

**PHYS3511-Biological Physics**  
**Fall 2018, Assignment #5, Due Wednesday October 7, 2018**  
**Read Chapter 5 before attempting the solution**

**Exercise 1) (10 points)** Chapter 5, Problem 5.2

First, I will state that sugar is made up of glucose that has chemical structure of  $C_6H_{12}O_6$ , and six **carbon** atoms. As stated in page 102 of the textbook, **one** E. Coli needs about  $10^{10}$  **extra carbons** to **divide** into **two** E. coli, i.e. an E. Coli is made of about  $10^{10}$

**carbons**. Hence, the number of glucose needed is  $\frac{10^{10}}{6} \sim 2 \times 10^9$ . Of course, ultimately **ATP** is the fuel that synthesize the proteins and lipids that make up the E. Coli. Biology textbooks will often state that one glucose can produce 38 ATP, 2 from glycolysis, 2 from the Krebs cycle, and about 34 from the electron transport system. We will not discuss these issues, rather I direct you to read the figure caption of table 5.1, on the last page of this solution. It states that one glucose produces about 2 ATP. Below we calculate the number of glucose to produce macromolecules:

**Proteins:** On page 199, equation 5.2 it is assumed that an E. Coli must produced  $3 \times 10^6$  proteins (see table 2.1), and it is assumed that a protein has on average 300 amino acid (aa), and that each aa needs 5.2 ATP. This works out to  $5.2 ATP \cdot aa^{-1} \times 300 aa \cdot proteins^{-1} \times 3 \times 10^6 proteins \sim 4.5 \times 10^9 ATP$ , which works out to about  $2.25 \times 10^9 g$  glucose. From assignment 1, exercise 4 (problem 2.5)  $\sim 4.3 \times 10^9$  carbons is needed, and since there are 6 carbons in a glucose, this works out to  $\sim 0.7 \times 10^9$ . Total number glucose needed is  $3.0 \times 10^9$ .

**DNA**

In figure 4.13, of the textbook the DNA of E. Coli is  $5 \times 10^6 bp$ . On page 199 it states “for RNA and DNA the energy to synthesize a nucleotide is to the order of 10 to 20 ATP.” I will assume that for DNA, 30 ATP is needed (10 is needed to incorporate the nucleotide into DNA). This gives  $30 ATP \cdot bp^{-1} \times 5 \times 10^6 bp = 1.5 \times 10^8 ATP$  is needed, and assuming one glucose produces 2 ATP, this give  $7.5 \times 10^7$  glucose. Since there are 2 copies of DNA in E. Coli, this gives  $2 \times 7.5 \times 10^7 glucose = 1.5 \times 10^8$  glucose. From exercise 4 of assignment 1,  $1.9 \times 10^8$  carbons need to be incorporated into 2 DNA, and since one glucose has 6 carbons, this works out to  $\sim 0.3 \times 10^8$  glucose, which gives finally  $\sim 2.0 \times 10^8$  glucose. This is similar to the value of table 5.2.

**RNA**

From assignment 1, exercise 4 (problem 2.5) I showed that there are about  $1 \times 10^9$  carbons from RNA. Since there are about 10 carbons per nucleotide (nt), this works out to about  $1 \times 10^8 nt$ . We will assume that we need 15 ATP to produce 1 nt of an RNA (half as for 1 bp of DNA). Hence, we need about  $1.5 \times 10^9 ATP$ , which is very similar to the value on Table 5.2. This converts to  $\frac{1.5 \times 10^9}{2} = 0.75 \times 10^9$  glucose. Since there are 6 carbons per glucose, the  $1 \times 10^9$  carbons will require  $\frac{1 \times 10^9}{6} = 2 \times 10^8$ . This adds to  $0.75 \times 10^9 + 0.2 \times 10^9 \sim 1 \times 10^9$  glucose.

**Phospholipid:**

The textbook does not state how many ATP is needed to make 1 phospholipid. But table 5.2 states  $3.2 \times 10^9$  ATP or  $1.6 \times 10^9$  glucose. Also, there are  $6.6 \times 10^8$  carbons (assignment 1), which will require  $1.1 \times 10^8$  glucose. Basically, we need  $1.7 \times 10^9$  glucose for lipids.

**Lipopolysaccharide:**

The textbook does not state how many ATP is needed to make 1 Lipopolysaccharide. But table 5.2 states  $3.8 \times 10^8$  ATP or  $1.9 \times 10^8$  glucose. Also, there are  $2.4 \times 10^8$  carbons, which will require  $0.8 \times 10^8$  glucose. Basically, we need  $2.7 \times 10^8$  glucose for Lipopolysaccharide.

**Peptidoglycan (Murien Wall):**

The textbook does not state how many ATP is needed to make 1 Peptidoglycan. But table 5.2 states  $1.7 \times 10^8$  ATP or  $8.5 \times 10^7$  glucose.

**Glycogen:**

The textbook does not state how many ATP is needed to make 1 glycogen. But table 5.2 states  $3.1 \times 10^7$  ATP or  $1.6 \times 10^7$  glucose. Also, there are  $2.6 \times 10^5$  carbons, which will require  $0.4 \times 10^5$  glucose. Basically, we need about  $1.6 \times 10^7$  glucose for Lipopolysaccharide.

Total number of glucose is  $3.0 \times 10^9 + 2.0 \times 10^8 + 1.0 \times 10^9 + 1.7 \times 10^9 + 2.7 \times 10^8 + 8.5 \times 10^7 + 1.6 \times 10^7 = 6.1 \times 10^9$ .

Assuming the cell division time of 3000s, the rate of glucose uptake is

$$\frac{6.1 \times 10^9 \text{ glucose}}{3000s} = 2 \times 10^6 \frac{\text{glucose}}{s}$$

On page 101 and 102 in the "Estimate Timing of E. Coli", the glucose uptake rate is calculated to be  $3 \times 10^5 \frac{\text{glucose}}{s}$ , which is a much lower rate.

**Exercise 2) (10 points) Chapter 5, Problem 5.5**

A) From 5.64,  $S_{gas} - S_{liquid} = k_B \ln \left( \frac{W_{gas}}{W_{liquid}} \right)$ , or in terms of the gas constant,

$S_{gas} - S_{liquid} = R \ln \left( \frac{W_{gas}}{W_{liquid}} \right)$ , which is equivalent to the macroscopic definition

$dS = S_{gas} - S_{liquid} = \frac{Q_{vaporization}}{T} = \frac{40.66 \times 10^3 \text{ J} \cdot \text{mol}^{-1}}{373 \text{ K}} = 109 \frac{\text{J}}{\text{K} \cdot \text{mol}}$ . Now note that we can also write

B) Part B assumes  $\frac{W_{gas}}{W_{liquid}} = \left( \frac{V_{gas}}{V_{liquid}} \right)^N$

**Exercise 3) (10 points)** An E. Coli of radius about  $r = 0.7 \mu\text{m}$  is observed to swim at  $v = 80 \mu\text{m} \cdot \text{s}^{-1}$ . Estimate the amount of ATP that it must produce per second, in order for the E. Coli to swim at this rate. Compare this with the number of ATP needed to produce one E. Coli per second. DATA: ATP hydrolysis produce  $\Delta G = -30 \text{ kJ} \cdot \text{mol}^{-1}$ .

The drag force is  $f = \zeta v$ , valid for the small size/low speed/high viscosity regime, where using stokes law  $\zeta = 6\pi\eta R$ , with the viscosity of water,  $\eta = 10^{-3} \text{ Pa} \cdot \text{s} = 10^{-3} \frac{\text{kg}}{\text{m} \cdot \text{s}}$

$$f = 6\pi\eta Rv = 6\pi \times 10^{-3} \frac{\text{kg}}{\text{m} \cdot \text{s}} \times 7 \times 10^{-7} \text{m} \times 8 \times 10^{-5} \text{m} \cdot \text{s}^{-1} = 1 \times 10^{-12} \text{N}.$$

In physics power = force x speed,  $P = fv = 1 \times 10^{-12} \text{N} \times 8 \times 10^{-5} \text{m} \cdot \text{s}^{-1} = 8 \times 10^{-17} \text{J} \cdot \text{s}^{-1} = 8 \times 10^{-17} \text{W}$ .

We know that an ATP hydrolysis produced  $30 \text{kJ} \cdot \text{mol}^{-1}$ , which works out to be an energy per ATP hydrolysis of  $30 \times 10^3 \frac{\text{J}}{\text{mol}} \times \frac{1}{6.023 \times 10^{23} \text{mol}^{-1}} = 4.98 \times 10^{-20} \text{J}$ , which in terms of thermal energy at room temperature  $T = 300 \text{ K}$ , works out to be  $\frac{4.98 \times 10^{-20} \text{J}}{k_B T} =$

$$\frac{4.98 \times 10^{-20} \text{J}}{(1.381 \times 10^{-23} \text{J} \cdot \text{K}^{-1})(300 \text{K})} = 12.$$

Hence for the E. Coli to swim that fast would require  $\frac{8 \times 10^{-17} \text{J} \cdot \text{s}^{-1}}{4.98 \times 10^{-20} \text{J} \cdot \text{ATP}^{-1}} = 1606$  ATP per second. Looking at Table 5.1 E. Coli needs about  $1 \times 10^{10}$  ATP to divide, and with division time of about 3000s, this gives  $\frac{1 \times 10^{10} \text{ATP}}{3000 \text{s}} = 3.3 \times 10^6 \frac{\text{ATP}}{\text{s}}$ . E. Coli produces enough ATP to swim at this rate.

On page 192, the book states that ATP hydrolysis produces  $20k_B T = 20(1.381 \times 10^{-23} \text{J} \cdot \text{K}^{-1})(300 \text{K}) = 8.3 \times 10^{-20} \text{J}$ , which would give  $\frac{8 \times 10^{-17} \text{J} \cdot \text{s}^{-1}}{4.98 \times 10^{-20} \text{J} \cdot \text{ATP}^{-1}} \sim 1000 \frac{\text{ATP}}{\text{s}}$  for the E. Coli to swim that fast.

**Exercise 4) (10 points)** From class note, I showed the 1<sup>st</sup> law of Thermodynamics:

$dE = TdS - PdV + \mu dN$ , which gives  $dS = \frac{1}{T} dE + \frac{P}{T} dV - \frac{\mu}{T} dN$ . Hence we know that the Entropy  $S(E, V, N)$  is a function of E, V and N. This gives the differential formula  $dS = \left(\frac{\partial S}{\partial E}\right)_{V,N} dE + \left(\frac{\partial S}{\partial V}\right)_{E,N} dV - \left(\frac{\partial S}{\partial N}\right)_{E,V} dN$ . Comparing coefficients we obtain:

$$\left(\frac{\partial S}{\partial E}\right)_{V,N} = \frac{1}{T}; \left(\frac{\partial S}{\partial V}\right)_{E,N} = \frac{P}{T}; \left(\frac{\partial S}{\partial N}\right)_{E,V} = -\frac{\mu}{T}$$

For an ideal gas of non-interacting particles the Entropy is given by the Sackur-Tetrode equation:

$$S = Nk_B \left[ \ln \left\{ \left( \frac{V}{N} \right) \left( \frac{4\pi m E}{3N h^2} \right)^{3/2} \right\} + \frac{5}{2} \right].$$

The above can be used to find the ideal gas equation,  $PV = Nk_B T$ , and the equipartition theorem,  $E = \frac{3}{2} Nk_B T$ .

Now we consider the entropy of a **dilute attractive gas** with **Entropy**:

$$S = Nk_B \left[ \ln \left\{ \left( \frac{V}{N} \right) \left( \frac{4\pi m}{3N h^2} \right)^{3/2} \left( E + a \frac{N^2}{V} \right)^{3/2} \right\} + \frac{5}{2} \right].$$

A) Use  $\left(\frac{\partial S}{\partial E}\right)_{V,N} = \frac{1}{T}$  to find an analogous equipartition equation.

Since derivative  $\left(\frac{\partial S}{\partial E}\right)_{V,N}$  holds V and N constant

$$\left(\frac{\partial S}{\partial E}\right)_{V,N} = \frac{3}{2} \frac{Nk_B}{E + a \frac{N^2}{V}} = \frac{1}{T} \rightarrow E = \frac{3}{2} Nk_B T - a \frac{N^2}{V}$$

B) and  $\left(\frac{\partial S}{\partial V}\right)_{E,N} = \frac{P}{T}$  to find an analogous equation to the ideal gas equation

Since  $\left(\frac{\partial S}{\partial V}\right)_{E,N}$  holds E and N constant.

$$\left(\frac{\partial S}{\partial V}\right)_{E,N} = Nk_B \left( \frac{1}{V} - a \frac{N^2}{V^2} \frac{3}{2} \frac{1}{E + a \frac{N^2}{V}} \right) = \frac{P}{T}$$

From part A)  $E + a \frac{N^2}{V} = \frac{3}{2} Nk_B T$ , gives

$$Nk_B \left( \frac{1}{V} - a \frac{N^2}{V^2} \frac{3}{2} \frac{1}{\frac{3}{2} Nk_B T} \right) = \frac{P}{T} \rightarrow \frac{Nk_B}{V} - a \frac{N^2}{V^2} \frac{1}{T} = \frac{P}{T}$$

$$\left( P + a \frac{N^2}{V^2} \right) V = Nk_B T$$

**BONUS: (5 points)** For the van der waals gas the Entropy is

$$S = Nk_B \left[ \ln \left\{ \left( \frac{V - Nb}{N} \right) \left( \frac{4\pi m}{3Nh^2} \right)^{3/2} \left( E + a \frac{N^2}{V} \right)^{3/2} \right\} + \frac{5}{2} \right]$$

Find the van der Waals equation of state (this equation is easily found online)

$$\left(\frac{\partial S}{\partial E}\right)_{V,N} = \frac{3}{2} \frac{Nk_B}{E + a \frac{N^2}{V}} = \frac{1}{T} \rightarrow E = \frac{3}{2} Nk_B T - a \frac{N^2}{V}, \quad (A)$$

$$\left(\frac{\partial S}{\partial V}\right)_{E,N} = Nk_B \left( \frac{1}{V - Nb} - a \frac{N^2}{V^2} \frac{3}{2} \frac{1}{E + a \frac{N^2}{V}} \right) = \frac{P}{T}, \quad (B)$$

Using equation A) to get  $E + a \frac{N^2}{V} = \frac{3}{2} Nk_B T$ , and substituting into B

$$\left(\frac{\partial S}{\partial V}\right)_{E,N} = Nk_B \left( \frac{1}{V - Nb} - a \frac{N^2}{V^2} \frac{3}{2} \frac{1}{\frac{3}{2} Nk_B T} \right) = \frac{P}{T}$$

$$\frac{Nk_B}{V - Nb} - a \frac{N^2}{V^2} \frac{1}{T} = \frac{P}{T} \rightarrow \frac{Nk_B T}{V - Nb} - a \frac{N^2}{V^2} = P \rightarrow P + a \frac{N^2}{V^2} = \frac{Nk_B T}{V - Nb} \rightarrow$$

$$\left( P + a \left( \frac{N}{V} \right)^2 \right) (V - Nb) = Nk_B T$$

**NOTE: van der Waals equation of state** is  $\left( P + a \left( \frac{N}{V} \right)^2 \right) (V - Nb) = Nk_B T$ . The equation of state of an attractive gas is found by setting  $b = 0$  in the **van der Waals equation of state**.

way? How many reducing equivalents of NADH and NADPH are consumed or created along the way? In order to answer this question completely, you may need to consider a few other pathways as well. For example, it is likely that the displayed glycolysis pathway does not actually start with glucose. To get glucose 6-phosphate from glucose requires 1 ATP. One of the steps in the serine synthesis pathway is coupled to a conversion of L-glutamate to 2-ketoglutarate. You will have to look up the "glutamate biosynthesis III" pathway to determine the cost of regenerating L-glutamate from 2-ketoglutarate. Assuming that each NADH or NADPH is equivalent to 2 ATP, which is a reasonable conversion factor for bacteria, what is the net energy cost to synthesize one molecule of serine in units of ATP and units of  $k_B T$ ?

### • 5.2 The sugar budget revisited

In Chapter 3, we worked out the rate of sugar uptake to provide the construction materials for a dividing bacterium. However, as shown in this chapter, sugar molecules also provide the *energy* needed to perform macromolecular synthesis. Amend the estimate of Chapter 3 to include the fact that sugar supplies construction materials and the energy needed to assemble them. You might find it useful to look at the macromolecular energy costs revealed in Table 5.2. How many sugars are needed to provide the energy and construction materials for making a new cell? Make an estimate for the average rate of sugar uptake for a dividing bacterium in light of this amendment to our earlier estimates.

### • 5.3 A feeling for the numbers: covalent bonds

(a) Based on a typical bond energy of  $150 k_B T$  and a typical bond length of 0.15 nm, use dimensional analysis to estimate the frequency of vibration of covalent bonds.

(b) Assume that the Lennard-Jones potential given by

$$V(r) = \frac{a}{r^{12}} - \frac{b}{r^6}$$

describes a covalent bond (though real covalent bonds are more appropriately described by alternatives such as the Morse potential that are not so convenient analytically).

### • 5.5 A feeling for the numbers: comparing multiplicities

Boltzmann's equation for the entropy (Equation 5.30) tells us that the entropy difference between a gas and a liquid is given by

$$S_{\text{gas}} - S_{\text{liquid}} = k_B \ln \frac{W_{\text{gas}}}{W_{\text{liquid}}}. \quad (5.64)$$

From the macroscopic definition of entropy as  $dS = dQ/T$ , we can make an estimate of the ratios of multiplicities by noting that boiling of water takes place at fixed  $T$  at 373 K.

(a) Consider a cubic centimeter of water and use the result that the heat needed to boil water (the latent heat of vaporization) is given by  $Q_{\text{vaporization}} = 40.66 \text{ kJ/mol}$  (at  $100^\circ\text{C}$ ) to estimate the ratio of multiplicities of water and water vapor for this number of molecules. Write your result as 10 to some power. If we think of multiplicities in terms of an ideal gas at fixed  $T$ , then

$$\frac{W_1}{W_2} = \left( \frac{V_1}{V_2} \right)^N. \quad (5.65)$$

What volume change would one need to account for the liquid/vapor multiplicity ratio? Does this make sense?

(b) In the chapter, we discussed the Stirling approximation and the fact that our results are incredibly tolerant of error. Let us pursue that in more detail. We have found that the typical types of multiplicities for a system like a gas are of the order of  $W \approx e^{10^{25}}$ . Now, let us say we are off by a factor of  $10^{1000}$  in our estimate of the multiplicities, namely,  $W = 10^{1000} e^{10^{25}}$ . Show that the difference in our evaluation of the entropy is utterly negligible whether we use the first or second of these results for the multiplicity. This is the error tolerance that permits us to use the Stirling approximation so casually! (This problem was adapted from Ralph Baierlein, *Thermal Physics*, Cambridge University Press, 1999.)

### • 5.6 Stirling approximation revisited

The Stirling approximation is useful in a variety of different settings. The goal of the present problem is to work through a more sophisticated treatment of this approximation than

**Table 5.2:** Biosynthetic cost in ATP equivalents to synthesize the macromolecules of a single *E. coli* cell.

Class	Biosynthetic cost (aerobic) – ATP equivalent
Protein	$4.5 \times 10^9$
DNA	$3.5 \times 10^8$
RNA	$1.6 \times 10^9$
Phospholipid	$3.2 \times 10^9$
Lipopolysaccharide	$3.8 \times 10^8$
Peptidoglycan	$1.7 \times 10^8$
Glycogen	$3.1 \times 10^7$

**Table 5.1:** Amino acid abundance and cost of synthesis for making the amino acids under both aerobic and anaerobic growth conditions. "Glucose equivalents" refers to the number of glucose molecules that must be used to generate the carbon skeletons of each amino acid (for example, one mole of alanine, an amino acid containing three carbons, can be synthesized from one half mole of glucose, a sugar containing six carbons). "ATP equivalents" refers to the approximate amount of biosynthetic energy required to synthesize the amino acid from glucose as a starting material. A negative value indicates that synthesis of the amino acid from glucose is favorable so energy is generated rather than consumed. These numbers are not absolute; they depend on several assumptions about metabolic energetics and pathway utilization. We have assumed that the energetic value of one molecule of NADH or NADPH is equivalent to two ATP molecules. We have not accounted for the biosynthetic cost of sulfate, ammonium, or single carbon units. (Data from F. C. Neidhardt et al., *Physiology of the Bacterial Cell*, Sinauer Associates, 1990; M. Schaechter et al., *Microbe*, ASM Press, 2006; and EcoCyc, *Encyclopedia of Escherichia coli K-12 Genes and Metabolism*, [www.ecocyc.org](http://www.ecocyc.org).)

Amino acid	Abundance (molecules per cell)	Glucose equivalents	ATP equivalents (aerobic)	ATP equivalents (anaerobic)
Alanine (A)	$2.9 \times 10^8$	0.5	–1	1
Arginine (R)	$1.7 \times 10^8$	0.5	5	13
Asparagine (N)	$1.4 \times 10^8$	0.5	3	5
Aspartate (D)	$1.4 \times 10^8$	0.5	0	2
Cysteine (C)	$5.2 \times 10^7$	0.5	11	15

