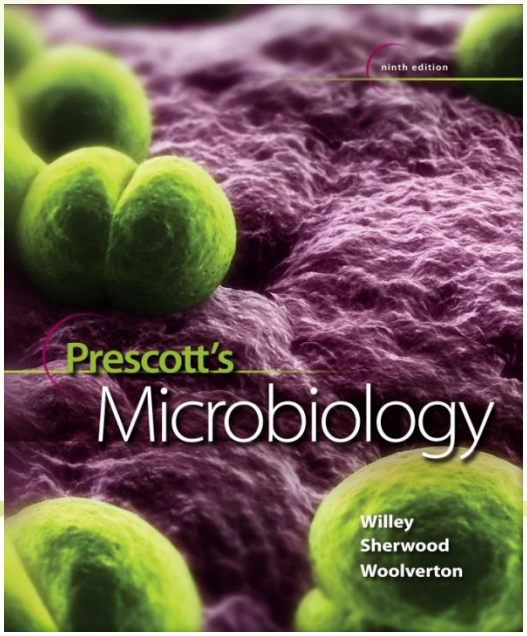
7




# Microbial Growth

# 7.1 Reproductive strategies

1. Describe binary fission as observed in bacteria and archaea
2. Compare the three reproductive strategies used by bacteria other than binary fission

# Reproductive Strategies

- The reproductive strategies of eukaryotic microbes
  - asexual and sexual, haploid or diploid
- *Bacteria* and *Archaea*
  - haploid only, asexual - binary fission, budding, filamentous
  - all must replicate and segregate the genome prior to division

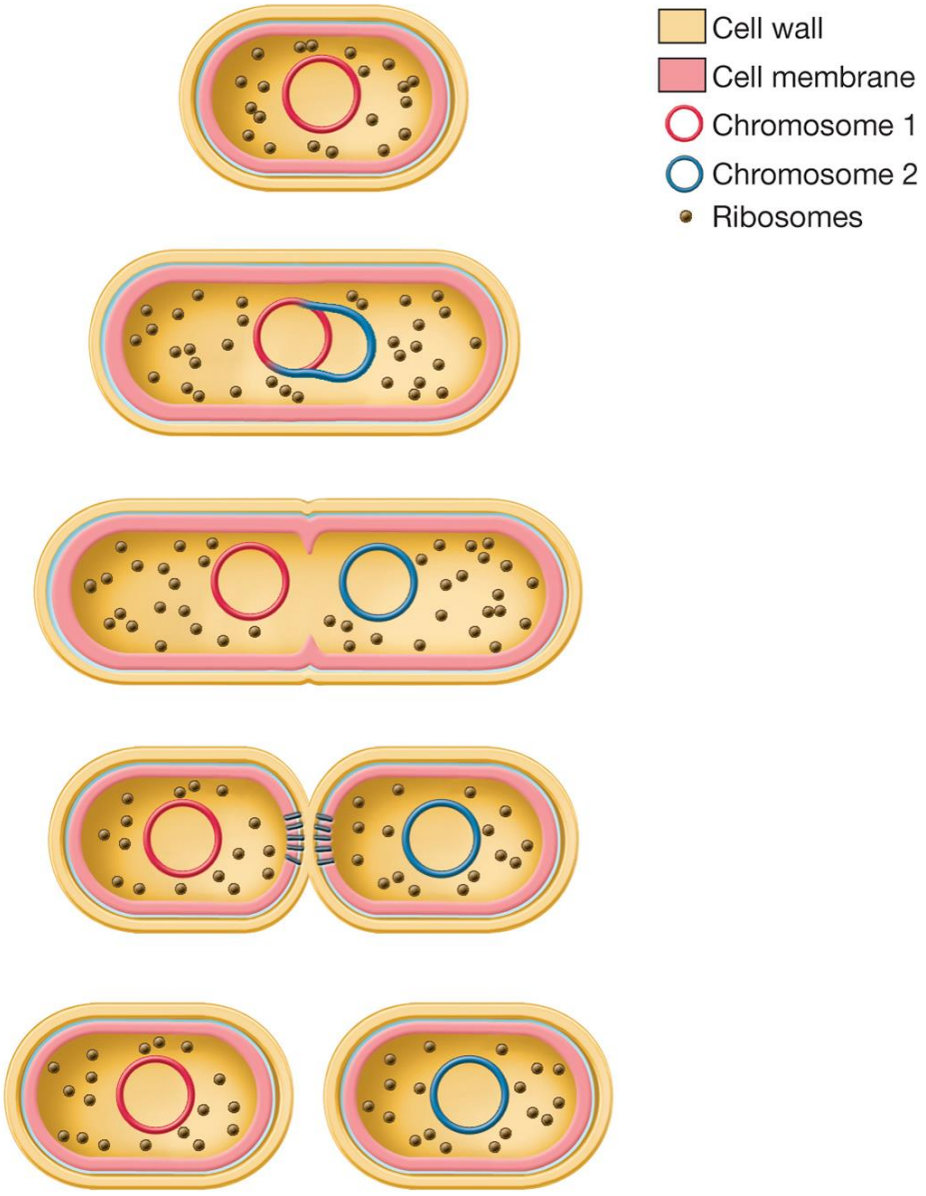
(a) A young cell at early phase of cycle

(b) A parent cell prepares for division by enlarging its cell wall, cell membrane, and overall volume. DNA replication then starts.

(c) The septum begins to grow inward as the chromosomes move toward opposite ends of the cell. Other cytoplasmic components are distributed to the two developing cells.

(d) The septum is synthesized completely through the cell center, creating two separate cell chambers.

(e) At this point, the daughter cells are divided. Some species separate completely as shown here, while others remain attached, forming chains, doublets, or other cellular arrangements.



# 7.2 Bacterial cell cycle

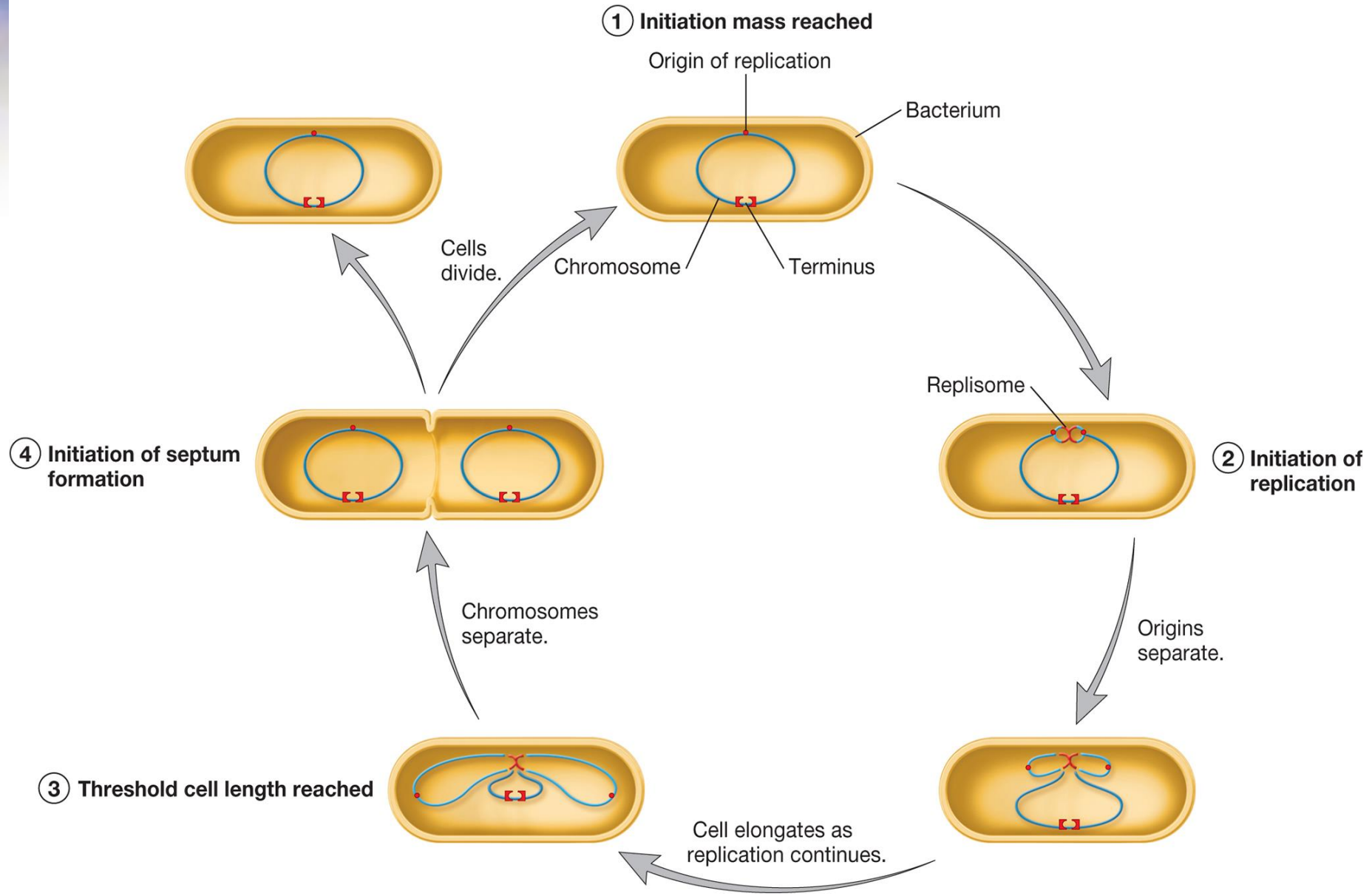
1. Summarize the two major events in a typical bacterial cell cycle
2. State the functions of cytoskeletal proteins in a typical bacterial cell cycle and in determining cell shape

# Bacterial Cell Cycle

- Cell cycle is sequence of events from formation of new cell through the next cell division
  - most bacteria divide by binary fission
- Two pathways function during cycle
  - DNA replication and partition
  - cytokinesis

# Chromosome Replication and Partitioning - 1

- Most bacterial chromosomes are circular
- Single origin of replication – site at which replication begins
- Terminus – site at which replication is terminated, located opposite of the origin
- Replisome – group of proteins needed for DNA synthesis
- DNA replication proceeds in both directions from the origin
- Origins move to opposite ends of the cell



# Chromosome Partitioning

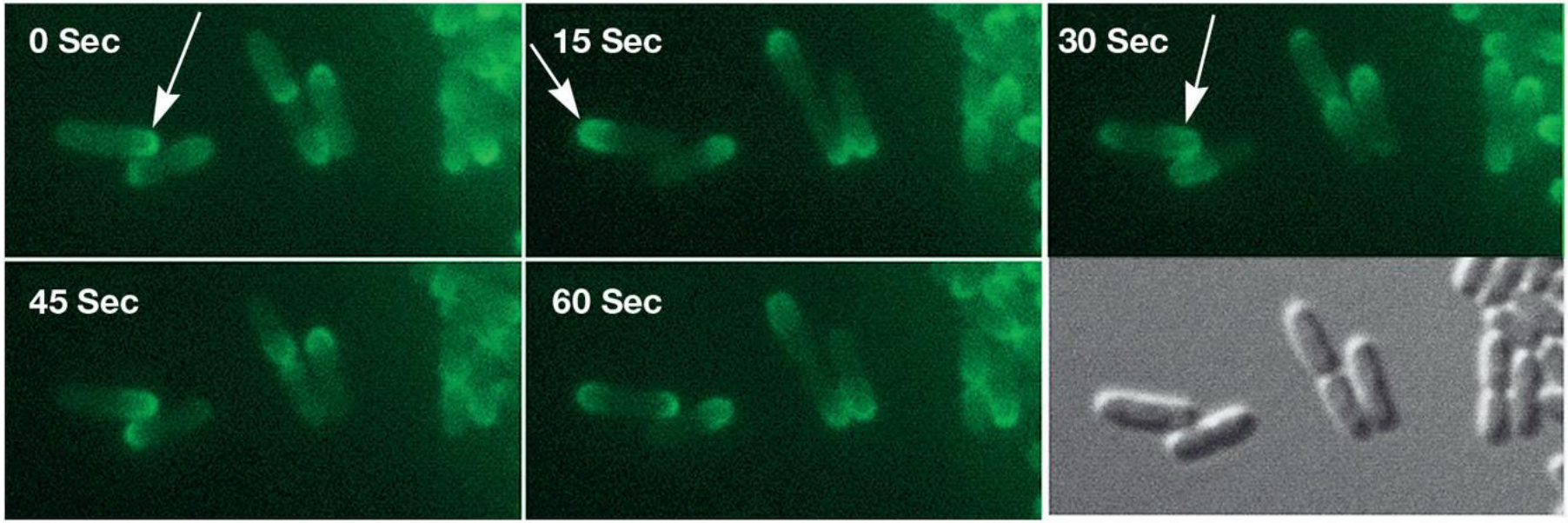
- Replisome pushes, or condensation of, daughter chromosomes to opposite ends
- MreB (*mur*ein cluster *B*) – an actin homolog, plays role in determination of cell shape as spiral inside cell periphery, and chromosome segregation
  - new origins associate with MreB tracks
  - if MreB is mutated, chromosomes do not segregate

# Cytokinesis - Septation

- Septation – formation of cross walls between daughter cells
- Several steps
  - selection of site for septum formation
  - assembly of Z ring
  - linkage of Z ring to plasma membrane (cell wall)
  - assembly of cell wall synthesizing machinery
  - constriction of cell and septum formation

# Z Ring Formation - Role in Septation

- Protein FtsZ
  - tubulin homologue, found in most bacteria and archaea
  - polymerization forms Z ring, filaments of meshwork
- MinCDE system in *E. coli* limits the Z ring to the center of the cell
  - MinC, MinD, MinE oscillate from one side of cell to other
  - link Z ring to cell membrane
  - Z ring constricts and cell wall synthesis of septal wall

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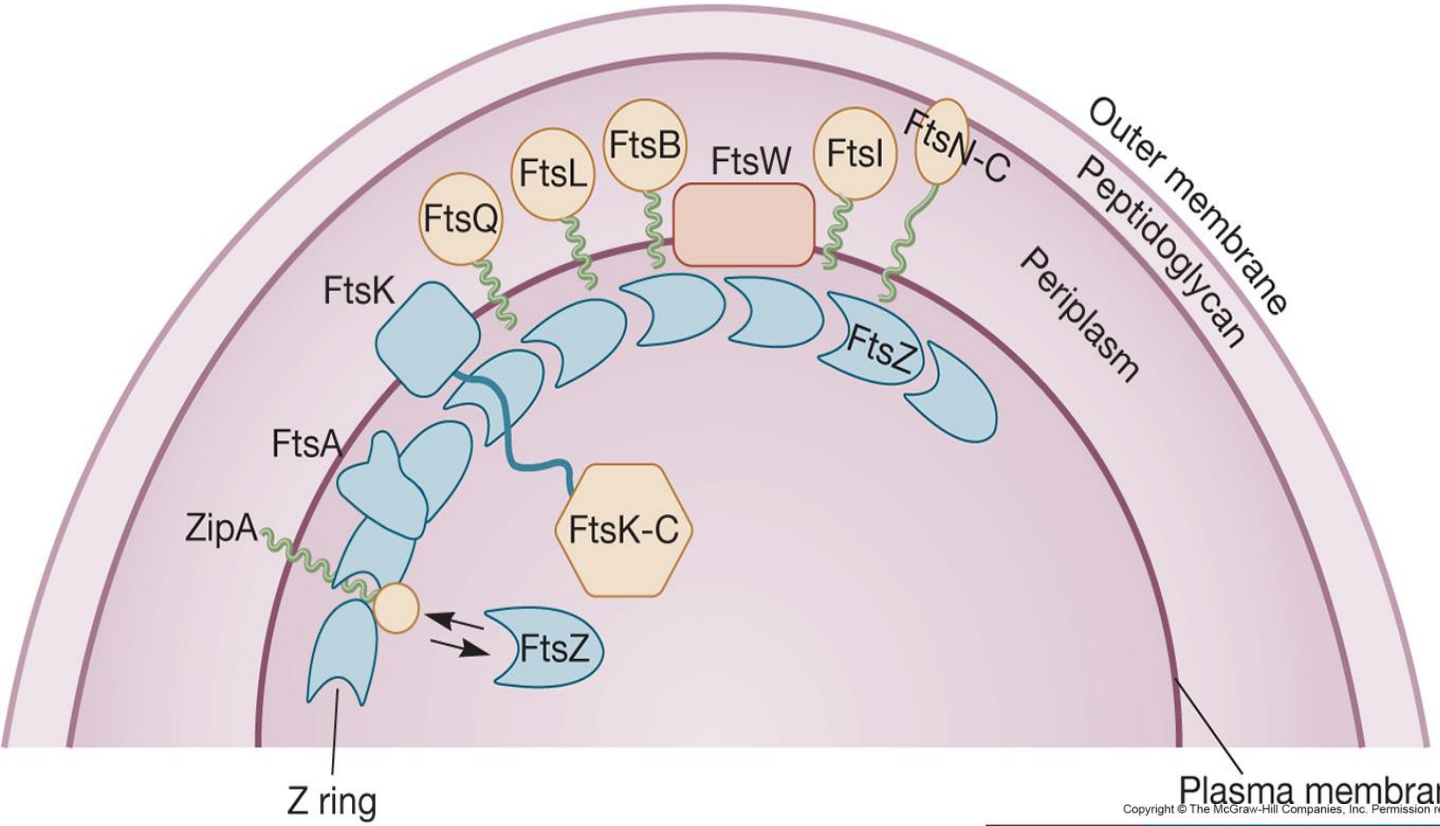




The *E. coli* divisome

**Table 7.1 Divisome Proteins and Their Functions**

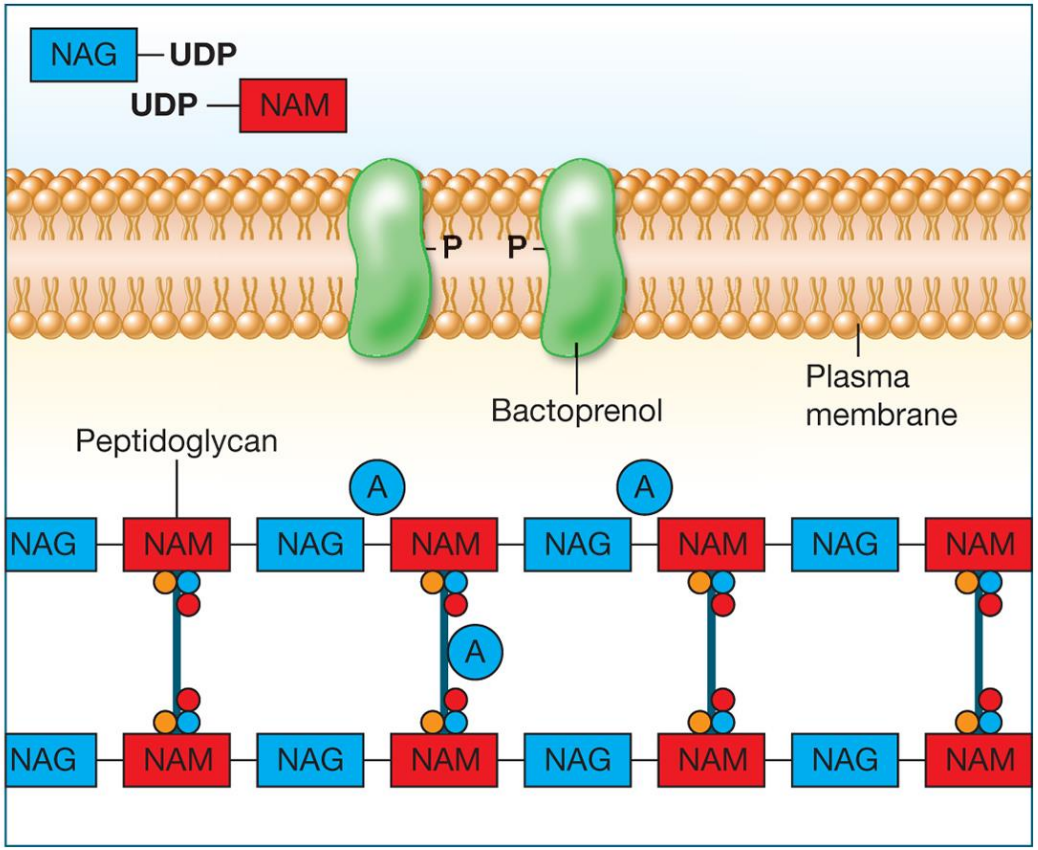
| Divisome Protein | Function |
|---|---|
| FtsA, ZipA | Anchor Z ring to plasma membrane |
| FtsZ | Forms Z ring |
| FtsK | Chromosome segregation and separation of chromosome dimers |
| FtsQLB | May provide a scaffold for assembly of proteins involved in peptidoglycan synthesis |
| FtsI[1], FtsW | Peptidoglycan synthesis |
| FtsN | Thought to trigger constriction initiation |

1 FtsI is also known as penicillin-binding protein 3 (PBP3).

1. **Peptidoglycan synthesis starts in the cytoplasm with the attachment of uridine diphosphate (UDP) to the sugar *N*-acetylglucosamine (NAG). Some of the UDP-NAG molecules are converted to UDP-NAM. Amino acid addition to NAM is not shown for simplicity.**

2. **NAM is transferred from UDP to bactoprenol, a carrier embedded in the plasma membrane. NAG is then attached to bactoprenol-NAM generating bactoprenol-NAM-NAG. Bactoprenol carries the NAM-NAG unit across the plasma membrane, delivering it to the periplasm.**

3. **Autolysins (cyan balls labeled "A") located at the divisome degrade bonds in the existing peptidoglycan sacculus. This permits the insertion of new NAM-NAG units into the sacculus.**



# 7.3 Influences of environmental factors on growth

1. Use the terms that describe a microbe's growth range or requirement for each of the factors that influence microbial growth
2. Summarize the adaptations of extremophiles to their natural habitats
3. Summarize the strategies used by nonextremophiles to acclimate to changes in their environment
4. Describe the enzymes observed in microbes that protect them against toxic $O_2$ products

# The Influence of Environmental Factors on Growth

- Most organisms grow in fairly moderate environmental conditions
- Extremophiles
  - grow under harsh conditions that would kill most other organisms

**Table 7.2 Microbial Responses to Environmental Factors**

| Descriptive Term | Definition | Representative Microorganisms |
|---|---|---|
| **Solute and Water Activity** | | |
| Osmotolerant | Able to grow over wide ranges of water activity or osmotic concentration | *Staphylococcus aureus, Saccharomyces rouxii* |
| Halophile | Requires high levels of sodium chloride, usually above about 0.2 M, to grow | *Halobacterium, Dunaliella, Ectothiorhodospira* |
| **pH** | | |
| Acidophile | Growth optimum between pH 0 and 5.5 | *Sulfolobus, Picrophilus, Ferroplasma, Acontium* |
| Neutrophile | Growth optimum between pH 5.5 and 8.0 | *Escherichia, Euglena, Paramecium* |
| Alkaliphile | Growth optimum between pH 8.0 and 11.5 | *Bacillus alcalophilus, Natronobacterium* |
| **Temperature** | | |
| Psychrophile | Grows at 0°C and has an optimum growth temperature of 15°C or lower | *Bacillus psychrophilus, Chlamydomonas nivalis* |
| Psychrotroph | Can grow at 0–7°C; has an optimum between 20 and 30°C and a maximum around 35°C | *Listeria monocytogenes, Pseudomonas fluorescens* |
| Mesophile | Has growth optimum between 20 and 45°C | *Escherichia coli, Trichomonas vaginalis* |
| Thermophile | Can grow at 55°C or higher; optimum often between 55 and 65°C | *Geobacillus stearothermophilus, Thermus aquaticus, Cyanidium caldarium, Chaetomium thermophile* |
| Hyperthermophile | Has an optimum between 85 and about 113°C | *Sulfolobus, Pyrococcus, Pyrodictium* |
| **Oxygen Concentration** | | |
| Obligate aerobe | Completely dependent on atmospheric $O_2$ for growth | *Micrococcus luteus,* most protists and fungi |
| Facultative anaerobe | Does not require $O_2$ for growth but grows better in its presence | *Escherichia, Enterococcus, Saccharomyces cerevisiae* |
| Aerotolerant anaerobe | Grows equally well in presence or absence of $O_2$ | *Streptococcus pyogenes* |
| Obligate anaerobe | Does not tolerate $O_2$ and dies in its presence | *Clostridium, Bacteroides, Methanobacterium* |
| Microaerophile | Requires $O_2$ levels between 2–10% for growth and is damaged by atmospheric $O_2$ levels (20%) | *Campylobacter, Spirillum volutans, Treponema pallidum* |
| **Pressure** | | |
| Piezophile (barophile) | Growth more rapid at high hydrostatic pressures | *Photobacterium profundum, Shewanella benthica* |

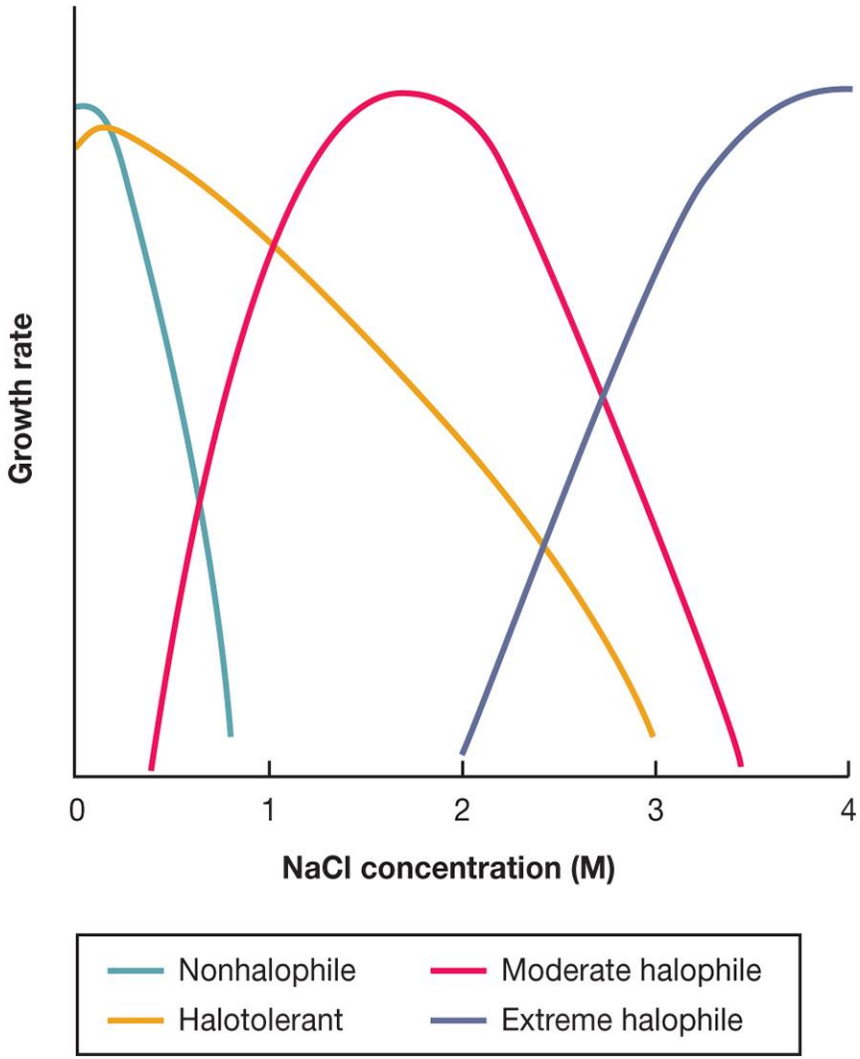
# Extremely Adapted Microbes

- Halophiles
  - grow optimally in the presence of NaCl or other salts at a concentration above about 0.2M
- Extreme halophiles
  - require salt concentrations of 2M and 6.2M
  - extremely high concentrations of potassium
  - cell wall, proteins, and plasma membrane require high salt to maintain stability and activity

# Effects of NaCl on Microbial Growth

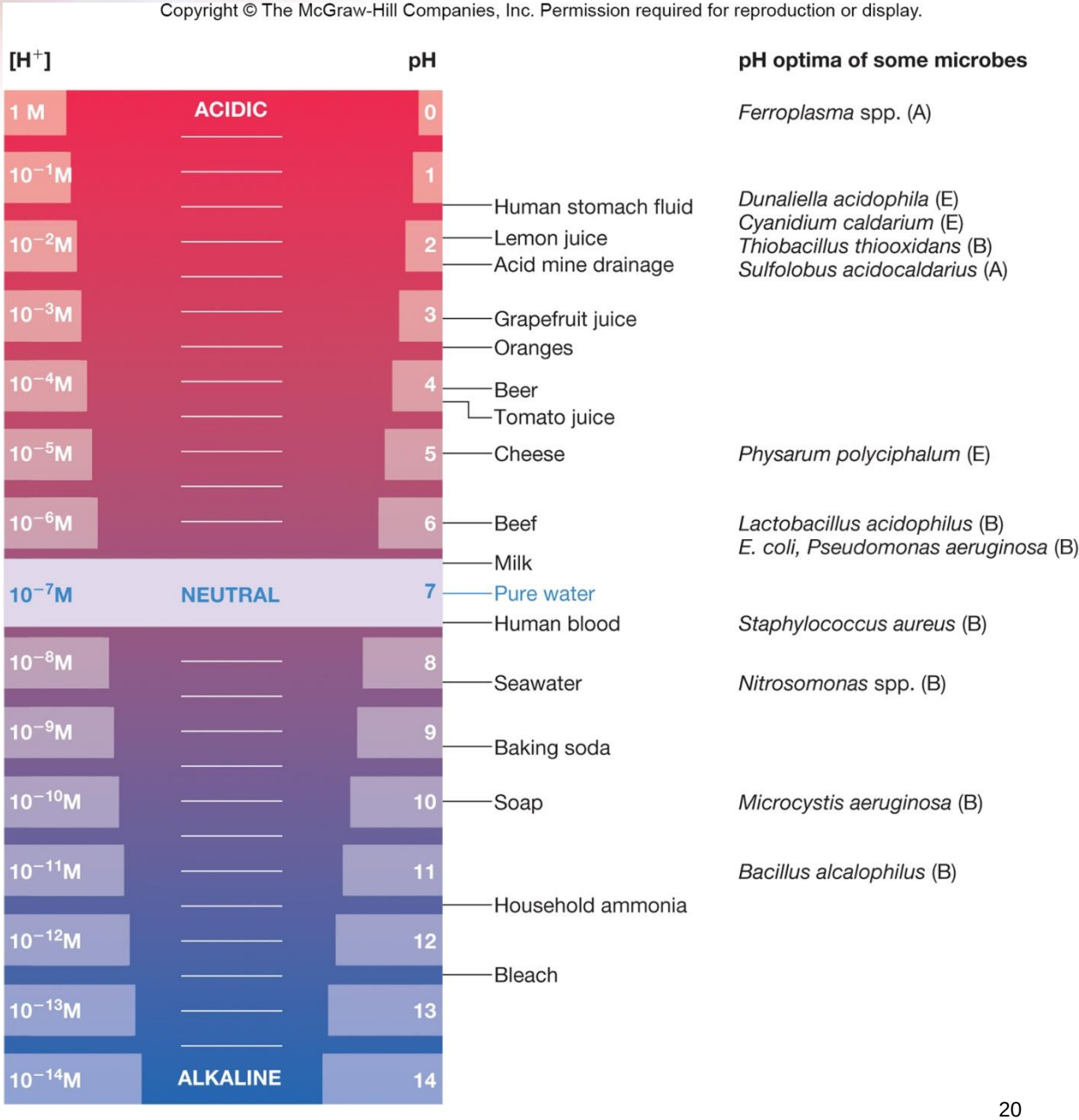


- Halophiles
  - grow optimally at >0.2 M
- Extreme halophiles
  - require >2 M



# pH

- measure of the relative acidity of a solution
- negative logarithm of the hydrogen ion concentration



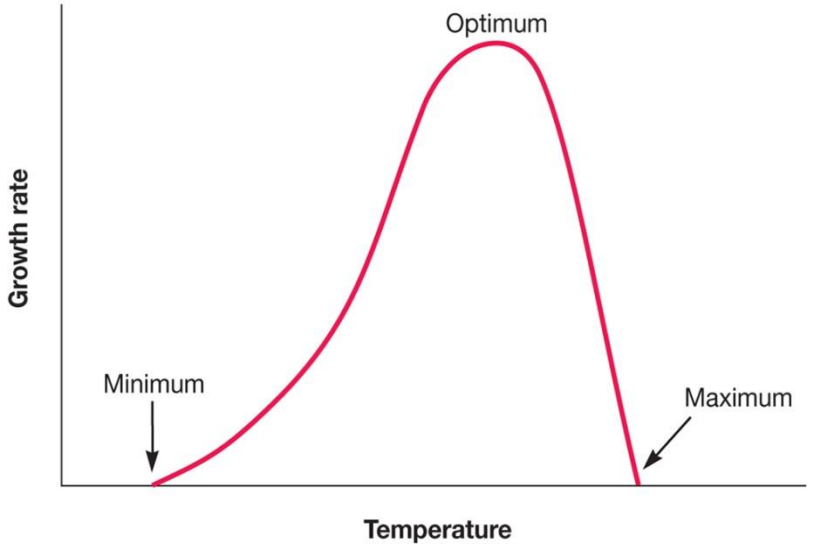
# pH

- Acidophiles
  - growth optimum between pH 0 and pH 5.5
- Neutrophiles
  - growth optimum between pH 5.5 and pH 7
- Alkaliphiles (alkalophiles)
  - growth optimum between pH 8.5 and pH 11.5

# Temperature

- Microbes cannot regulate their internal temperature
- Enzymes have optimal temperature at which they function optimally
- High temperatures may inhibit enzyme functioning and be lethal
- Organisms exhibit distinct cardinal growth temperatures
  - minimal
  - maximal
  - optimal





# Temperature Ranges for Microbial Growth

- psychrophiles – 0º C to 20º C
- psychrotrophs – 0º C to 35º C
- mesophiles – 20º C to 45º C
- thermophiles – 55º C to 85º C
- hyperthermophiles – 85º C to 113º C



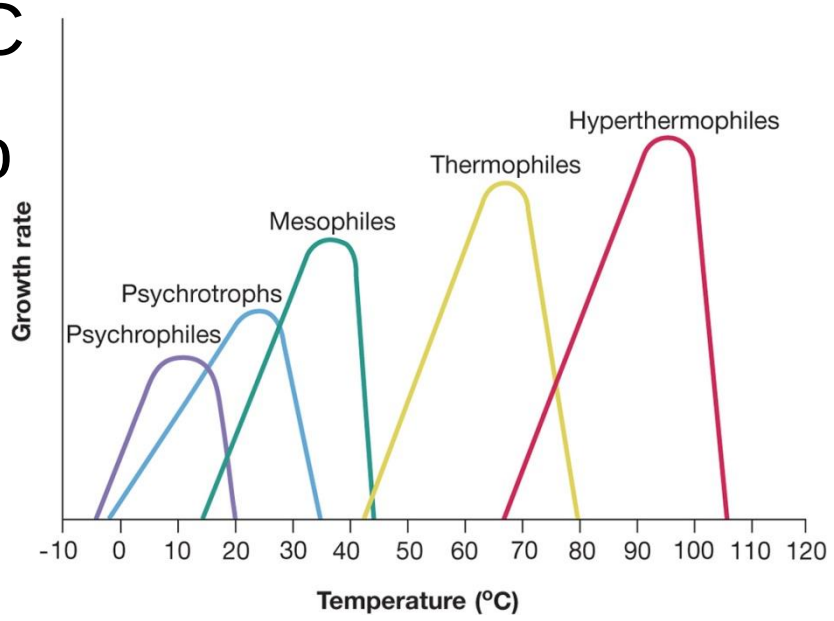


**Table 7.3 Temperature Ranges for Microbial Growth**

| | CARDINAL TEMPERATURES (°C) | | |
|---|---|---|---|
| **Microorganism** | **Minimum** | **Optimum** | **Maximum** |
| ***Nonphotosynthetic Bacteria and Archaea*** | | | |
| *Bacillus psychrophilus* | –10 | 23–24 | 28–30 |
| *Pseudomonas fluorescens* | 4 | 25–30 | 40 |
| *Enterococcus faecalis* | 0 | 37 | 44 |
| *Escherichia coli* | 10 | 37 | 45 |
| *Neisseria gonorrhoeae* | 30 | 35–36 | 38 |
| *Thermoplasma acidophilum* | 45 | 59 | 62 |
| *Thermus aquaticus* | 40 | 70–72 | 79 |
| *Pyrococcus abyssi* | 67 | 96 | 102 |
| *Pyrodictium occultum* | 82 | 105 | 110 |
| *Pyrolobus fumarii* | 90 | 106 | 113 |
| ***Photosynthetic Bacteria*** | | | |
| *Anabaena variabilis* | ND[1] | 35 | ND |
| *Synechococcus eximius* | 70 | 79 | 84 |
| ***Protists*** | | | |
| *Chlamydomonas nivalis* | –36 | 0 | 4 |
| *Amoeba proteus* | 4–6 | 22 | 35 |
| *Skeletonema costatum* | 6 | 16–26 | >28 |
| *Trichomonas vaginalis* | 25 | 32–39 | 42 |
| *Tetrahymena pyriformis* | 6–7 | 20–25 | 33 |
| *Cyclidium citrullus* | 18 | 43 | 47 |
| ***Fungi*** | | | |
| *Candida scotti* | 0 | 4–15 | 15 |
| *Saccharomyces cerevisiae* | 1–3 | 28 | 40 |
| *Mucor pusillus* | 21–23 | 45–50 | 50–58 |

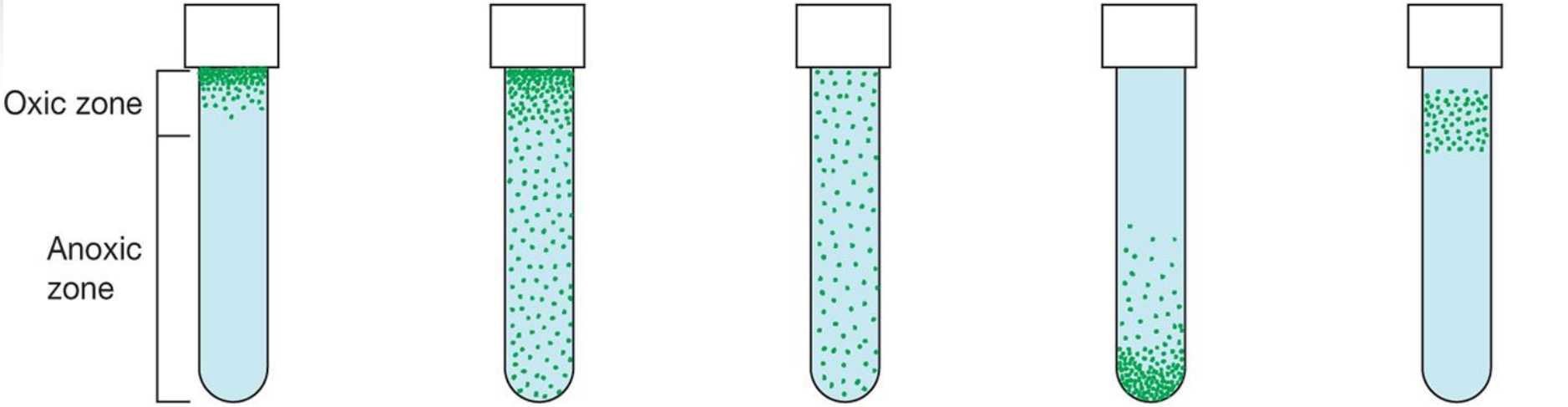
1 ND, not determined.

# Adaptations of Thermophiles

- Protein structure stabilized by a variety of means
  - e.g., more H bonds
  - e.g., more proline
  - e.g., chaperones
- Histone-like proteins stabilize DNA
- Membrane stabilized by variety of means
  - e.g., more saturated, more branched and higher molecular weight lipids
  - e.g., ether linkages (archaeal membranes)

# Oxygen Concentration

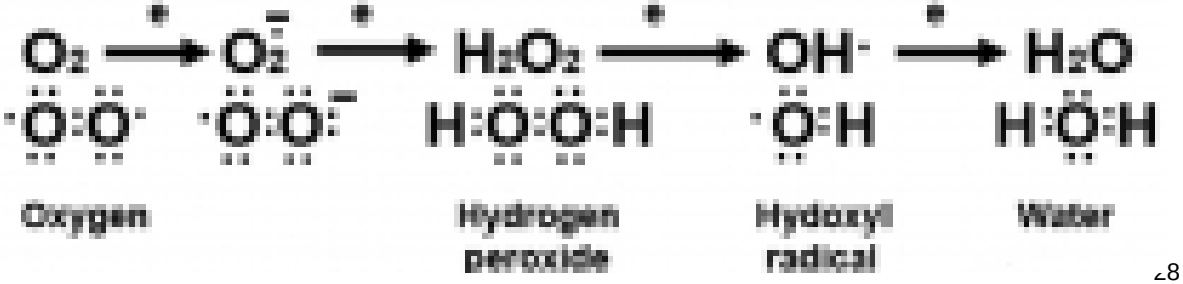
- growth in oxygen correlates with microbes energy conserving metabolic processes and the electron transport chain (ETC) and nature of terminal electron acceptor




| | Obligate aerobe | Facultative anaerobe | Aerotolerant anaerobe | Strict anaerobe | Microaerophile |
|---|---|---|---|---|---|
| **Enzyme content** | | | | | |
| | + SOD<br>+ Catalase | + SOD<br>+ Catalase | + SOD<br>– Catalase | – SOD<br>– Catalase | + SOD<br>+/– Catalase (low levels) |

# Basis of Different Oxygen Sensitivities

- Oxygen easily reduced to toxic reactive oxygen species (ROS)
  - superoxide radical
  - hydrogen peroxide
  - hydroxyl radical
- Aerobes produce protective enzymes
  - superoxide dismutase (SOD)
  - catalase
  - peroxidase



# Strict Anaerobic Microbes

- All strict anaerobic microorganisms lack or have very low quantities of
  - superoxide dismutase
  - catalase
- These microbes cannot tolerate $O_2$
- Anaerobes must be grown without $O_2$
  - work station with incubator
  - gaspak anaerobic system

# Pressure

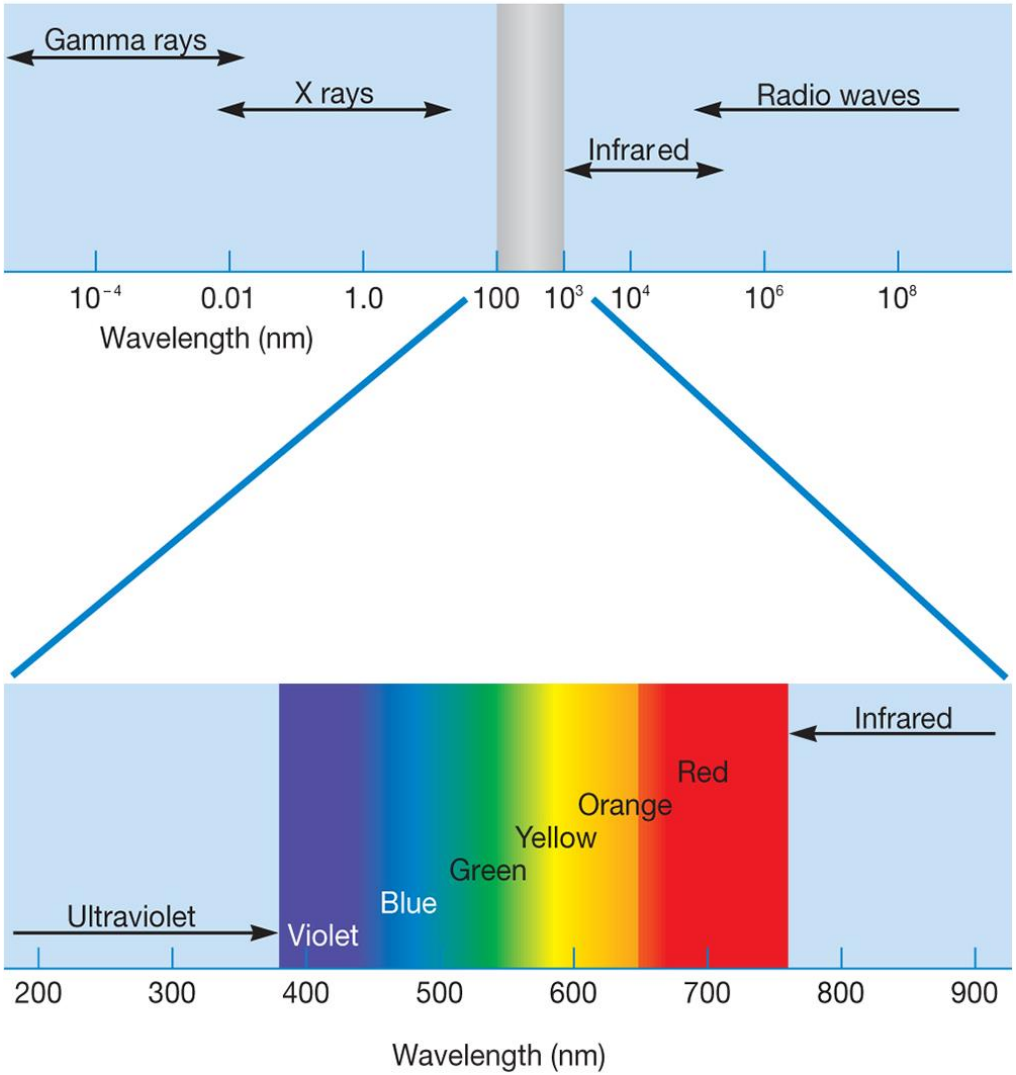
- Microbes that live on land and water surface live at 1 atmosphere (atm)
- Some *Bacteria* and *Archaea* live in deep sea with very high hydrostatic pressures

# Pressure

- Barotolerant
  - adversely affected by increased pressure, but not as severely as nontolerant organisms
- Barophilic (peizophilic) organisms
  - require or grow more rapidly in the presence of increased pressure
  - change membrane fatty acids to adapt to high pressures

- The Electromagnetic Spectrum





# Radiation Damage

- Ionizing radiation
  - x-rays and gamma rays
  - mutations → death (sterilization)
  - disrupts chemical structure of many molecules, including DNA
    - damage may be repaired by DNA repair mechanisms if small dose
  - *Deinococcus radiodurans*
    - extremely resistant to DNA damage

# Radiation Damage…

- Ultraviolet (UV) radiation
  - wavelength most effectively absorbed by DNA is 260 nm
  - mutations $\rightarrow$ death
  - causes formation of thymine dimers in DNA
  - requires direct exposure on microbial surface
  - DNA damage can be repaired by several repair mechanisms

# Radiation Damage…

- Visible light
  - at high intensities generates singlet oxygen ($^1O_2$)
    - powerful oxidizing agent
  - carotenoid pigments
    - protect many light-exposed microorganisms from photooxidation

# 7.4 Microbial growth in natural environments

1. Discuss the mechanisms used by microbes to survive starvation
2. Distinguish sessile and planktonic microbial life styles
3. Describe the formation of biofilms and summarize their importance in natural environments, industrial settings, and medicine
4. Define quorum sensing and provide examples of cellular processes regulated by quorum sensing
5. Discuss in general terms the communication that occurs between rhizobia and their plant hosts

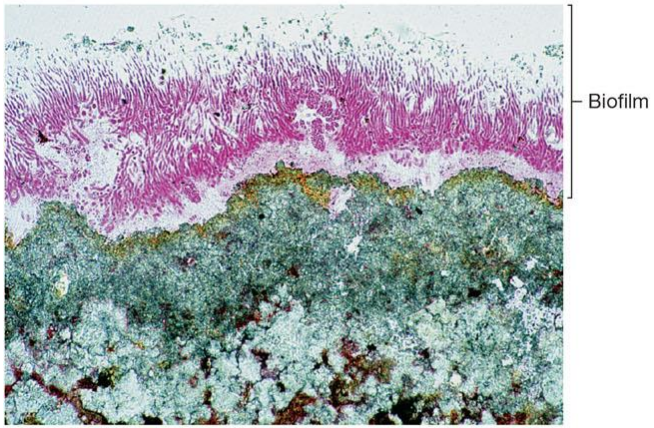
# Microbial Growth in Natural Environments

- Microbial environments are complex, constantly changing, often contain low nutrient concentrations (oligotrophic environment) and may expose a microorganism to overlapping gradients of nutrients and environmental factors

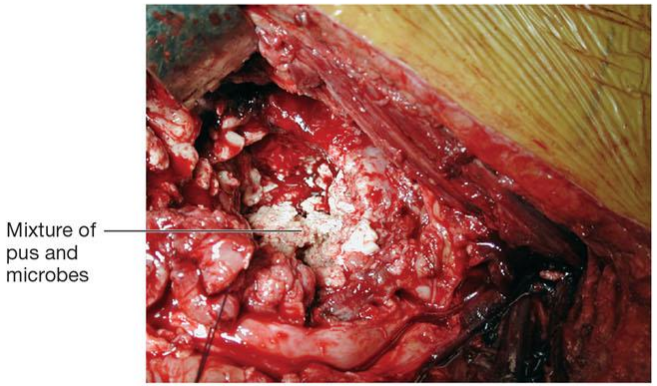
# Biofilms

- Most microbes grow attached to surfaces (sessile) rather than free floating (planktonic)
- These attached microbes are members of complex, slime enclosed communities called a biofilm
- Biofilms are ubiquitous in nature in water
- Can be formed on any conditioned surface



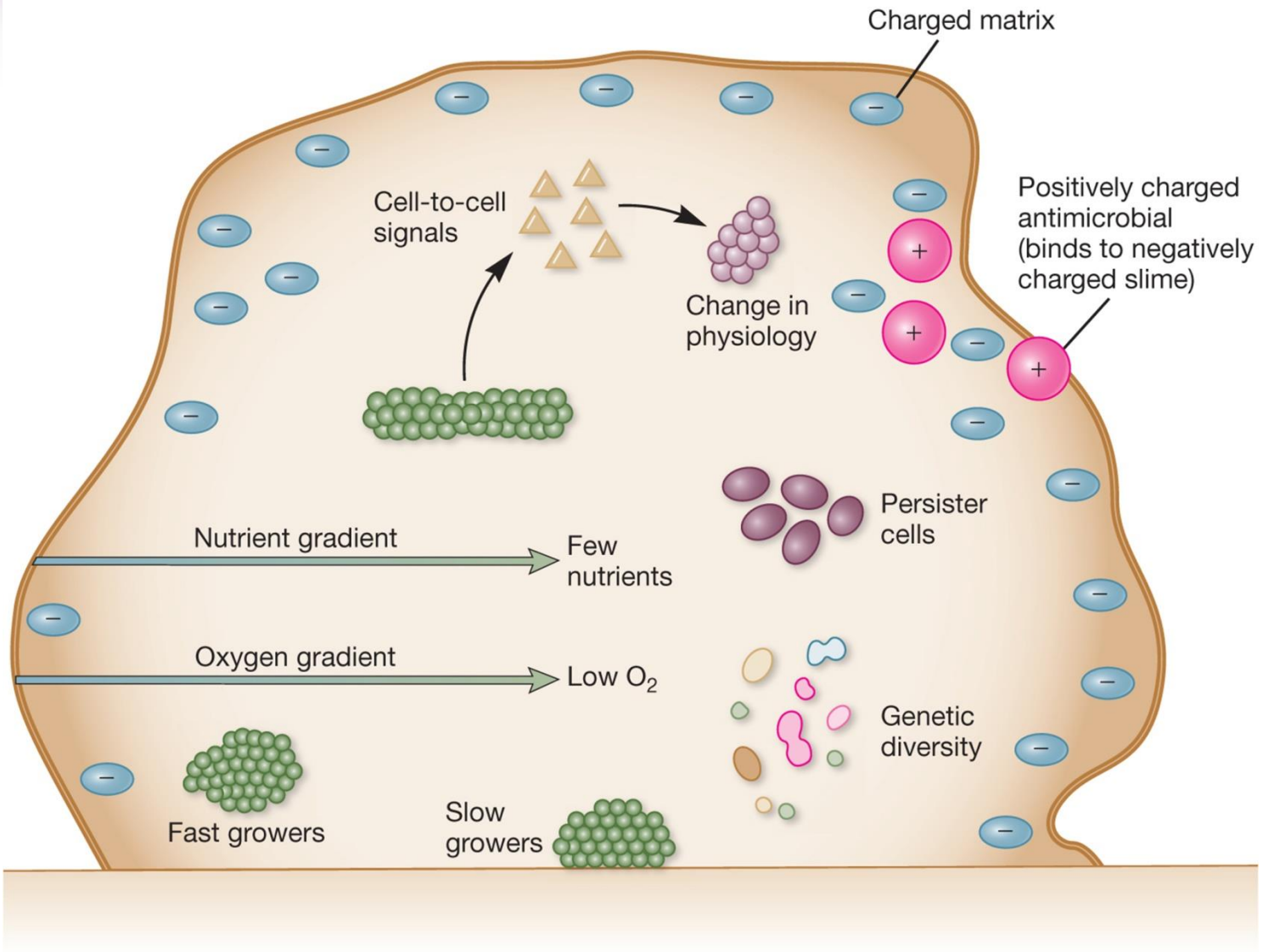



**(a)** Biofilm on surface of a stromatolite



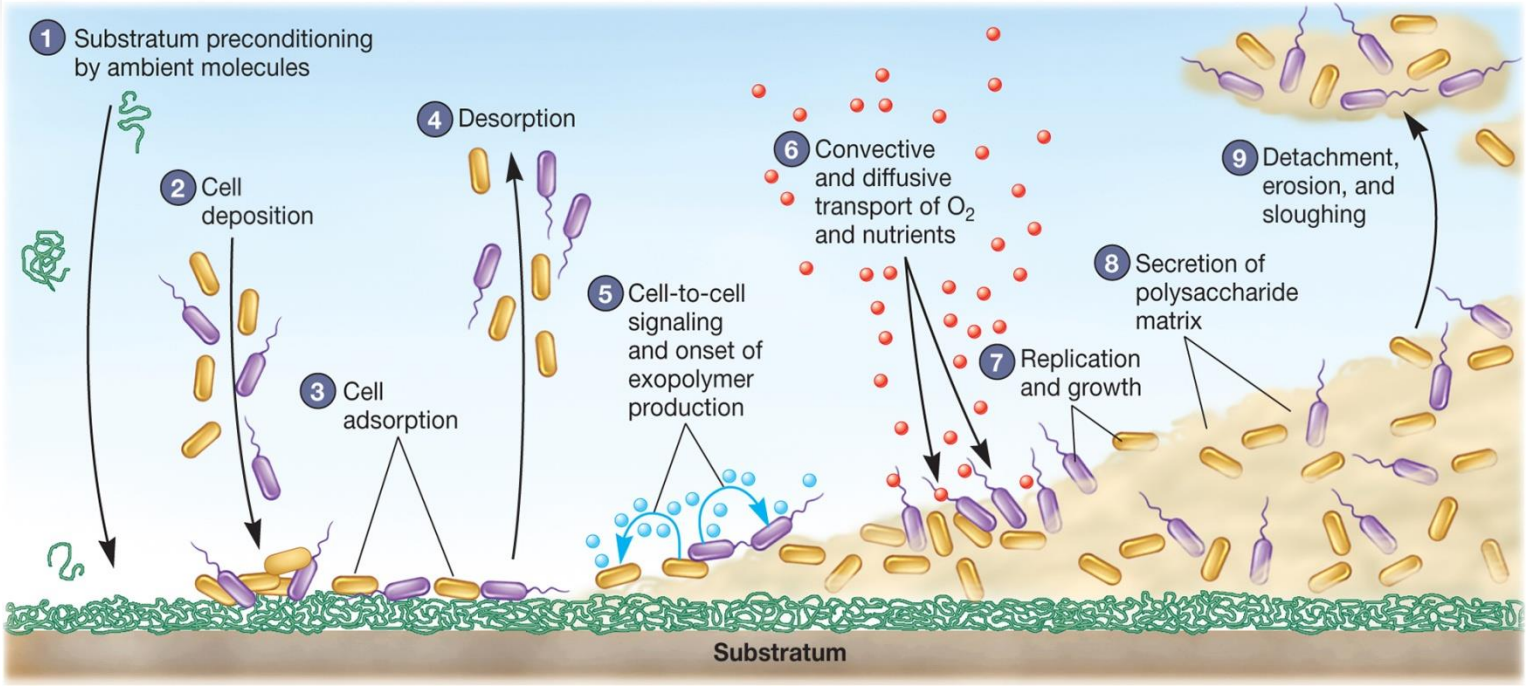

**(b)** Infected tissue after hip replacement

a: Dr. Joachim Reitner; b: Courtesy Nicholas G. Sotereanos, M.D.



# Biofilm Formation






- Microbes reversibly attach to conditioned surface and release polysaccharides, proteins, and DNA to form the extracellular polymeric substance (EPS)
- Additional polymers are produced as microbes reproduce and biofilm matures

# Biofilms

- a mature biofilm is a complex, dynamic community of microorganisms
- heterogeneity is differences in metabolic activity and locations of microbes
- interactions occur among the attached organisms
  - exchanges take place metabolically, DNA uptake and communication

# Biofilm Microorganisms

- The EPS and change in attached organisms' physiology protects microbes from harmful agents
  - UV light, antibiotics, antimicrobials
- When formed on medical devices, such as implants, often lead to illness
- Sloughing off of organisms can result in contamination of water phase above the biofilm such as in a drinking water system

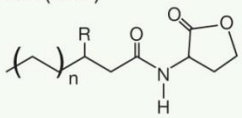
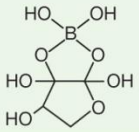
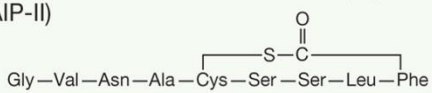
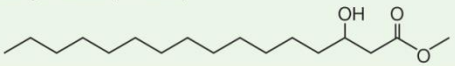
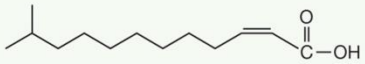
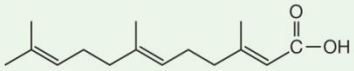
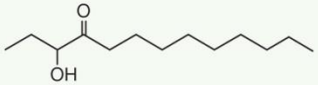
# Cell to Cell Communication Within the Microbial Populations

- Bacterial cells in biofilms communicate in a density-dependent manner called quorum sensing
- Produce small proteins that increase in concentration as microbes replicate and convert a microbe to a competent state
  - DNA uptake occurs, bacteriocins are released

# Quorum Sensing

- Acylhomoserine lactone (AHL) is an autoinducer molecule produced by many gram-negative organisms
  - diffuses across plasma membrane
  - once inside the cell, induces expression of target genes regulating a variety of functions



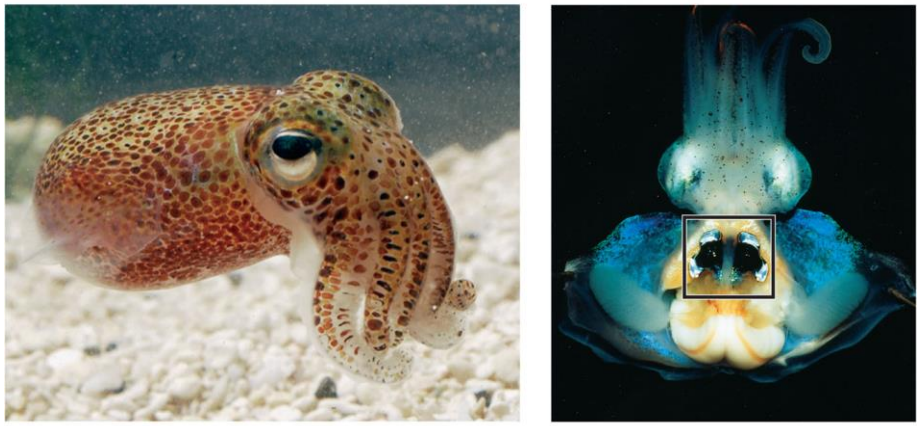
| Signal and Structure | Representative Organism | Function Regulated |
|---|---|---|
| *N*-acylhomoserine lactone (AHL)  | *Vibrio fischeri*<br>*Agrobacterium tumefaciens*<br>*Erwinia carotovora*<br>*Pseudomonas aeruginosa*<br>*Burkholderia cepacia* | Bioluminescence<br>Plasmid transfer<br>Virulence and antibiotic production<br>Virulence and biofilm formation<br>Virulence |
| Furanosylborate (AI-2)  | *Vibrio harveyi*[a] | Bioluminescence |
| Cyclic thiolactone (AIP-II)  | *Staphylococcus aureus* | Virulence |
| Hydroxy-palmitic acid methyl ester (PAME)  | *Ralstonia solanacearum* | Virulence |
| Methyl dodecenoic acid  | *Xanthomonas campestris* | Virulence |
| Farnesoic acid  | *Candida albicans* | Dimorphic transition and virulence |
| 3-hydroxytridecan-4-one  | *Vibrio cholerae* | Virulence |

[a] Other bacteria make a form of AI-2 that lacks boron.

# Quorum Sensing Systems

- Processes regulated by quorum sensing involve host-microbe interactions
  - symbiosis – *Vibrio fischeri* and bioluminescence in squid
  - pathogenicity and increased virulence factor production
  - DNA uptake for antibiotic resistance genes





**(a)** *E. scolopes*, the bobtail squid **(b)** Light organ

a: Chris Frazee, UW-Madison; b: Courtesy Dr. Margaret Jean McFall-Ngai

# 7.6 Growth curve: When one becomes two and two become four… - 1

1. Describe the four phases of a microbial growth curve observed when microbes are grown in a batch culture
2. Describe three hypotheses proposed to account for the decline in cell numbers during the death phase of a growth curve
3. Predict how the presence of viable but nonculturable cells in food or water systems might impact public health

# 7.6 Growth curve: When one becomes two and two become four… - 2

4. Correlate changes in nutrient concentrations in natural environments with the four phases of a microbial growth curve
5. Relate growth rate constant to generation (doubling) time and suggest how these values might be used by microbiologists doing basic research or working in industrial settings

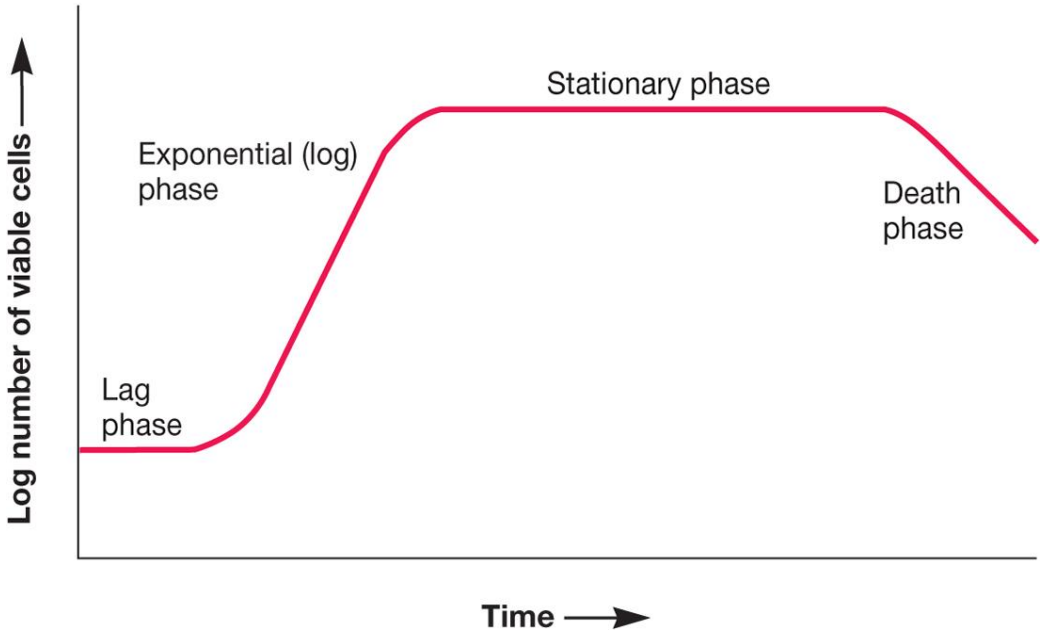
# Growth

- Increase in cellular constituents that may result in:
  - increase in cell number
  - increase in cell size
- Growth refers to population growth rather than growth of individual cells

# The Growth Curve

- Observed when microorganisms are cultivated in batch culture
- Usually plotted as logarithm of cell number versus time
- Has four distinct phases





# Lag Phase

- Cell synthesizing new components
  - e.g., to replenish spent materials
  - e.g., to adapt to new medium or other conditions
- Varies in length
  - in some cases can be very short or even absent

# Exponential Phase

- Also called log phase
- Rate of growth and division is constant and maximal
- Population is most uniform in terms of chemical and physical properties during this phase

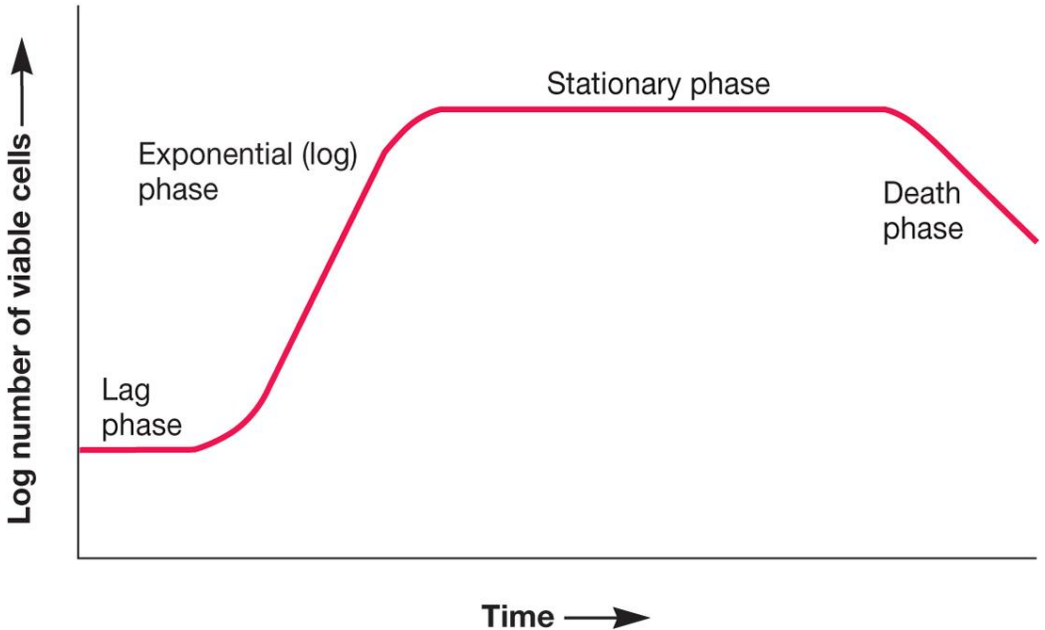
# Balanced Growth

- During log phase, cells exhibit balanced growth
  - cellular constituents manufactured at constant rates relative to each other

# The Growth Curve

- Observed when microorganisms are cultivated in batch culture
- Usually plotted as logarithm of cell number versus time
- Has four distinct phases

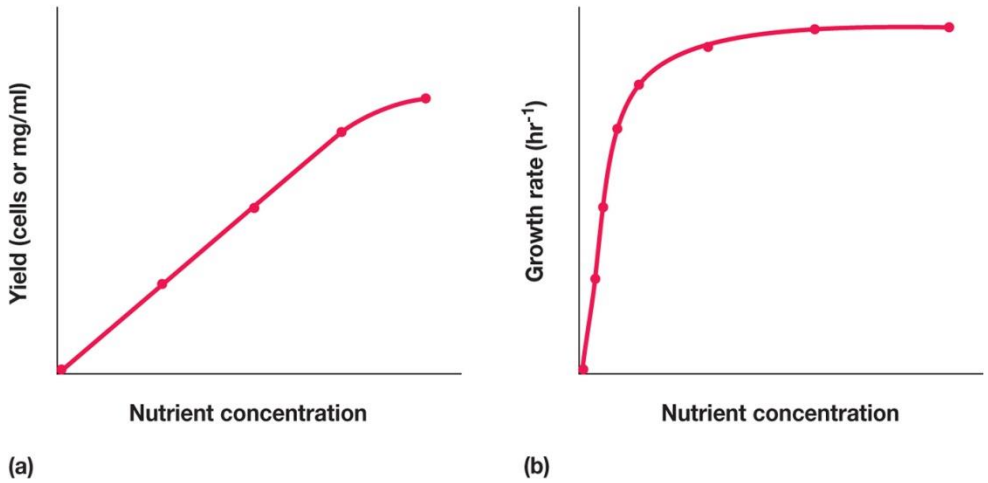




# Unbalanced Growth

- Rates of synthesis vary relative to each other
- Occurs under a variety of conditions
  - change in nutrient levels
    - shift-up (poor medium to rich medium)
    - shift-down (rich medium to poor medium)
  - change in environmental conditions





# Stationary Phase

- Closed system population growth eventually ceases, total number of viable cells remains constant
  - active cells stop reproducing or reproductive rate is balanced by death rate

# Possible Reasons for Stationary Phase

- Nutrient limitation
- Limited oxygen availability
- Toxic waste accumulation
- Critical population density reached

# Stationary Phase and Starvation Response

- Entry into stationary phase due to starvation and other stressful conditions activates survival strategy
  - morphological changes
    - e.g., endospore formation
  - decrease in size, protoplast shrinkage, and nucleoid condensation
  - RpoS protein assists RNA polymerase in transcribing genes for starvation proteins

# Starvation Responses

- Production of starvation proteins
  - increase cross-linking in cell wall
  - Dps protein protects DNA
  - chaperone proteins prevent protein damage
- Cells are called persister cells
  - long-term survival
  - increased virulence

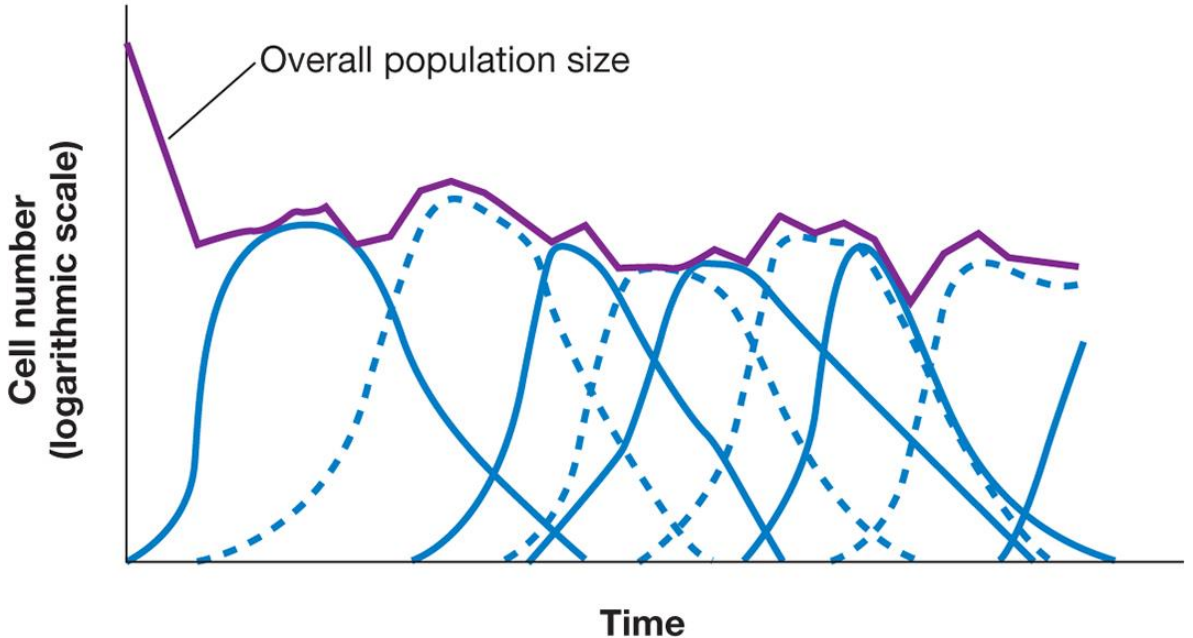
# Senescence and Death Phase

- Two alternative hypotheses
  - cells are Viable But Not Culturable (VBNC)
    - cells alive, but dormant, capable of new growth when conditions are right
- Programmed cell death
  - fraction of the population genetically programmed to die (commit suicide)

# Prolonged Decline in Growth

- Bacterial population continually evolves
- Process marked by successive waves of genetically distinct variants
- Natural selection occurs





# The Mathematics of Growth

- Generation (doubling) time
  - time required for the population to double in size
  - varies depending on species of microorganism and environmental conditions
  - range is from 10 minutes for some bacteria to several days for some eukaryotic microorganisms

## Table 7.8 An Example of Exponential Growth

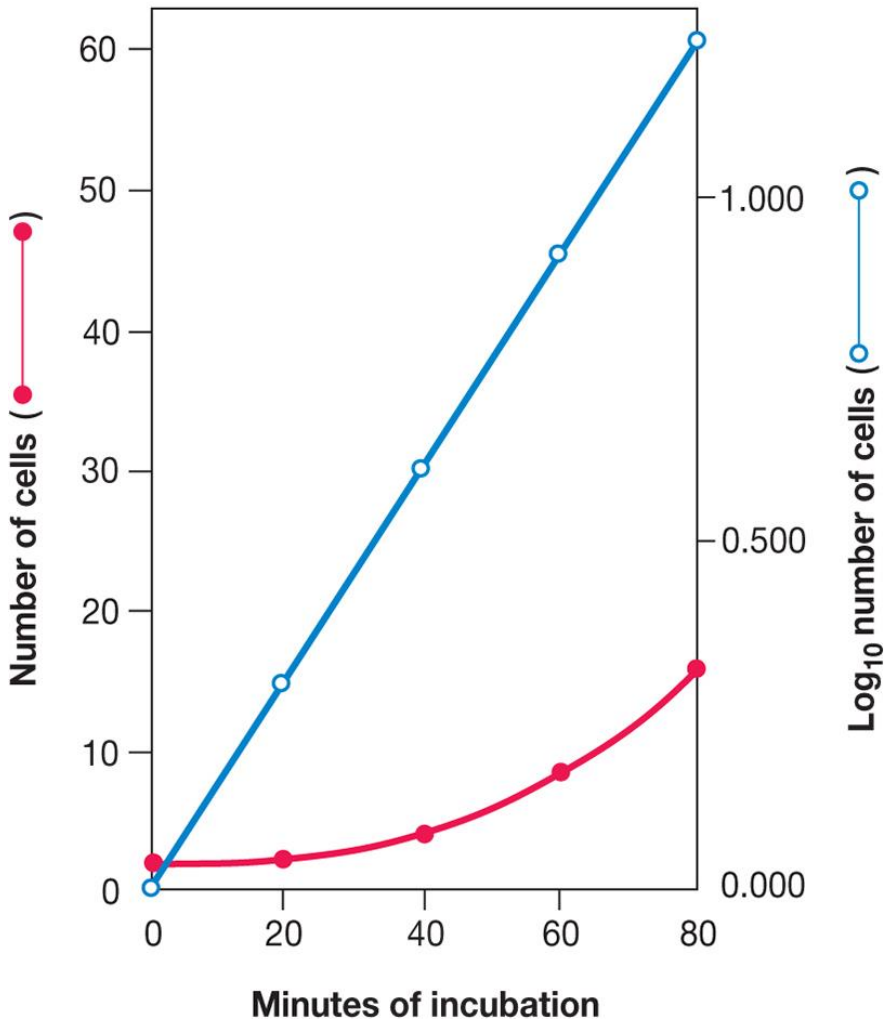
| Time[1] | Division Number | $2^n$ | Population[2] ($N_0 \times 2^n$) | $\log_{10} N_t$ |
|---|---|---|---|---|
| 0 | 0 | $2^0 = 1$ | 1 | 0.000 |
| 20 | 1 | $2^1 = 2$ | 2 | 0.301 |
| 40 | 2 | $2^2 = 4$ | 4 | 0.602 |
| 60 | 3 | $2^3 = 8$ | 8 | 0.903 |
| 80 | 4 | $2^4 = 16$ | 16 | 1.204 |

1 The hypothetical culture begins with one cell having a 20-minute generation time.
2 Number of cells in the culture.

# Exponential Population Growth

- Population is doubling every generation





# Measurement of Growth Rate and Generation Time



**Calculation of the growth rate constant**

Let $N_0$ = the initial population number

$N_t$ = the population at time $t$

$n$ = the number of generations in time $t$

For populations reproducing by binary fission

$$N_t = N_0 \times 2^n$$

Solving for $n$, the number of generations, where all logarithms are to the base 10,

$$\log N_t = \log N_0 + n \cdot \log 2, \text{ and}$$

$$n = \frac{\log N_t - \log N_0}{\log 2} = \frac{\log N_t - \log N_0}{0.301}$$

The growth rate constant ($k$) is the number of generations per unit time $\left(\frac{n}{t}\right)$. Thus

$$k = \frac{n}{t} = \frac{\log N_t - \log N_0}{0.301t}$$

**Calculation of generation (doubling) time**

If a population doubles, then

$$N_t = 2N_0$$

Substitute $2N_0$ into the growth rate constant equation and solve for

$$k = \frac{\log (2N_0) - \log N_0}{0.301g} = \frac{\log 2 + \log N_0 - \log N_0}{0.301g}$$

$$k = \frac{1}{g}$$

The generation time is the reciprocal of the growth rate constant.

$$g = \frac{1}{k}$$

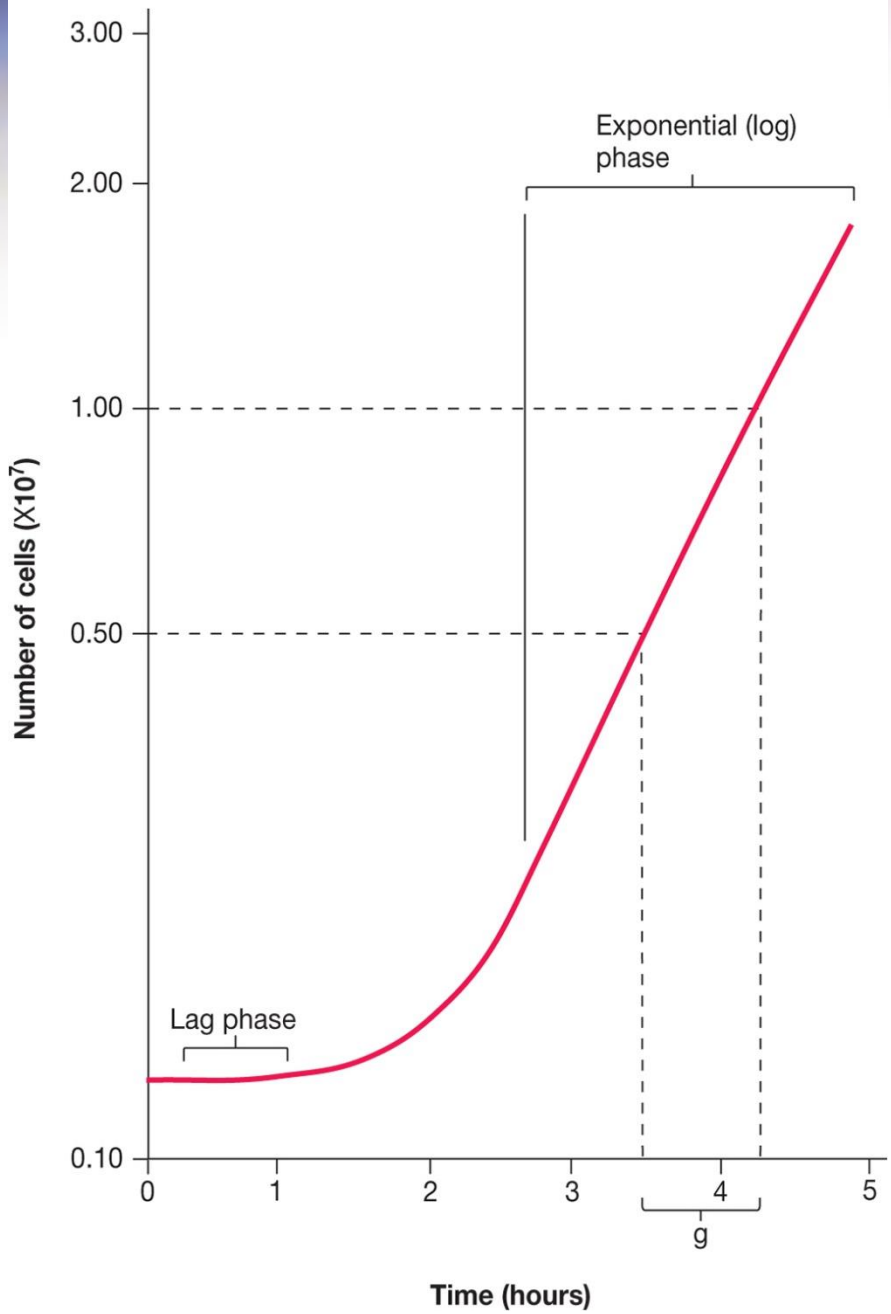





**Table 7.9 Examples of Generation Times[1]**

| Microorganism | Incubation Temperature (°C) | Generation Time (Hours) |
|---|---|---|
| **Bacteria** | | |
| *Escherichia coli* | 40 | 0.35 |
| *Bacillus subtilis* | 40 | 0.43 |
| *Staphylococcus aureus* | 37 | 0.47 |
| *Pseudomonas aeruginosa* | 37 | 0.58 |
| *Clostridium botulinum* | 37 | 0.58 |
| *Mycobacterium tuberculosis* | 37 | ≈12 |
| *Treponema pallidum* | 37 | 33 |
| **Protists** | | |
| *Tetrahymena geleii* | 24 | 2.2–4.2 |
| *Chlorella pyrenoidosa* | 25 | 7.75 |
| *Paramecium caudatum* | 26 | 10.4 |
| *Euglena gracilis* | 25 | 10.9 |
| *Giardia lamblia* | 37 | 18 |
| *Ceratium tripos* | 20 | 82.8 |
| **Fungi** | | |
| *Saccharomyces cerevisiae* | 30 | 2 |
| *Monilinia fructicola* | 25 | 30 |

# 7.8 Continuous culture of microorganisms

1. Distinguish batch culture and continuous culture
2. Differentiate chemostats and turbidostats
3. Discuss the relationship between the dilution rate of a chemostat and population size and growth rate

# The Continuous Culture of Microorganisms

- Growth in an open system
  - continual provision of nutrients
  - continual removal of wastes
- Maintains cells in log phase at a constant biomass concentration for extended periods
- Achieved using a continuous culture system

# Importance of Continuous Culture Methods

- Constant supply of cells in exponential phase growing at a known rate
- Study of microbial growth at very low nutrient concentrations, close to those present in natural environment
- Study of interactions of microbes under conditions resembling those in aquatic environments
- Food and industrial microbiology

# The Chemostat

- Rate of incoming medium = rate of removal of medium from vessel
- An essential nutrient is in limiting quantities