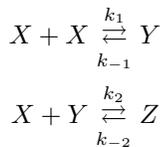


**MTH 370, Fall 2009**  
**Solutions to Homework 10**

**Instructions:** Do these calculations by hand (you may use a computer or calculator for simple arithmetic and function evaluations) and show your work.

1. In the real world, trimolecular reactions are rare, although trimers are not. Consider the following trimerization reaction in which three monomers of X combine to form the trimer Z:



- (a) Write down the mass-action equations for these reactions.  
(b) Show that

$$\frac{dx}{dt} + 2\frac{dy}{dt} + 3\frac{dz}{dt} = 0.$$

Why does this equation hold?

- (c) Letting  $x_0$  denote the initial concentration of monomers, suppose

$$k_{-1} \gg k_{-2}, \quad k_{-1} \gg k_2 x_0.$$

Use a quasi-steady-state approximation to find the rate of production of Z, and show that it is proportional to  $x^3$ .

**Solutions:**

- (a)

$$\begin{aligned} \frac{dx}{dt} &= -2k_1 x^2 - k_2 xy + 2k_{-1} y + k_{-2} z \\ \frac{dy}{dt} &= k_1 x^2 + k_{-2} z - k_2 xy - k_{-1} y \\ \frac{dz}{dt} &= k_2 xy - k_{-2} z \end{aligned}$$

- (b) This is equation represents the conservation of total monomer concentration.  
(c) Setting

$$a = \frac{x}{x_0}, \quad b = \frac{y}{x_0}, \quad c = \frac{z}{x_0}, \quad \tau = k_2 x_0 t, \quad \lambda = \frac{k_{-2}}{k_2 x_0}, \quad \mu = \frac{k_1 x_0}{k_{-1}}, \quad \epsilon = \frac{k_2 x_0}{k_{-1}},$$

the above equations can be written

$$\begin{aligned} \epsilon \frac{da}{d\tau} &= \epsilon(\lambda c - ab) - 2\mu a^2 + 2b \\ \epsilon \frac{db}{d\tau} &= \epsilon(\lambda c - ab) + \mu a^2 - b \\ \frac{dc}{d\tau} &= ab - \lambda c \end{aligned}$$

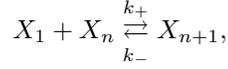
Setting  $\epsilon = 0$  gives the “slow” equations in which  $a$  and  $b$  have already reached quasi-equilibrium, and during which

$$b = \mu a^2.$$

Substituting this into the equation for  $c$  yields

$$\frac{dc}{d\tau} = \mu a^3 - \lambda c.$$

2. The length of a microtubule changes by a process called *treadmilling* – monomer is added to one end of the microtubule and removed from the other. A simple set of reactions for this process is the following. Let  $X_n$  denote a microtubule comprised of  $n$  monomers. We say that  $n$  is the *length* of such a microtubule. Then for each  $n \geq 1$ ,



where  $k_+$  is the rate of adding monomer, and  $k_-$  is the rate of removing it. Assuming that there is a total concentration  $c$  of monomers, find the equilibrium distribution of microtubule lengths.

**Solutions:** The mass-action equations are

$$\begin{aligned} \frac{dx_1}{dt} &= -k_+x_1 \left( \sum_{n=1}^{\infty} x_n + x_1 \right) + k_- \left( \sum_{n=2}^{\infty} x_n + x_2 \right), \\ \frac{dx_n}{dt} &= k_+x_1x_{n-1} - (k_+x_1 + k_-)x_n + k_-x_{n+1} \quad (n > 1). \end{aligned}$$

It is “easy” to check that the following conservation equation holds,

$$\sum_{n=1}^{\infty} nx_n = c. \tag{1}$$

At equilibrium, the equation above for  $n > 1$  can be written

$$0 = \mu x_{n-1} - (1 + \mu)x_n + x_{n+1} \quad \left( \mu = \frac{k_+x_1}{k_-} \right)$$

which is a second-order linear difference equations for  $x_n$ . Setting  $x_n = \lambda^n$ , the above equation is reduced to a quadratic equation for  $\lambda$ ,

$$0 = \mu - (1 + \mu)\lambda + \lambda^2,$$

whose solutions are

$$\lambda_{\pm} = \frac{1 + \mu \pm \sqrt{(1 + \mu)^2 - 4\mu}}{2} = \frac{1 + \mu \pm \sqrt{(1 - \mu)^2}}{2} \Rightarrow \lambda_+ = 1, \lambda_- = \mu.$$

Therefore, the general form of  $x_n$  is

$$x_n = c_1 + c_2\mu^n$$

for some constants  $c_1$  and  $c_2$  to be determined. From (1) it is clear that  $c_1 = 0$  and  $\mu < 1$  else the sum would be infinite. Substituting  $x_n = c_2\mu^n$  into (1) yields

$$c = c_2 \sum_{n=1}^{\infty} n\mu^n = c_2\mu \frac{d}{d\mu} \left( \sum_{n=1}^{\infty} \mu^n \right) = c_2\mu \frac{d}{d\mu} \left( \frac{1}{1 - \mu} - 1 \right) = \frac{c_2\mu}{(1 - \mu)^2} \Rightarrow c_2 = \frac{c(1 - \mu)^2}{\mu}.$$

Therefore,

$$x_n = c(1 - \mu)^2\mu^{n-1} \quad (n \geq 1). \tag{2}$$

Recall that  $\mu = k_+x_1/k_-$ , hence setting  $n = 1$  in the equation above and multiplying by  $k_+/k_-$  yields

$$\mu = \frac{ck_+}{k_-}(1 - \mu)^2 \Rightarrow 0 = 1 - \left( 2 + \frac{k_-}{ck_+} \right) \mu + \mu^2,$$

so

$$\mu_{\pm} = 1 + \frac{k_-}{2ck_+} \pm \sqrt{\left( 1 + \frac{k_-}{2ck_+} \right)^2 - 1}.$$

Since

$$\sqrt{\left(1 + \frac{k_-}{2ck_+}\right)^2} - 1 = \sqrt{\frac{k_-}{ck_+} + \left(\frac{k_-}{2ck_+}\right)^2} > \frac{k_-}{2ck_+},$$

we find  $\mu_+ > 1$  but  $\mu_- < 1$ . Thus  $\mu = \mu_-$  in (2).

Of course,  $x_n$  is only the equilibrium concentration of microtubules of length  $n$ . To find the distribution, we must first calculate the total concentration of microtubules,

$$C = \sum_{n=1}^{\infty} x_n = c(1 - \mu)^2 \sum_{n=1}^{\infty} \mu^n = c(1 - \mu)^2 \frac{\mu}{1 - \mu} = c\mu(1 - \mu)$$

and then divide  $x_n$  by  $C$ ,

$$p_n = \frac{x_n}{C} = (1 - \mu)\mu^{n-2}.$$

Therefore, the lengths are distributed geometrically. The number  $p_n$  is the probability of finding a microtubule of length  $n$  amongst all the microtubules at equilibrium.