Distributions, abundance, and activities of marine bacteria
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Marine Microplankton Ecology
OCN 626

“The evolution of a given material system is a process which may be expressed as the progressive change in the distribution of matter among specific components of the said material system...”

Alfred J. Lotka (1911)
Outline

1. Defining the terms – biomass, productivity, and growth
2. Methods of measuring cell abundance, volumes, biomass
3. Distribution of bacterial biomass in the world’s oceans
4. Bacterial growth and production
The Microbial Loop: A central theme in marine microplankton ecology

Classic Food web

Phytoplankton

Herbivores

Higher trophic levels (zooplankton, fish, etc.)

A simplified depiction of the microbial loop

Inorganic Nutrients

Dissolved organic matter

Heterotrophic bacteria

Protozoa
Microbial Loop

• Heterotrophic bacterial growth results in recovery of non-living pool of dissolved organic matter back into living pool of biomass.
• Transfer of bacterial biomass to higher trophic levels
• Remineralization of nutrients through the various stages of growth and predation.
Bacterial growth regulates fluxes of carbon and nutrients, and dictates energy flow through marine ecosystems.
To determine the importance of microbes to ocean food webs/carbon/nutrient fluxes, we need to:

1. **Quantify bacterial population size and mass**  
   • Biomass, abundance, cell sizes

2. **Quantify growth rates and production**  
   • Biomass production, respiration, cell division, and turnover

3. **Understand factors limiting microbial growth**  
   • Metabolic flexibility, physiology
The importance of the microbial loop in different marine ecosystems depends on at least four factors:

1. The rate that DOC is produced

2. The rate that bacteria convert DOC into biomass (this is bacterial production)

3. The rate that DOC is respired during growth

4. The rate of bacterial removal and subsequent passage of material to higher trophic levels
What is it we want to know?

• **Carbon fluxes** (bacterial production, respiration, DOC utilization rates)

• **Bacterial growth** (cell physiology, nutritional status)

• **Standing biomass** (biogenic carbon, trophic linkages)
## The Elemental Composition of *E. coli*

<table>
<thead>
<tr>
<th>Element</th>
<th>% dry</th>
<th>Substrate Source</th>
<th>Cellular Components</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>55</td>
<td>DOC, CO₂</td>
<td>Main constituent of cellular material</td>
</tr>
<tr>
<td>O</td>
<td>20</td>
<td>O₂, DOM, CO₂</td>
<td>Constituent of cell material and cell water; O₂ primary electron acceptor in aerobic respiration</td>
</tr>
<tr>
<td>N</td>
<td>10</td>
<td>NH₃, NO₃⁻, NO₂⁻, DON, N₂</td>
<td>Constituent of amino acids, nucleic acids, nucleotides, and coenzymes</td>
</tr>
<tr>
<td>H</td>
<td>8</td>
<td>DOM, H₂</td>
<td>Main constituent of organic compounds and cell water</td>
</tr>
<tr>
<td>P</td>
<td>3</td>
<td>PO₄³⁻, DOP</td>
<td>Constituent of nucleic acids, nucleotides, phospholipids, LPS, teichoic acids in gram positives</td>
</tr>
<tr>
<td>S</td>
<td>1</td>
<td>SO₄, H₂S, HS, DOM</td>
<td>Constituent of cysteine, methionine, glutathione, several coenzymes</td>
</tr>
<tr>
<td>K</td>
<td>1</td>
<td>Potassium salts</td>
<td>Main cellular inorganic cation and cofactor for certain enzymes</td>
</tr>
<tr>
<td>Mg</td>
<td>0.5</td>
<td>Magnesium salts</td>
<td>Inorganic cellular cation, cofactor for certain enzymatic reactions</td>
</tr>
<tr>
<td>Ca</td>
<td>0.5</td>
<td>Calcium salts</td>
<td>Inorganic cellular cation, cofactor for certain enzymes</td>
</tr>
<tr>
<td>Fe</td>
<td>0.002</td>
<td>Iron salts, DOM</td>
<td>Component of cytochromes and Fe-proteins; cofactor for many enzymes</td>
</tr>
</tbody>
</table>
The Struggle for Composition

Bacterial biomass relatively enriched in P, N, C, Fe compared to the surface seawater.
Methods of Determining Biomass in a Growing Culture

- Dry weight
- Wet Weight
- Total C
- Total protein
- Total DNA content
- ATP
- Chlorophyll (photosynthetic microbes)
Determining Biomass in Seawater is Much More Difficult

• Cell densities in seawater are orders of magnitude lower than typically found in cultures.

• Cell sizes are often smaller in natural populations than cultivated populations.
## Methods of Estimating Bacterial Biomass and Production in Seawater

### Biomass

<table>
<thead>
<tr>
<th>Biomass</th>
<th>Production</th>
</tr>
</thead>
<tbody>
<tr>
<td>(mg C L(^{-1}))</td>
<td>(Δ biomass/time)</td>
</tr>
<tr>
<td></td>
<td>(mg C L(^{-1}) d(^{-1}))</td>
</tr>
<tr>
<td>ATP</td>
<td>FDC</td>
</tr>
<tr>
<td>Muramic acid</td>
<td>3H-thymidine</td>
</tr>
<tr>
<td>Cell abundance</td>
<td>3H or 14C-leucine</td>
</tr>
<tr>
<td>Cell volume</td>
<td>3H-adenine</td>
</tr>
<tr>
<td>LPS</td>
<td>Bromodeoxyuridine</td>
</tr>
<tr>
<td>Chlorophyll</td>
<td></td>
</tr>
</tbody>
</table>

Note: none of these are direct measures of biomass or productivity (i.e. carbon)
Most Widely Used Determinations of Bacterial Biomass (mg C L\(^{-1}\))

- Cell abundance and cell volume (by microscopy and more recently by flow cytometry)
Determining Bacterial Biomass by Microscopy

- Filter seawater onto nucleopore polycarbonate filter (typically 0.2 µm)
- Stain bacterial cells using nucleic acid or protein stain (e.g. DAPI or acridine orange)
- Visualize cells by epifluorescence microscopy
- Count cells and measure cell sizes
Epifluorescence microscopy

EPIFLUORESCENCE MICROSCOPE

- Eyepiece
- Barrier filter
- Long λ light
- Chromatic beam splitter
- Excitation light
- Objective as condenser
- Specimen

Excitation Light Path

- Eyepiece
- Fluorescence
- Barrier filter
- Chromatic beam splitter
- Short λ excitation light
- Objective
- Specimen

Emission Light Path

Image of an epifluorescence microscope
Application of flow cytometry to bacterial abundance/cell sizing

- Greater sensitivity.
- Ability to distinguish non-pigmented bacteria from bacteria with weak autofluorescence.
- Provides cell abundances and sometimes estimated cell sizes.
Vertical distributions of bacteria

Bacterial abundance varies ~2-fold (5 x 10⁵ to 1 x 10⁶ cells ml⁻¹) across very different ocean ecosystems—except the Ross Sea.
Bacterial cell densities in marine ecosystems

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Cell density (cells ml$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estuaries</td>
<td>$&gt;5 \times 10^6$</td>
</tr>
<tr>
<td>Coastal (near shore)</td>
<td>1-5 $\times 10^6$</td>
</tr>
<tr>
<td>Open Ocean</td>
<td>0.5-1 $\times 10^6$</td>
</tr>
<tr>
<td>Deep Sea</td>
<td>&lt;0.01 $\times 10^6$</td>
</tr>
</tbody>
</table>
Remember that cell abundance ≠ carbon biomass
Size matters

Smaller organisms have higher surface area (SA) to volume (V) ratios. Consider a spherical microbe:

\[ SA = 4\pi r^2 \]
\[ V = \frac{4}{3} \pi r^3 \]

The smaller the cell, the larger the SA : V.
Greater SA : V increases number of transport sites (per unit biomass), and may allow smaller cells to out compete larger cells under limiting nutrient conditions.
Determinations of cell volume

- Need to measure 300-400 cells per sample for statistical precision.
- Assumes spherical cells
- No standards; calibrated with microspheres that have different fluorescence and shape characteristics than bacterial cells
- Image analyses is highly dependent on edge determination
Bacterial cell volumes by depth in several ocean ecosystems

<table>
<thead>
<tr>
<th>Location</th>
<th>Cell Volume ($\mu$m$^3$)</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Escherichia coli</em></td>
<td>0.9-2.4</td>
<td>Watson et al. (1977)</td>
</tr>
<tr>
<td><em>Vibrio natriegens</em></td>
<td>0.9-3.5</td>
<td>Fagerbakke et al. (1996)</td>
</tr>
<tr>
<td>Sargasso Sea</td>
<td>0.03-0.06</td>
<td>Carlson et al. (1996)</td>
</tr>
<tr>
<td>North Sea</td>
<td>0.1-0.4</td>
<td>Fagerbakke et al. (1996)</td>
</tr>
<tr>
<td>Ross Sea, Antarctica</td>
<td>0.04-0.15</td>
<td>Ducklow et al. (2001)</td>
</tr>
<tr>
<td>Sargasso Sea</td>
<td>0.03-0.1</td>
<td>Gundersen et al. (2002)</td>
</tr>
</tbody>
</table>

Cell abundance (cells ml$^{-1}$) x Cell volume ($\mu$m$^3$ cell$^{-1}$) = Biovolume ($\mu$m$^3$ ml$^{-1}$)
Why are oceanic bacteria so small?

• Inactive or dormant – low growth rates?

• High S/V advantageous for growth in limiting nutrient media?

• Predation defense?
Non-living and inactive bacteria?

- Various staining, destaining, and microautoradiography methods have suggested ~30-60% of the "DAPI" stainable cells are inactive or dormant.

Zweifel and Hagstrom (1995)

Choi et al. (1996)
Alive but inactive?

Addition of organic nutrients to seawater culture increased the abundance of nucleoid-visible cells and the proportion of actively respiring cells. These data suggest inactive cells may have low cellular DNA concentrations.

Fig. 2. Results of a long-term (24 d) culture experiment with the marine isolate. A. Change in abundance with time (cells ml\(^{-1}\)) of total bacterial counts (DAPI), nucleoid-visible cells (NV), and ETS-active cells (active). B. Changes in NV and active cell abundance with time expressed as a percentage of total DAPI counts. Error bars represent 1 SE of three replicate samples.

Choi et al. (1996)
To get from abundance and volume to biomass requires carbon conversion factors

<table>
<thead>
<tr>
<th>Location</th>
<th>Density (fg C μm⁻³)</th>
<th>C content (fg C cell⁻¹)</th>
<th>Method</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>E. coli</em></td>
<td>126-132</td>
<td>109-323</td>
<td>CHN analyses</td>
<td>Watson et al. (1977)</td>
</tr>
<tr>
<td><em>E. coli, P. putida, B. subtilius</em></td>
<td>160-930</td>
<td></td>
<td>CHN analyses</td>
<td>Bratbak et al. (1985)</td>
</tr>
<tr>
<td>Natural plankton</td>
<td>280</td>
<td>20</td>
<td>CHN</td>
<td>Lee and Fuhrman (1987)</td>
</tr>
<tr>
<td>Station ALOHA</td>
<td></td>
<td>3.5-8.8</td>
<td>Biomass constraint</td>
<td>Christian and Karl (1994)</td>
</tr>
<tr>
<td>Southern Ocean</td>
<td></td>
<td>12</td>
<td>Direct Measure by TOC</td>
<td>Fukuda et al. (1998)</td>
</tr>
<tr>
<td>Ross Sea, Antarctica</td>
<td>77-165</td>
<td>7-13</td>
<td>C mass balance</td>
<td>Carlson et al. (1999)</td>
</tr>
<tr>
<td>Sargasso Sea</td>
<td>148</td>
<td>4-9</td>
<td>X-Ray microanalyses</td>
<td>Gunderson et al. (2002)</td>
</tr>
</tbody>
</table>
### Bacterial and phytoplankton biomass in the upper ocean in various ecosystems

<table>
<thead>
<tr>
<th>Location</th>
<th>Bacterial Biomass (mg C m(^{-2}))</th>
<th>Phytoplankton Biomass (mg C m(^{-2}))</th>
<th>B:P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sargasso Sea</td>
<td>659</td>
<td>573</td>
<td>1.2</td>
</tr>
<tr>
<td>North Atlantic</td>
<td>500</td>
<td>4500</td>
<td>0.11</td>
</tr>
<tr>
<td>North Pacific</td>
<td>571</td>
<td>447</td>
<td>1.2</td>
</tr>
<tr>
<td>Station ALOHA</td>
<td>750</td>
<td>447</td>
<td>1.7</td>
</tr>
<tr>
<td>Arabian Sea</td>
<td>724</td>
<td>1248</td>
<td>0.58</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>641</strong></td>
<td><strong>1443</strong></td>
<td><strong>0.96</strong></td>
</tr>
<tr>
<td><strong>Stand dev.</strong></td>
<td><strong>105</strong></td>
<td><strong>1740</strong></td>
<td><strong>0.62</strong></td>
</tr>
<tr>
<td><strong>CV (%)</strong></td>
<td><strong>16%</strong></td>
<td><strong>120%</strong></td>
<td><strong>64%</strong></td>
</tr>
</tbody>
</table>

**Main point:**

Bacterial biomass constitutes a large pool of living carbon in marine ecosystems.

Note greater variation between ecosystems in phytoplankton biomass relative to bacterial biomass.
Plankton biomass pyramids

In regions with low Chl a, bacterial biomass constitutes a large component of plankton biomass. With increasing ecosystem productivity, bacterial biomass appears to be a proportionately smaller component of total plankton biomass.

Note that these determinations are highly dependent on the conversion factors used to derive the various pools of biomass.

In open ocean ecosystems, bacterial biomass is relatively enriched implying that resources must cycle rapidly to support the elevated biomass.

\[
P_B = \mu_B B_B \quad \text{and} \quad P_P = \mu_P B_P, \quad (i.e. \quad B = P/\mu)
\]

If \( B_B = B_P \) then \( P_B/\mu_B = P_P/\mu_P \) and \( P_P > P_B \)

then

\[\mu_B < \mu_P\]
### Upper ocean biomass inventories at Station ALOHA in the oligotrophic North Pacific Ocean

<table>
<thead>
<tr>
<th>Carbon reservoir</th>
<th>Depth integration (m)</th>
<th>Method</th>
<th>Average concentration (g m⁻³)</th>
<th>Total carbon (g C m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dissolved inorganic carbon</td>
<td>0-50</td>
<td>Coulometry</td>
<td>24.1 (±0.1) g</td>
<td>1,205</td>
</tr>
<tr>
<td></td>
<td>50-200</td>
<td></td>
<td>24.6 (±0.1) g</td>
<td>36090</td>
</tr>
<tr>
<td></td>
<td>200-1000</td>
<td></td>
<td>27.2 (±0.3) g</td>
<td>21,760</td>
</tr>
<tr>
<td>Dissolved organic carbon</td>
<td>0-50</td>
<td>High temperature combustion</td>
<td>1.12 (±0.12) g</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>50-200</td>
<td></td>
<td>0.93 (±0.07) g</td>
<td>140</td>
</tr>
<tr>
<td></td>
<td>200-1000</td>
<td></td>
<td>0.57 (±0.04) g</td>
<td>456</td>
</tr>
<tr>
<td>Particulate organic carbon</td>
<td>0-50</td>
<td>High temperature combustion</td>
<td>27 (±5.2) mg</td>
<td>1.35</td>
</tr>
<tr>
<td></td>
<td>50-200</td>
<td></td>
<td>17 (±0.3.7) mg</td>
<td>2.55</td>
</tr>
<tr>
<td></td>
<td>200-1000</td>
<td></td>
<td>5.1 (±0.1.6) mg</td>
<td>4.08</td>
</tr>
<tr>
<td>Total microbial biomass</td>
<td>0-50</td>
<td>ATP</td>
<td>36 (±15) µg</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>50-200</td>
<td></td>
<td>24 (±11) µg</td>
<td>0.90</td>
</tr>
<tr>
<td></td>
<td>200-1000</td>
<td></td>
<td>2.4 (±1.2) µg</td>
<td>0.48</td>
</tr>
<tr>
<td>Phototrophic biomass</td>
<td>0-50</td>
<td>Chl a</td>
<td>93 (±30) µg</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>50-200</td>
<td></td>
<td>126 (±33) µg</td>
<td>0.28</td>
</tr>
<tr>
<td>Heterotrophic bacteria</td>
<td>0-50</td>
<td>Flow cytometry</td>
<td>5 x 10¹¹ cells</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>50-200</td>
<td></td>
<td>3.3 x 10¹¹ cells</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>200-1000</td>
<td></td>
<td>7 x 10¹⁰ cells</td>
<td>0.56</td>
</tr>
</tbody>
</table>
Contribution of various carbon pools to total inventories at Station ALOHA

Red = 0-50 m
Green = 50-200 m
Yellow = 200-1000 m
The phases of bacterial growth in a closed system

Closed system; variable growth rate – cells are inoculated into media and grow until resources are depleted (logistic growth model).
Ideally we could estimate $B$ and $\mu$ to get BP ...

Unfortunately, $\mu$ of marine bacteria is very difficult to measure.

- From an exponentially growing population the specific growth rate ($\mu$) can be derived from:
  
  $\frac{dN}{dt} = \mu N$

  $N_t = N_0 e^{\mu t}$

  or alternatively:

  $\mu = (\ln N_t - \ln N_0) / t$

  $\mu$ has units of $\text{time}^{-1}$

**Doubling time ($d$)** is the time required for the population to increase by 100%; it is related to $\mu$ by:

- $N_t = N_0 e^{\mu d}$
- $N_t/N_0 = e^{\mu d} = 2$
- $d = \ln 2/\mu$
- $d$ has units of days or hours.
Bacterial growth in a chemostat

Open system: constant supply of limiting nutrients; growth rate held constant by rate of substrate addition (or removal). Typically use an exponential growth model.
Measuring bacterial growth in seawater

• Most direct method is to measure changes in cell abundance + volume (biomass) over time in the absence of predation.

But, in a natural seawater sample….

• Mixed assemblage of microbes with variable growth rates.

• Losses via predation and/or viral lysis tend to balance growth (i.e. no net change in population standing stock over time).
Bacterial Production

• Bacterial production (BP) is the rate that bacterial biomass is produced. It is the net movement of organic matter from a nonliving pool (DOM) to a living pool (bacterial biomass).

• Typically the term bacterial production refers only to heterotrophic production.

• Mathematically

\[ BP = \mu B \]

\[ \mu = \text{specific growth rate (time}^{-1}) \]

\[ B = \text{bacterial biomass (mg C L}^{-1}) \]

• **Note that \( \mu = \frac{BP}{B} \)

• Thus, BP has units of mg C L\(^{-1}\) d\(^{-1}\)
Commonly used methods of estimating bacterial production

Production
\((\Delta \text{ biomass/time})\)
\((\text{mg C L}^{-1} \text{ d}^{-1})\)

- $^3\text{H}$-thymidine
- $^3\text{H}/^{14}\text{C}$-leucine
- $^3\text{H}$-adenine
Bacterial Production – Advantages and Disadvantages of selected methods

- **Adenine** - purine base, RNA and DNA precursor (see Karl 1979). Measures nucleic acid production rates.
  - **Pros**: ability to determine isotope dilution by measuring intracellular pools of ATP.
  - **Cons**: non-specific; incorporated by all microbes

- **Thymidine** - nucleoside of thymine; DNA precursor (see Fuhrman and Azam 1980). Measures DNA production rates.
  - **Pros**: specific to heterotrophic bacteria
  - **Cons**: difficult to measure intracellular dilution, undergoes catabolism

- **Leucine** - amino acid; incorporated into protein (see Kirchman et al. 1992). Measures Protein production rates.
  - **Pros**: more sensitive than thymidine (intracellular protein >> DNA)
  - **Cons**: some cyanobacteria can utilize; difficult to measure isotope dilution.
**Measuring Bacterial Production**

1. Whole SW + isotope

   - Incubate at *in situ* temperature, typically in the dark (if interested in heterotrophic production)

2. Concentrate plankton on filter (0.2 µm)

   - Extract RNA, DNA, protein from filters.
   - Count radioactivity and convert to rate of incorporation (nmol leu L⁻¹ hr⁻¹)

   - SW + isotope

   - ³H-adenine, ³H-thymidine

   - ³H or ¹⁴C-leucine
The pathways of intracellular precursor incorporation, degradation, and dilution

- **Salvage pathway**
  - DNA (thymidine)
  - Protein (leucine)
  - RNA/DNA (adenine)

- **Degradation pathway**
  - Possible metabolism and non-specific labeling of proteins, RNA, DNA

- **De novo synthesis**
  - of leucine, adenine, thymidine from cellular pools of C, N, P

- **$^3$H-Thymidine/adenine/leucine**
More Conversion Factors

<table>
<thead>
<tr>
<th>Region</th>
<th>Thymidine conversion ((10^{18} \text{ cells mole}^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligotrophic Mediterranean</td>
<td>1.7</td>
</tr>
<tr>
<td>Ross Sea, Antarctica</td>
<td>0.2-1.3</td>
</tr>
<tr>
<td>Subarctic North Pacific</td>
<td>1.74</td>
</tr>
<tr>
<td>Sargasso Sea</td>
<td>0.2-5.6</td>
</tr>
<tr>
<td>Oligotrophic North Pacific</td>
<td>1.46</td>
</tr>
</tbody>
</table>

Variability in conversion factors directly influences resulting estimate of bacterial production. Conversion factors also vary in time and space.

Ducklow et al. (1999)
Vertical Profiles of Bacterial Production

Bacterial Production (ng C L⁻¹ d⁻¹)

Depth (m)

Bacterial Production (ng C L⁻¹ d⁻¹)

Eq-Pac
HOT
Arabian Sea
## Bacterial production and growth in several ocean ecosystems

<table>
<thead>
<tr>
<th>Location</th>
<th>Bacteria Biomass (mg C m(^{-2}))</th>
<th>Phyto. Biomass (mg C m(^{-2}))</th>
<th>BB:PB</th>
<th>BP (mg C m(^{-2}) d(^{-1}))</th>
<th>PP (mg C m(^{-2}) d(^{-1}))</th>
<th>BP:PP</th>
<th>BP/BB (d(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sargasso Sea</td>
<td>659</td>
<td>573</td>
<td>1.2</td>
<td>70</td>
<td>465</td>
<td>0.15</td>
<td>0.11</td>
</tr>
<tr>
<td>North Atlantic</td>
<td>500</td>
<td>4500</td>
<td>0.11</td>
<td>275</td>
<td>1083</td>
<td>0.25</td>
<td>0.55</td>
</tr>
<tr>
<td>Subarctic North Pacific</td>
<td>571</td>
<td>447</td>
<td>1.2</td>
<td>56</td>
<td>629</td>
<td>0.09</td>
<td>0.10</td>
</tr>
<tr>
<td>Station ALOHA</td>
<td>750</td>
<td>447</td>
<td>1.7</td>
<td>106</td>
<td>486</td>
<td>0.22</td>
<td>0.14</td>
</tr>
<tr>
<td>Arabian Sea</td>
<td>724</td>
<td>1248</td>
<td>0.58</td>
<td>257</td>
<td>1165</td>
<td>0.22</td>
<td>0.35</td>
</tr>
<tr>
<td>Average</td>
<td>641</td>
<td>1443</td>
<td>0.96</td>
<td>153</td>
<td>765</td>
<td>0.18</td>
<td>0.25</td>
</tr>
<tr>
<td>Stand dev.</td>
<td>105</td>
<td>1740</td>
<td>0.62</td>
<td>105</td>
<td>334</td>
<td>0.06</td>
<td>0.20</td>
</tr>
<tr>
<td>CV (%)</td>
<td>16%</td>
<td>120%</td>
<td>64%</td>
<td>69%</td>
<td>44%</td>
<td>35%</td>
<td>79%</td>
</tr>
</tbody>
</table>
Quantifying fluxes of carbon/nutrients through bacteria, requires knowledge of bacterial growth.
Bacterial biomass, growth and production in the oceans

• Bacterial biomass is typically 30-100% of phytoplankton biomass. In oligotrophic ecosystems, bacterial biomass may exceed phytoplankton biomass.

• Bacterial production typically ranges ~10-20% of photosynthetic production of particulate organic matter.

• Bacterial growth rates range 0.1 to 1.0 d\(^{-1}\) (equivalent to doubling times of ~0.7 to 7 days).