What happens to the 90-99% of organic matter production that does not get exported as particles?

DOM does not sink, but can be physically transported

~1-10% of net organic matter production is exported to deep sea

Organic matter production

Dissolved Organic Matter

Particulate Organic Matter

Heterotrophic Bacterial Growth

Grazing

Export
• Labile DOC turnover over time scales of hours to days.

• Semi-labile DOC turnover on time scales of weeks to months.

• Refractory DOC cycles over on time scales ranging from decadal to multi-decadal...perhaps longer.

• So what consumes labile and semi-labile DOC?

**Figure 5** Conceptual cartoon of the various pools of refractory, semilabile, and labile DOC in the open ocean. This figure is based on the mean profile for all DOC data collected at the Bermuda Atlantic Time-series Study (BATS) site in the Northwestern Sargasso Sea. The magnitude and distribution of the various pools of lability will vary depending on the location of the study site and the degree of thermal stratification of the water column (see Hansell, Chapter 15). The refractory pool is divided into two broad pools based on the deep ocean gradient observed by Hansell and Carlson (1998a). They observed the lowest concentration of DOC (34 μM C) in the north Pacific and used this concentration to represent refractory DOC which turns over on time scales of greater than ocean mixing (A, white box). The deep DOC concentrations in excess of the 34 μM C represents the fraction of the biologically refractory pool that turns over on time scales of ocean mixing (i.e., centuries; B, light gray box).
How much carbon passes through the microbial loop?

Phytoplankton

Herbivores

Higher trophic levels (zooplankton, fish, etc.)

Dissolved organic matter

Heterotrophic bacteria

Protozoa

??

??

??
• Very difficult to directly measure the flux of carbon from primary producers into the microbial loop.
  – The microbial loop is mostly run on labile (recently produced organic matter) -- very low concentrations (nM) turning over rapidly against a high background pool (µM).
  – Unclear exactly which types of organic compounds support bacterial growth.
Bacterial Production

• Step 1: Determine how much carbon is consumed by bacteria for production of new biomass.

• Bacterial production (BP) is the rate that bacterial biomass is created. It represents the amount of material that is transformed from a nonliving pool (DOC) to a living pool (bacterial biomass).

• Mathematically
  \[ P = \mu B \]
  \[ \mu = \text{specific growth rate (time}^{-1}) \]
  \[ B = \text{bacterial biomass (mg C L}^{-1}) \]
  \[ P = \text{bacterial production (mg C L}^{-1} \text{ d}^{-1}) \]

• Note that \( \mu = P/B \)

• Thus, \( P \) has units of mg C L\(^{-1} \) d\(^{-1} \)

Bacterial production provides one measurement of carbon flow into the microbial loop
How do we measure bacterial production?

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

- \(^3\text{H}\)-thymidine
- \(^3\text{H}\) or \(^{14}\text{C}\)-leucine

Note: these are NOT direct measures of biomass production (i.e. carbon)
Bacterial Production –
Advantages and Disadvantages of two common methods

• **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**
   - SW + isotope

2. **SW + isotope**
   - Incubate at *in situ* temperature, typically in the dark (if interested in heterotrophic production)

3. **3H-thymidine or leucine**
   - Concentrate plankton or nucleic acids

4. **Extract DNA and protein**
   - Count radioactivity and convert to rate of production (ng C L$^{-1}$ d$^{-1}$)
Across a wide range of aquatic ecosystems, bacterial production co varies with primary production.

Based on these relationships, BP accounts for ~10 to 30% of PP.
## Phytoplankton and bacterial biomass, production and growth in various ocean ecosystems

<table>
<thead>
<tr>
<th>Location</th>
<th>Bact. Biomass (mg C m(^{-2}))</th>
<th>Phyto. Biomass (mg C m(^{-2}))</th>
<th>BactB: PhytoB</th>
<th>BactP (mg C m(^{-2}) d(^{-1}))</th>
<th>1(^{o}) Pro (mg C m(^{-2}) d(^{-1}))</th>
<th>1(^{o}) Pro: PhytoB (d(^{-1}))</th>
<th>BactP: BactB (d(^{-1}))</th>
<th>1(^{o}) Pro: BactP</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>0.8</td>
<td>0.1</td>
<td>0.15</td>
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<tr>
<td>North Atlantic Bloom</td>
<td>500</td>
<td>4500</td>
<td>0.1</td>
<td>275</td>
<td>1083</td>
<td>0.2</td>
<td>0.6</td>
<td>0.25</td>
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<tr>
<td>Subarctic North Pacific</td>
<td>571</td>
<td>447</td>
<td>1.2</td>
<td>56</td>
<td>629</td>
<td>1.4</td>
<td>0.1</td>
<td>0.09</td>
</tr>
<tr>
<td>Station ALOHA</td>
<td>750</td>
<td>447</td>
<td>1.7</td>
<td>106</td>
<td>486</td>
<td>1.1</td>
<td>0.1</td>
<td>0.22</td>
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<tr>
<td>Arabian Sea</td>
<td>724</td>
<td>1248</td>
<td>0.6</td>
<td>257</td>
<td>1165</td>
<td>0.9</td>
<td>0.4</td>
<td>0.22</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td><strong>641</strong></td>
<td><strong>1443</strong></td>
<td><strong>1.0</strong></td>
<td><strong>153</strong></td>
<td><strong>766</strong></td>
<td><strong>0.9</strong></td>
<td><strong>0.3</strong></td>
<td><strong>0.19</strong></td>
</tr>
<tr>
<td><strong>Stand dev. CV (%)</strong></td>
<td><strong>105</strong></td>
<td><strong>1741</strong></td>
<td><strong>0.6</strong></td>
<td><strong>105</strong></td>
<td><strong>334</strong></td>
<td><strong>0.4</strong></td>
<td><strong>0.2</strong></td>
<td><strong>0.07</strong></td>
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<tr>
<td></td>
<td><strong>16</strong></td>
<td><strong>121</strong></td>
<td><strong>65</strong></td>
<td><strong>69</strong></td>
<td><strong>44</strong></td>
<td><strong>48</strong></td>
<td><strong>79</strong></td>
<td><strong>35</strong></td>
</tr>
</tbody>
</table>
Bacterial biomass, growth and production in the oceans

- Bacterial biomass is typically 50 to >100% of phytoplankton biomass. In oligotrophic ecosystems, bacterial biomass can exceed phytoplankton biomass.

- Bacterial production typically ranges ~10-30% of primary production.

- Bacterial growth rates range 0.1 to 0.5 d\(^{-1}\) (equivalent to doubling times of ~1 to 7 days), while phytoplankton growth rates range ~0.5-1.4 d\(^{-1}\) (doubling times of 0.5 to ~2 days)
What factors control variability in bacterial production?

- Changes in growth rate and changes in biomass.
- Top down pressures control biomass, bottom up factors control growth.

- Bottom up: light, nutrients, temperature
- Top down: predation, viruses
The total carbon used to support bacterial production also includes DOC that is resired during growth.

DOM

Bacterial Biomass

BP ~10-30% PP

Higher trophic levels

Available to food web

Regeneration of nutrients/CO₂

CO₂, NH₄⁺, PO₄³⁻
Respiration by various plankton size classes

Figure 6. Distribution of respiratory activity with size. (□) CEPEX, samples from bag; (○) Loch Ewe, samples from bag; (●) Loch Ewe samples from outside bag. Data are expressed as cumulative respiration up to various size limits, normalized against the rate in the unfiltered sample. All the data points are for a single size horizon and are not replicates.

Williams (1984)
Energetic costs of growth

del Giorgio and Cole (2001)

a. Oxidation of organic matter to form ATP, b. energy expense of active transport, c. anabolic reactions utilize energy, d. maintenance energy expenditures, e. degradation of biomass via endogenous metabolism.
We can estimate carbon that supports biomass production…but we really need to know the total carbon flux required to support bacterial growth

• Total amount of carbon that supports growth includes carbon used for biomass synthesis and carbon metabolized.

• Bacterial growth efficiency (BGE) is the growth yield or the amount of biomass synthesized relative to total carbon required for growth.
  \[ = \text{BGE} = \frac{\text{BP}}{\text{BP} + \text{Respiration}} \]

If we can constrain BGE, then

\[ \frac{\text{BP}}{\text{BGE}} = \text{the total DOC flux entering the microbial loop} \]
In this example, $^{14}$C-glucose was added to seawater and passage of this radiolabeled DOC through the food web (or lack thereof) was monitored over time.

Conclusion: very little of the DOC consumed by bacteria passes to higher trophic levels—the vast majority appears respired by bacteria.

Bacteria appeared to be a SINK for carbon in this example.

Ducklow et al. (1986)
Evaluating BGE based on changes in CO₂, DOC, and cell biomass. This approach requires eliminating the sources of DOM production in order to determine the net change over time.

\[
BGE = \frac{\Delta BB}{\Delta BB + \Delta BR}
\]

or

\[
BGE = \frac{\Delta BB}{\Delta DOC}
\]

Fig. 3. AESOPS II bag 1 provides an example of time varying changes in (A) ΔTOC ( ■) and ΔTCO₂ ( ●) and (B) ΔDOC ( ●) and bacterial biovolume (▲). Error bars represent standard error of mean.

Carlson et al. (1999)
## Estimates of BGE in various ocean ecosystems

<table>
<thead>
<tr>
<th>Ecosystem</th>
<th>BGE (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sargasso Sea</td>
<td>4-9</td>
</tr>
<tr>
<td>Coastal /Shelf waters</td>
<td>8-40</td>
</tr>
<tr>
<td>Central North Pacific</td>
<td>1-33</td>
</tr>
<tr>
<td>North Atlantic</td>
<td>4-6</td>
</tr>
</tbody>
</table>
Abstract. The global ocean apparently consumes more organic carbon than it produces. The excess heterotrophy probably occurs in the nearshore zone. This nearshore heterotrophy has significant implications with respect to processes such as organic matter transport from the nearshore zone to the adjacent open ocean, nutrient limitation of primary production, and the role of the coastal zone as a short-term sink for anthropogenic CO₂.

### Table 1. Estimates of Primary Production and Respiration in the Global Ocean.

<table>
<thead>
<tr>
<th>Reference</th>
<th>p</th>
<th>r</th>
<th>p-r</th>
<th>p/r</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reiners [1973]</td>
<td>4167</td>
<td>5417</td>
<td>-1250</td>
<td>0.769</td>
</tr>
<tr>
<td>Likens et al. [1973]</td>
<td>3750</td>
<td>3784b</td>
<td>-34</td>
<td>0.991</td>
</tr>
<tr>
<td>Olson et al. [1985]</td>
<td>2500</td>
<td>2497</td>
<td>+3</td>
<td>1.001</td>
</tr>
</tbody>
</table>

Fluxes in units of $10^{12}$ mol C yr$^{-1}$.

a."Respiration" includes the terms respiration, decay, and decomposition, as used in the various models.

b.Average of a range of estimates: 3767-3800.

### Figure 3

Fig. 3. The distribution of the P/R ratio at different depths in the subtropical NE Atlantic. Surface (~5 m), mixed (30–50 m), deep chlorophyll a maximum (DCM, 50–110 m), and bottom of photic layer (BEZ, the depth receiving 1% of the surface irradiance [60–130 m]). The boxes enclose the 25 and 75% percentiles of the data, the central line represents the median, and the bars encompass 95% of the data.