(0<a<t)} + \underbrace{\int_t^\infty b(a)n(t,a)\mathrm{d}a}_{(t<a<\infty)}, \tag{3.21}$$

and, hence,

$$n(t,0) \equiv \int_0^t \left(b(a)n(t-a,0)\exp\left\{-\int_0^a \mu(\theta)\mathrm{d}\theta\right\}\right)\mathrm{d}a + \int_t^\infty \left(b(a)f(a-t)\exp\left\{-\int_{a-t}^a \mu(\theta)\mathrm{d}\theta\right\}\right)\mathrm{d}a. \tag{3.22}$$

Equation (3.22) defines $n(t,0)$ in terms of known functions and $n(\tau,0)$ (where $0 \le \tau < t$). Although this is a linear equation for $n(t,0)$, it is usually difficult to solve.

3.1.2 Worked Example

Consider a population with a constant death rate, $\mu(a) = \mu$, and a piecewise constant birth rate, $b(a) = bH(a_R - a)$. In more detail, suppose that $n(t,a)$ satisfies

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu n, \tag{3.23}$$

with $n(0,a) = 1$ and $n(t,0) = \int_0^\infty b(a)n(t,a)\mathrm{d}a$, where

$$b(a) = \begin{cases} b & \text{for } 0 < a < a_R, \\ 0 & \text{otherwise.} \end{cases} \tag{3.24}$$

As above, when constructing solutions for $n(t,a)$, we consider separately the regions for which $0 < t < a$ and $0 < a < t$.

Region 1. In this region $0 < t < a$ and so we have $\mu(a) = \mu$ and $f(a) = 1$ in Equation (3.14). It is straightforward to show that in this region

$$n(t,a) = e^{-\mu t}. \tag{3.25}$$

Region 2. In this region $0 < a < t$ and so Equations (3.20) and (3.22) supply

$$n(t,a) = n(t-a,0)e^{-\mu a} \qquad \text{where} \qquad n(t,0) = b\int_0^{a_R} n(t,a)\mathrm{d}a. \tag{3.26}$$

When solving Equation (3.26), we must consider separately the cases for which $0 < t < a_R$ and $a_R < t < \infty$.

Case 1. If $0 < t < a_R$, then

$$\begin{aligned} n(t,0) &= b\int_0^{a_R} n(t,a)\mathrm{d}a \\ &= b\int_0^{t} n(t,a)\mathrm{d}a + b\int_t^{a_R} n(t,a)\mathrm{d}a \\ &= b\int_0^{t} n(t-a,0)e^{-\mu a}\mathrm{d}a + b\int_t^{a_R} e^{-\mu t}\mathrm{d}a, \end{aligned} \tag{3.27}$$

where we have exploited the fact that $n(t,a) = e^{-\mu t}$ for $0 < t < a$. We rewrite Equation (3.27) in terms of $N(t) = n(t,0)$:

$$\begin{aligned} N(t) &= b\int_0^{t} N(t-a)e^{-\mu a}\mathrm{d}a + b(a_R - t)e^{-\mu t} \\ &= b\int_0^{t} N(\tau)e^{-\mu(t-\tau)}\mathrm{d}\tau + b(a_R - t)e^{-\mu t}. \end{aligned} \tag{3.28}$$

Differentiating this expression for $N(t)$ with respect to t we obtain the following ordinary differential equation for $N(t)$:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (b-\mu)N - be^{-\mu t}, \tag{3.29}$$

and hence we have

$$N(t) = \hat{N}e^{(b-\mu)t} + e^{-\mu t}, \tag{3.30}$$

where $\hat{N}$ is a constant of integration.

Substituting the expression for $N(t) = n(t,0)$ into Equation (3.26) and recalling that $n(t,a) = e^{-\mu t}$ for $0 < t < a$, we deduce that, for $0 < t < a_R$, our age-structured population evolves as follows:

$$n(t,a) = \begin{cases} N(t-a)e^{-\mu a} = e^{-\mu t}\left(\hat{N}e^{b(t-a)} + 1\right) & \text{for } 0 < a < t; \\ e^{-\mu t} & \text{for } 0 < t < a. \end{cases} \tag{3.31}$$

Case 2. For $a_R < t$, and with $N(t) = n(t,0)$, Equation (3.26) gives

$$N(t) = b\int_0^{a_R} N(t-a)e^{-\mu a}\mathrm{d}a = b\int_{t-a_R}^{t} N(\tau)e^{-\mu(t-\tau)}\mathrm{d}\tau. \tag{3.32}$$

If we differentiate this expression for $N(t)$ with respect to t we obtain a delay differential equation for $N(t)$:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (b-\mu)N(t) - bN(t-a_R)e^{-\mu a_R}. \tag{3.33}$$

We seek solutions of the form $N(t) = \tilde{N}e^{\omega t}$ where

$$\omega = (b-\mu) - be^{-(\omega+\mu)a_R}. \tag{3.34}$$

With $N(t) = \tilde{N}e^{\omega t}$, Equation (3.31) supplies

$$n(t,a) = N(t-a)e^{-\mu a} = \tilde{N}e^{\omega(t-a)}e^{-\mu a}. \tag{3.35}$$

If $\Re e(\omega) > 0$ then the age-dependent population increases over time; if $\Re e(\omega) < 0$ then it decays. For a stable, age-structured population, we require $\omega = 0$. From Equation (3.34) we deduce that the population will be stable if the birth rate b, the death rate μ and the parameter a_R satisfy

$$b = \frac{\mu}{1 - e^{-\mu a_R}}. \tag{3.36}$$

In this case where $\omega = 0$, we have

$$n(t,a) = \begin{cases} e^{-\mu a} & \text{for } 0 < a < t, \\ e^{-\mu t} & \text{for } a_R < t < a. \end{cases} \tag{3.37}$$

Notes and conclusions. Equation (3.36) states how the birth and death rates should be related in order to achieve a stable, age-structured population (*i.e.* one which neither explodes nor dies out). We can use this equation to draw the following conclusions:

- we must have $b > \mu$ – since only individuals of age $0 < a < a_R$ reproduce, the birth rate b must exceed the death rate to achieve a stable population;
- if $a_R \to \infty$, then $b \to \mu$ – if all individuals reproduce, then a stable population will only be achieved if the birth and death rates balance;
- if $a_R \to 0$, then $b \to 1/a_R \gg 1$ – as the reproductive lifespan of the population decreases, their birth rate must increase in order to maintain a stable population.

3.1.3 Separable solutions for age-structured models

Guided by the solution for the worked example, we now seek separable solutions to von Foerster's equation of the form

$$n(t,a) = e^{\gamma t}F(a), \tag{3.38}$$

i.e. we assume that the age distribution is altered by a time-dependent factor which decays or grows depending on whether $\Re e(\gamma) < 0$ or $\Re e(\gamma) > 0$. Substituting this separable form into Equation (3.4) supplies the following ordinary differential equation for $F(a)$:

$$\frac{\mathrm{d}F}{\mathrm{d}a} = -\left(\mu(a) + \gamma\right) F \quad \Longrightarrow \quad F(a) = F(0)\exp\left\{-\gamma a - \int_0^a \mu(\theta)\mathrm{d}\theta\right\}. \tag{3.39}$$

Imposing the boundary conditions stated in Equation (3.5) we deduce

$$\begin{aligned} n(t,0) &= e^{\gamma t}F(0) \\ &= \int_0^\infty b(a)e^{\gamma t}F(a)\mathrm{d}a \\ &= e^{\gamma t}F(0)\int_0^\infty b(a)\exp\left\{-\gamma a - \int_0^a \mu(\theta)\mathrm{d}\theta\right\}\mathrm{d}a. \end{aligned} \tag{3.40}$$

Cancelling by the nonzero factor $e^{\gamma t}F(0)$, we deduce

$$1 = \int_0^\infty b(a)\exp\left\{-\gamma a - \int_0^a \mu(\theta)\mathrm{d}\theta\right\}\mathrm{d}a \;\equiv\; \Phi(\gamma). \tag{3.41}$$

Since $\Phi(\gamma)$ is a monotonic decreasing function of γ, we deduce that Equation (3.41) admits a unique solution for γ.

In general, a separable solution will not satisfy the initial conditions $n(0,a) = f(a)$. However, in the limit as $t \to \infty$, Equation (3.22) supplies

$$n(t,0) \sim \int_0^t b(a)n(t-a,0)\exp\left\{-\int_0^a \mu(\theta)\mathrm{d}\theta\right\}\mathrm{d}a. \tag{3.42}$$

If we seek solutions to this equation of the form $n(t,a) \sim e^{\gamma t}F(a)$, then Equation (3.41) is recovered.

Exercise. By seeking separable solutions to the worked example, verify that Equation (3.41) is a necessary condition for obtaining a stable, age-structured population.

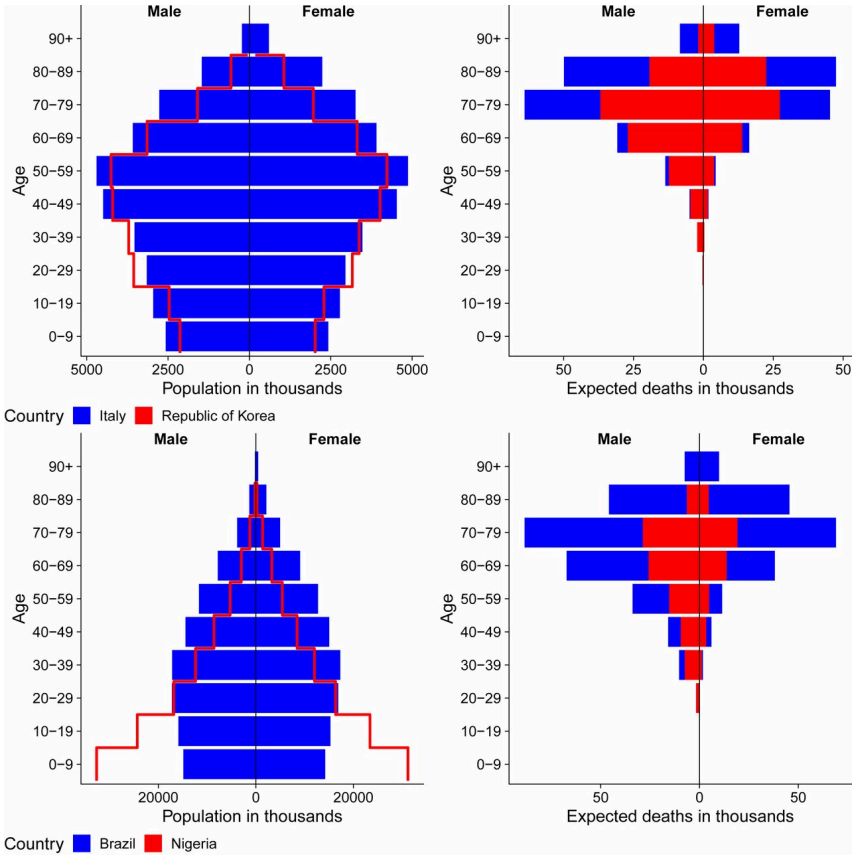

Figure 3.3: Population composition (left) and expected deaths in population (right) for Italy and Republic of Korea (top) and Nigeria and Brazil (bottom). Projections assume 10% population infection rate and age-sex-specific case fatality rates from Italy. Imaged reproduced from [1].

Exercise. Suppose that $\mu(a) = \mu$, constant, $n(0, a) = 1$ and $b(a)$ is given by

$$b(a) = \begin{cases} b, & \text{for } a_L < a < a_R, \\ 0, & \text{otherwise.} \end{cases} \tag{3.43}$$

By seeking separable solutions to von Foerster's equation, show that

$$b = \mu/(e^{-\mu a_L} - e^{-\mu a_R}), \tag{3.44}$$

is a necessary condition for obtaining a stable, age-structured population. Explain what happens in the limit at $(a_R - a_L) \to 0$.

3.2 Age-dependent epidemic models

One of the main reasons for developing age-structured models is to study the spread of diseases for which age is an important factor for susceptibility, infectiousness or death. For example, vulnerability to COVID increases dramatically with age (see Figure 3.3). In this section, we

will extend our previous age-structured model of population growth to describe the spread of a disease. In order to do this, we divide the population into two age-structured sub-populations: Susceptibles, $S(t,a)$, and Infectives, $I(t,a)$.

Applying the arguments used to derive Equation (3.4), we assume that $S(t,a)$ and $I(t,a)$ satisfy

$$\frac{\partial S}{\partial t}+\frac{\partial S}{\partial a} = -\underbrace{\left(\int_0^\infty r(\alpha)I(t,\alpha)\mathrm{d}\alpha\right)S(t,a)}_{\text{infection}}-\underbrace{\mu S}_{\text{death}}, \tag{3.45}$$

$$\frac{\partial I}{\partial t}+\frac{\partial I}{\partial a} = \underbrace{\left(\int_0^\infty r(\alpha)I(t,\alpha)\mathrm{d}\alpha\right)S(t,a)}_{\text{infection}}-\underbrace{\mu I}_{\text{death}}, \tag{3.46}$$

where, for simplicity, we assume that susceptibles and infectives die at the same, constant rate μ.

We close Equations (3.45)–(3.46) by prescribing the following initial and boundary conditions

$$S(0,a)=S_0(a), \qquad I(0,a)=I_0(a), \qquad S(t,0)=\int_0^\infty b(a)S(t,a)\mathrm{d}a, \qquad I(t,0)=0, \tag{3.47}$$

where the last condition results from the assumption that all newborns are susceptible.

In general, solutions for $S(t,a)$ and $I(t,a)$ require numerical approaches. Here, however, we attempt to make progress by seeking separable solutions of the form

$$S(t,a)=e^{\gamma t}S(a), \quad I(t,a)=e^{\gamma t}I(a), \tag{3.48}$$

with $\gamma=0$, *i.e.* we seek time-independent solutions. Then Equations (3.45)–(3.46) supply

$$\frac{\mathrm{d}S}{\mathrm{d}a} = -\left(\int_0^\infty r(\alpha)I(\alpha)\mathrm{d}\alpha\right)S(a)-\mu S, \tag{3.49}$$

$$\frac{\mathrm{d}I}{\mathrm{d}a} = \left(\int_0^\infty r(\alpha)I(\alpha)\mathrm{d}\alpha\right)S(a)-\mu I, \tag{3.50}$$

and hence

$$\frac{\mathrm{d}}{\mathrm{d}a}(S+I)=-\mu(S+I) \quad \Longrightarrow \quad S+I=\Lambda e^{-\mu a}, \tag{3.51}$$

where Λ is a constant of integration.

If $r(a)=r$, constant, then

$$\frac{\mathrm{d}I}{\mathrm{d}a}=r\underbrace{\left(\int_0^\infty I(\alpha)\mathrm{d}\alpha\right)}_{I_{\text{tot}}}S(a)-\mu I=rI_{\text{tot}}\Lambda e^{-\mu a}-\left(\mu+rI_{\text{tot}}\right)I, \tag{3.52}$$

which can be integrated to give

$$I(a) = Ae^{-(\mu+rI_{\text{tot}})a} + \Lambda e^{-\mu a}, \tag{3.53}$$

where

$$I_{\text{tot}} = \int_0^\infty I(a)\mathrm{d}a = \frac{A}{\mu + rI_{\text{tot}}} + \frac{\Lambda}{\mu}. \tag{3.54}$$

As a result,

$$I(a) = \left(I_{\text{tot}} - \frac{\Lambda}{\mu}\right)(\mu + rI_{\text{tot}})\, e^{-(\mu+rI_{\text{tot}})a} + \Lambda e^{-\mu a}. \tag{3.55}$$

and

$$S(a) = \Lambda e^{-\mu a} - I(a) = \left(\frac{\Lambda}{\mu} - I_{\text{tot}}\right)(\mu + rI_{\text{tot}})\, e^{-(\mu+rI_{\text{tot}})a} \tag{3.56}$$

where $S(0) = \int_0^\infty b(a)S(a)\mathrm{d}a$. Substituting for $S(0)$ and $S(a)$ we deduce that I_{tot} satisfies

$$1 = \int_0^\infty b(a)e^{-(\mu+rI_{\text{tot}})}\mathrm{d}a. \tag{3.57}$$

If $b(a) = b^{-\theta a}$, *i.e.* an individual's birth rate decreases with age, then

$$I_{\text{tot}} = \frac{b - \mu - \theta}{r}. \tag{3.58}$$

Exercise. Derive an expression for I_{tot} when $b(a) = bae^{-\theta a}$.

3.3 Structured models for populations of proliferating cells

Cells reproduce by duplicating their contents and then dividing in two (see Figure 3.4). The duration of the cell cycle varies widely: from eight minutes in fly embryos to more than a year for mammalian liver cells. In this subsection we will adapt the age-structured models developed above to study cell cycle dynamics.

We suppose that a tissue contains two types of cells:

- $p(t, s)$ = number of cycling cells at position $0 \leq s < T$ of the cell cycle at time t;
- $q(t, s)$ = number of quiescent (or non-cycling) cells arrested at position $0 \leq s < t$ at time t.

The evolution of the cycling population is governed by a nonlinear partial differential equation similar to Equation (3.4); as quiescent cells do not progress around the cell cycle, their evolution

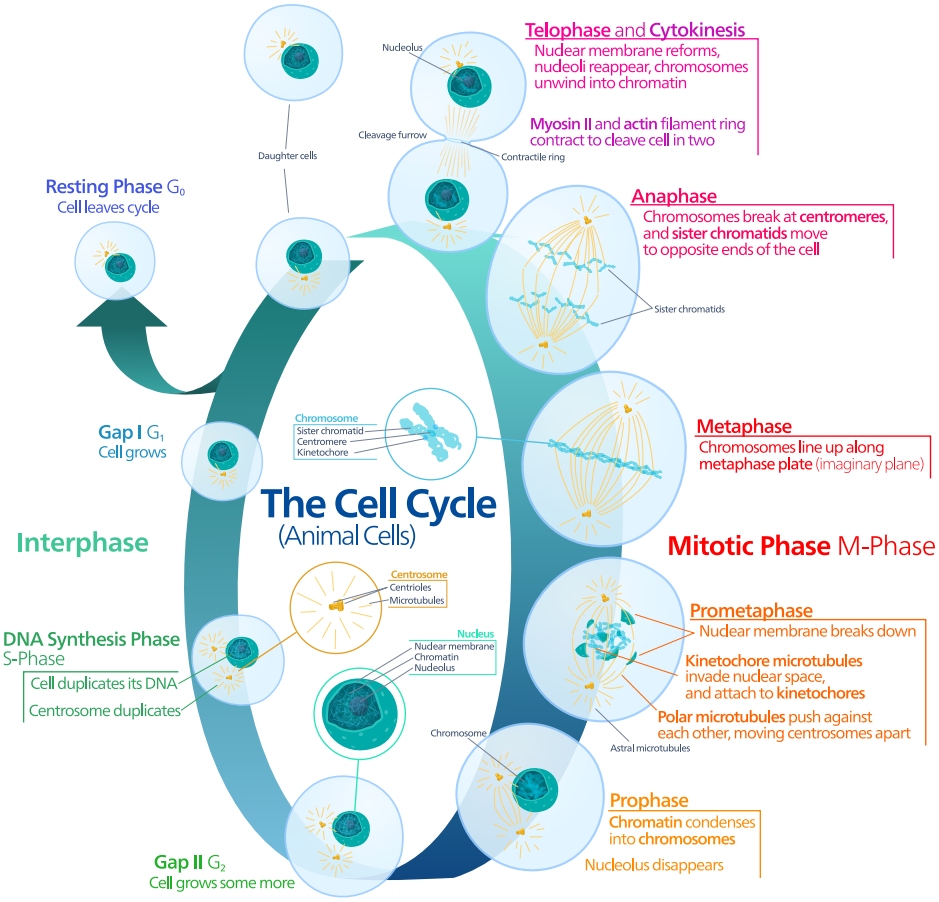

Figure 3.4: Schematic showing the different phases of the cycle cycle [16].

is governed by a time-dependent ordinary differential equation. In particular,

$$\frac{\partial p}{\partial t} + \frac{\partial p}{\partial s} = -\underbrace{\mu N p}_{\text{cell death}} - \underbrace{\Lambda N p}_{\text{exit cell cycle}} + \underbrace{\frac{\gamma q}{N_0 + N}}_{\text{re-enter cell cycle}}, \tag{3.59}$$

$$\frac{\partial q}{\partial t} = -\mu N q + \Lambda N p - \frac{\gamma q}{N_0 + N}. \tag{3.60}$$

where

$$N(t) = \int_0^T (p(t,s) + q(t,s))\mathrm{d}s, \tag{3.61}$$

is the total number of cells at time t, and μ, λ, γ and N_0 are positive constants.

In addition, we impose the following boundary and initial conditions:

$$p(0,s) = p_0(s), \qquad q(0,s) = q_0(s), \qquad p(t,0) = 2p(t,T). \tag{3.62}$$

The final condition states that at the end of the cell cycle (when $s = T$) a dividing cell produces two cells of age $s = 0$.

We seek separable solutions of the form

$$p(t,s) = e^{\theta t}P(s) \quad \text{and} \quad q(t,s) = e^{\theta t}Q(s), \tag{3.63}$$

with $\theta = 0$. Then $N(t)$, the total number of cells, is constant, and

$$\frac{\mathrm{d}P}{\mathrm{d}s} = -(\mu+\lambda)NP + \frac{\gamma Q}{N_0+N}, \tag{3.64}$$

$$0 = \Lambda NP - \left(\mu N + \frac{\gamma}{N_0+N}\right)Q, \tag{3.65}$$

hence

$$\frac{\mathrm{d}P}{\mathrm{d}s} = -\mu N(P+Q), \tag{3.66}$$

$$Q = \left(\frac{\Lambda N(N_0+N)}{\gamma+\mu N(N_0+N)}\right)P. \tag{3.67}$$

Eliminating Q we deduce

$$\frac{1}{P}\frac{\mathrm{d}P}{\mathrm{d}s} = -\mu N\left(1+\frac{\Lambda N(N_0+N)}{\gamma+\mu N(N_0+N)}\right) \equiv -\omega, \text{ say,} \tag{3.68}$$

and therefore

$$P(s) = P_\infty e^{-\omega s}, \tag{3.69}$$

$$Q(s) = Q_\infty e^{-\omega s} = \left(\frac{\Lambda N(N_0+N)}{\gamma+\mu N(N_0+N)}\right)P_\infty e^{-\omega s}. \tag{3.70}$$

Now using the fact that $P(s=0) = 2P(s=T)$ gives

$$1 = 2e^{-\omega T}, \tag{3.71}$$

and so

$$\frac{\ln 2}{T} = \omega = \mu N\left(1+\frac{\Lambda N(N_0+N)}{\gamma+\mu N(N_0+N)}\right). \tag{3.72}$$

This equation defines the total population size, N, in terms of the cell cycle length, T, and other model parameters.

We determine the proportion of cycling cells by noting that

$$N = \int_0^T [P(s)+Q(s)]\,\mathrm{d}s = \left(\frac{1-e^{-\omega T}}{\omega}\right)(P_\infty + Q_\infty), \tag{3.73}$$

which gives

$$2\omega N = \frac{\omega}{\mu N} P_\infty \quad \text{or} \quad P_\infty = 2\mu N^2, \tag{3.74}$$

and therefore

$$P(s) = 2\mu N^2 e^{-\omega s} \tag{3.75}$$

$$Q(s) = 2\mu N^2 \left(\frac{\Lambda N(N_0 + N)}{\gamma + \mu N(N_0 + N)} \right) e^{-\omega s}. \tag{3.76}$$

Exercise.

- Suppose $\gamma \to 0$: how are N, P and Q defined? Interpret your results.
- Suppose $\Lambda \to 0$: how are N, P and Q defined? Interpret your results.

Suggested reading.

- J. D. Murray, *Mathematical Biology, Volume I* – Chapter 1.
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