Aquatic respiration and ocean metabolism
• Remember what life is all about:
  • Energy (ATP)
  • Reducing power (NADPH)
  • Nutrients (C, N, P, S, Fe, etc., etc.)

Photosynthetic organisms use sunlight, $\text{H}_2\text{O}$, and dissolved nutrients

Heterotrophic microorganisms rely mostly on dissolved nutrients—both organic and inorganic (with some energy from sunlight)
• Where does primary production go?
  – Grazing
  – Bacteria
  – Dissolved organic matter
  – Export

The vast majority of marine primary production is respired during microorganism growth.
Quantifying fluxes of carbon/nutrients through bacteria, requires knowledge of bacterial growth and respiration.
Energy via oxidation of organic matter

- Glycolysis, the citric acid cycle (TCA cycle), and electron transport together generate ATP and NADPH via the oxidation of reduced carbon. End products are CO₂ and H₂O.

\[
C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{heat}
\]

36 ATP produced in the complete oxidation of one glucose molecule.
Most aquatic respiration is microbial

Note that 50-100% of plankton respiration in this example passes through a 10 µm filter; ~60% of the total respiration is by organisms <1 µm.

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

- Oxidation of organic matter to form ATP
- Energy expense of active transport
- Anabolic reactions utilize energy
- Maintenance energy expenditures
- Degradation of biomass via endogenous metabolism

del Giorgio and Cole (2001)
Major energy consuming processes for growth

- Solute transport
- Synthesis of macromolecules
- Maintenance
- Growth and reproduction
• The total amount of carbon required for growth includes that used for creating new biomass (production) and carbon that gets metabolized for energy (respiration).

• Total flux of carbon supporting growth:

Carbon demand = Production + Respiration
Bacterial growth efficiency (BGE) is the term used to describe the amount of biomass produced relative to total carbon required for growth.

\[ BGE = \frac{BP}{BP + \text{Respiration}} \]

Usually reported as %

The efficiency of cell growth determines the flux of carbon through bacteria in aquatic food webs. Variability in growth efficiencies (in space or time) could have large influences on CO$_2$ and O$_2$ fluxes, biomass production, organic matter consumption.
Methods of determining BGE

- Bacterial uptake and respiration of “model” DOM substrates ($^{14}$C-labeled DOC).
- Estimate increases in bacterial biomass relative to utilization of ambient DOC.
- Measure bacterial production in conjunction with respiration (changes in $O_2$ and/or $CO_2$ over time).
Examples of bacterial growth efficiencies based on uptake of model dissolved substrates

<table>
<thead>
<tr>
<th>Region</th>
<th>Substrate</th>
<th>BGE (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>N.E. Atlantic, Mediterranean Sea</td>
<td>Amino Acids</td>
<td>66-87</td>
</tr>
<tr>
<td></td>
<td>Glucose</td>
<td>51-76</td>
</tr>
<tr>
<td>North Sea</td>
<td>Amino acids</td>
<td>16-50</td>
</tr>
<tr>
<td></td>
<td>Glucose</td>
<td>20-50</td>
</tr>
<tr>
<td>Coastal California</td>
<td>Amino acids</td>
<td>60-90</td>
</tr>
</tbody>
</table>
Link vs Sink

1. Measure growth efficiency.
2. Add $^{14}$C DOM (glucose) and follow its transfer through the food web (into larger size fractions).

In this example, $^{14}$C-glucose was added to seawater and passage of this DOC through the food web was monitored over time. Conclusion: very little of the DOC channeled into biomass passes to higher trophic levels—the vast majority is respired.

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

Ducklow et al. (1986)
Measuring bacterial growth efficiency on naturally occurring DOC

Evaluating BGE based on changes in CO$_2$, DOC, and cell biomass. This approach requires eliminating the sources of DOM production in order to determine the net change over time.

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

Fig. 3. AESOPS II bag 1 provides an example of time varying changes in (A) $\Delta$TOC (■) and $\Delta$TCO$_2$ (●) and (B) $\Delta$DOC (●) 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>8-69</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>
Factors influencing BGE

- DOM composition (energetic and nutritional value)
- Temperature
- Growth rate
Growth efficiencies vary widely depending on the DOC source. DOC exudates from actively growing cells appears to support higher growth yields (40-70%) than growth on cellular constituents. The source of the DOC partly determines its suitability as a growth substrate.

*Figure 5*  Summary of literature data on direct measurements of BGE for organic matter grouped according to source. Box-and-whisker plot shows median and upper/lower quartiles (box), and range of values (bars). Extreme outliers are marked as open circles. The sources of the data are in Table 2.
Bacterial growth efficiencies across aquatic ecosystems

BGE in the open ocean \(~10\text{-}30\%\). Growth efficiency tends to increase along a productivity gradient from oligotrophic to eutrophic environments.

Figure 2  Summary of literature data on direct measurements of BGE in natural aquatic systems. Box-and-whisker plot shows median, and upper/lower quartiles (box), and range of values (bars). Extreme outliers are marked as open circles. The sources of the data are in Table 1.

del Giorgio and Cole (1999)
BCD relative to PP (%) or DOM uptake/Primary production (%)

<table>
<thead>
<tr>
<th>BP/PP</th>
<th>BGE 0.50</th>
<th>BGE 0.20</th>
<th>BGE 0.15</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.30</td>
<td>60%</td>
<td>150%</td>
<td>200%</td>
</tr>
<tr>
<td>0.20</td>
<td>40%</td>
<td>100%</td>
<td>133%</td>
</tr>
<tr>
<td>0.10</td>
<td>20%</td>
<td>50%</td>
<td>67%</td>
</tr>
</tbody>
</table>

Current estimates: BP/PP = 0.10 and BGE = 0.15
Motivation

Bacterial growth regulates fluxes of carbon and nutrients, and dictates energy flow in marine ecosystems.

DOM (C, N, P, Fe, O, S, Zn, etc., etc.)

Bacterial Biomass

\[ \text{CO}_2, \text{NH}_4^+, \text{PO}_4^{3-} \]

Sink

30-50%

Higher trophic levels

10-30% of PP into BP

BGE

Link
The ocean "appears" to be net heterotrophic, i.e. NCP is negative...

The ocean should soon have no free oxygen

Massive carbon shortfall (upwards of $1.3 \times 10^{15}$ mol C yr$^{-1}$)

---

**TABLE 1. Estimates of Primary Production and Respiration in the Global Ocean.**

<table>
<thead>
<tr>
<th>Reference</th>
<th>p</th>
<th>$r^a$</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>3784$^b$</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.

Net Community Production (NCP): Gross primary production less all autotrophic and heterotrophic losses due to respiration ($R_{A+H}$).

\[ \text{NCP} = P_G - R_{A+H} \]
Productivity and respiration by changes in $\text{O}_2$

- Measures changes in oxygen concentrations in light and dark bottles following incubation.
- Light bottle = net community production (photosynthesis and community respiration).
- Dark bottle: community respiration.
- Light + Dark = Gross primary production

$\text{GPP} = \Delta \text{O}_2 (\text{light}) - \Delta \text{O}_2 (\text{dark})$
• Net heterotrophy throughout the upper ocean

*Duart* et al. (2001)*

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.
Serret et al. (2001)
The structure of the food web matters!

Classic Food web

- Phytoplankton
- Herbivores
- Higher trophic levels (zooplankton, fish, etc.)

The more links - the less efficient...

- Inorganic Nutrients
- Dissolved organic matter
- Mesozooplankton
- Microzooplankton
- Heterotrophic bacteria
- Protozoa
Respiration rates in bacteria exceed phytoplankton production in unproductive aquatic systems

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Planktonic bacteria are a fundamental component of the organic carbon cycle in aquatic systems. Organic carbon consumption by planktonic bacteria is the sum of bacterial production (BP) and bacterial respiration (BR). It is now estimated that 30–60% of phytoplankton production (the amount of inorganic carbon fixed by phytoplankton photosynthesis, corrected for phytoplankton respiration) in marine and freshwater systems is processed by bacteria. These estimates of carbon flow through bacteria are conservative, however, because losses due to bacterial respiration are seldom directly measured. We report here that bacterial respiration is generally high, and tends to exceed phytoplankton net production in unproductive systems (less than 70 to 120 µg carbon per litre per day). A large proportion of the world's aquatic systems have phytoplankton productivities below this value. Bacterial growth efficiency (BGE) is the result of BP and BR [BGE = BP/(BR + BP)]. Comparisons of our models of bacterial respiration with published models of bacterial secondary production show that bacterial growth efficiency must range from less than 10% to 25% in most freshwater and marine systems, well below the values commonly assumed in many current ecological models. The imbalance between respiration and production in unproductive aquatic systems is substantial and may represent a major sink of organic carbon.

The CO₂ Balance of Unproductive Aquatic Ecosystems

Carlos M. Duarte* and Susana Agustí

Community respiration (R) rates are scaled as the two-thirds power of the gross primary production (P) rates of aquatic ecosystems, indicating that the role of aquatic biota as carbon dioxide sources or sinks depends on its productivity. Unproductive aquatic ecosystems support a disproportionately higher respiration rate than that of productive aquatic ecosystems; tend to be heterotrophic (R > P), and act as carbon dioxide sources. The average P required for aquatic ecosystems to become autotrophic (P > R) is over an order of magnitude greater for marshes than for the open sea. Although four-fifths of the upper ocean is expected to be net heterotrophic, this carbon demand can be balanced by the excess production over the remaining one-fifth of the ocean.

Aquatic ecosystems cover 70% of Earth's surface and contribute 45% of the global primary production. Yet, the role of their biota in the global CO₂ budget remains a subject of debate. Many freshwater ecosystems act as CO₂ sources; in contrast, oceanic ecosystems are assumed to act as CO₂ sinks. This assumption has been challenged by calculations suggesting that the coastal ocean may be net heterotrophic and by the finding that bacterial metabolism exceeds phytoplankton production in unproductive waters, which make up >30% of the ocean. These conclusions are based on indirect calculations and controversial assumptions. Here, we compare the gross primary production (P) and respiration (R) rates of aquatic communities to elucidate whether the biota of aquatic ecosystems acts as net CO₂ sources (R > P) or sinks (R < P). We compiled data obtained over the past five decades from studies in which oxygen evolution was used as a surrogate for carbon fluxes. The community metabolism varied by over four orders of magnitude across aquatic ecosystems (Table 1). Marshes tended to be more productive than other aquatic ecosystems, whereas open sea communities showed the lowest production and respiration rates. The
The balance of plankton respiration and photosynthesis in the open oceans

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Carbon balance. There is no evidence of the large regional imbalances observed previously. I conclude that the form of data analysis is critical.

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Regional Carbon Imbalances in the Oceans

Recent studies (1, 2) have suggested that respiration exceeds photosynthetic oxygen production in large areas of the oceans. If correct, the conclusion has profound implications for our understanding of the oceanic carbon cycle. C. M. Duarte and S. Agustí conclude that four fifths of the ocean are not is the gross primary production rate. This equation is an unsatisfactory model when extrapolating across ecosystems of widely different productivities because the term “a” is no constant, but dependent on the scale of lo photosynthesis [table 1 in the report (2)]. The "P = aR" relationship attempt to fit a sin
Respiration in the open ocean

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†† These authors contributed equally to this work

A key question when trying to understand the global carbon cycle is whether the oceans are net sources or sinks of carbon. This will depend on the production of organic matter relative to the decomposition due to biological respiration. Estimates of respiration are available for the top layers, the mesopelagic layer, and the abyssal waters and sediments of various ocean regions. Although the total open ocean respiration is uncertain, it is probably substantially greater than most current estimates of particulate organic matter production. Nevertheless, whether the biota act as a net source or sink of carbon remains an open question.

brief communications:

COMMUNICATIONS ARISING

Global carbon cycle

Metabolic balance of the open sea

The rise of oxygenic photosynthesis nearly three billion years ago led to the accumulation of free oxygen and to the subsequent diversification of life on Earth; today, nearly half of all oxygen production derives from the photosynthetic activities of marine phytoplankton. The conclusion that the open sea — and therefore much of our planet’s surface — is in a net heterotrophic metabolic state is enigmatic and is a first-order question in the global carbon cycle, as discussed by del Giorgio and Duarte. Our

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Mixed layer $\text{O}_2$ is in equilibrium with the atmosphere.

Rate of subsurface $\text{O}_2$ accumulation provides information on NCP.

But remember this study?
Net autotrophic not heterotrophic…
Late summer primary production event.
Organic matter export from the upper ocean implies that production exceeds respiration.
What processes control DIC gradients in the sea?

- Abiotic and biotic processes control carbon distributions in the sea.
- Need to understand controls on the variability of these processes.
Total organic carbon at BATS
Remember that DOC = ~98% of the TOC.

Note the build up in DOC through the spring and summer, with subsequent export the following winter.

Figure courtesy of Craig Carlson, UCSB
DOC has been characterized based on the turnover times of the various constituent pools.

- Labile pools cycle over time scales of hours to days.
- Semi-labile pools persist for weeks to months.
- Refractory material cycles over on time scales ranging from decadal to multi-decadal...perhaps longer...

**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).