

- > SECTION IV. PROCESSES
> CHAPTER 8. ENERGY DISSIPATION, RESPIRATION, AND GROWTH

Microbes and the Dissipation of Energy and Respiration: From Cells to Ecosystems

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In the year 1974, Larry Pomeroy first proposed that microbes were true movers of energy and nutrients in marine food webs (Pomeroy, 1974). This idea was later formalized as the “microbial loop” (Azam et al., 1983; Pomeroy et al., this issue) in which energy and carbon lost from the planktonic food web in the form of dissolved organic matter (DOM) was recovered and repackaged by heterotrophic bacterioplankton to particulate organic matter (POM). Their ecological role within the microbial loop is to facilitate the transformation of DOM to POM (a trophic “link”) (Azam et al., 1983) or to remineralize DOM back to its inor-

chemistry is elucidated in studies of how the flow of energy through microbial processes manifests itself as demand for and recycling of elemental nutrients.

Prokaryotes (bacteria and archaea) are now recognized as the most abundant living component of the biosphere with approximately 12×10^{28} cells found in the oceanic water column (Whitman et al., 1998). This prokaryotic biomass is comprised of vast phylogenetic diversity (Venter et al., 2004; Giovannoni and Stingl, 2005; Moran et al., this issue; Edwards and Dinsdale, this issue, Breitbart et al., this issue) as well as metabolic diversity (King, 2005; DeLong

In the contemporary aerobic ocean, the metabolic strategy for the vast majority of prokaryotes is chemoheterotrophy. Heterotrophic bacterioplankton are the major respirers (Sherr and Sherr, 1996; Rivkin and Legendre, 2001), with organic compounds serving as both the electron donors as well as carbon sources, and oxygen functioning as electron acceptor. As organic matter is catabolized, both organic matter and O_2 are consumed, resulting in anabolism (biosynthesis) and CO_2 production. In terms of energy and carbon cycling within the ocean, it is these chemoorganotrophic organisms that are the most important physiological group. They are instrumental in the transformation of organic matter, its remineralization to inorganic constituents (Ducklow et al.,

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ganic constituents (a respiratory “sink”) (Ducklow et al., 1986). These early studies laid the conceptual framework for investigations that linked microbial processes to the flow of energy in marine food webs (microbial ecology or trophodynamics). The link to ocean biogeo-

et al., 2006). Although prokaryotic processes and trophic interactions occur on the spatial scale of nanometers (Azam, 1998), their sheer numbers and the rates at which they operate have major biogeochemical implications on the scale of ecosystems.

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1986), and shaping of the organic and inorganic environment (Williams and del Giorgio, 2005). These organisms and their associated processes will be the focus of this article.

One of the fundamental properties that determines bacterioplankton's ecological or biogeochemical role in the marine ecosystem is the amount of biomass produced per unit of organic C consumed, or the bacterial growth efficiency (BGE) (Sherr and Sherr, 1996; del Giorgio and Cole, 1998). BGE is a measure of the coupling between catabolic (energy-yielding) reactions to anabolic (biosynthetic; energy-requiring) reactions and is expressed by the formula,

$$\text{BGE} = \text{BP} / (\text{BP} + \text{BR}) \quad [1]$$

where BP is bacterial production and BR is bacterial respiration. Here we will examine how microbial energetics of heterotrophic bacteria partition energy and carbon on a cellular level (Figure 1), how that partitioning affects their growth efficiency, and how that growth efficiency affects their ecological and biochemical roles in the sea.

CELLULAR BIOENERGETICS

The first law of thermodynamics states that the total amount of energy in the universe is conserved and cannot be created nor destroyed. As a result, all organisms have evolved physiological strategies to conserve energy by collecting, converting, and storing that energy principally via the synthesis of adenosine-5'-triphosphate (ATP). Energy is harvested from light (phototrophy), the oxidation of inorganic compounds (chemolithotrophy) (see Kolber

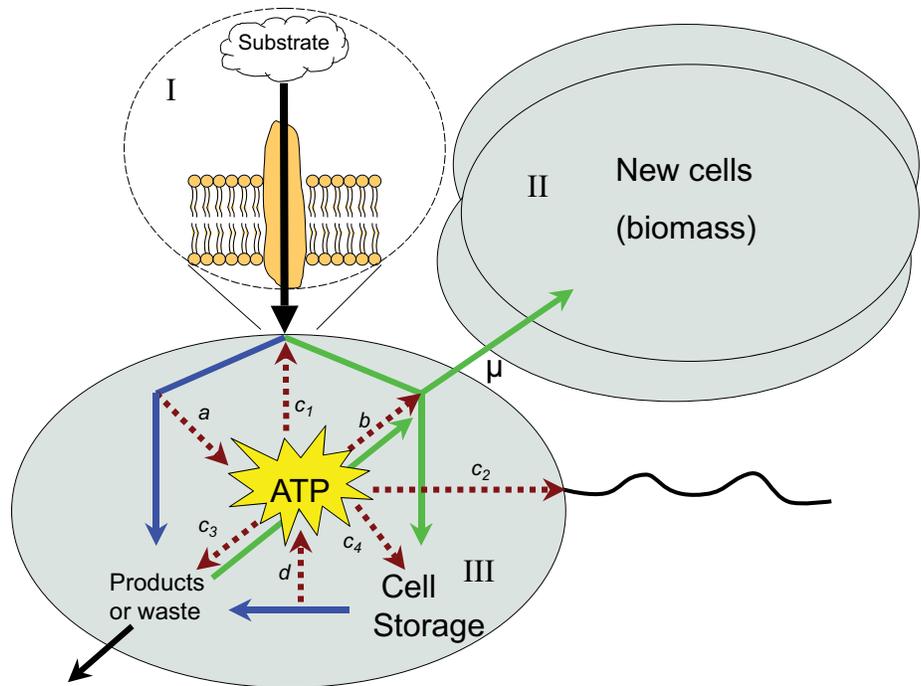


Figure 1. Substrate and energy flow within a cell. Substrate < 700 Da are actively taken up via membrane proteins (I). As the substrate enters the cell via active uptake, it either enters into catabolic pathways (blue lines) or anabolic pathways (green lines). Monomers for anabolism can come preformed from the environment or as products of catabolism. The red-dashed lines represent the flow of energy to and from these metabolic pathways. Energy is conserved via substrate catabolism and ATP is produced at a rate a . As ATP is hydrolyzed, energy is released and utilized at rate b to drive anabolic processes such as production of new cells (growth; II) and production cell storage products (III). Energy is also utilized at various rates to support processes that are independent of anabolism. This maintenance energy is used at rates c_1 to activate uptake systems, c_2 to fuel cell motility, c_3 to actively eliminate waste, and c_4 to repair cellular machinery. In the absence of exogenous organic substrates, the cell can yield ATP at rate d by catabolizing storage material (endogenous substrates). Adapted from del Giorgio and Cole (1998)

et al., this issue, for details on these two metabolic strategies), or the oxidation of organic compounds (chemoorganotrophy). ATP is synthesized via one of three distinct mechanisms: substrate-level phosphorylation (fermentation), photophosphorylation, or oxidative phosphorylation (respiration). Except for obligate fermenters, all microbes carry out respiration. On the cellular level, respiration is the key process of energy conservation in which an electrochemical potential is generated from the flow of electrons from reduced compounds

through a membrane transport system to an electron acceptor. The generated chemical energy is used to drive the cells' metabolic processes (Jones, 1983).

The second law of thermodynamics states that in all processes or reactions, some of the energy involved irreversibly loses its ability to do work as a system moves from order to disorder (entropy). From the standpoint of energy flow within a cell, the hydrolysis of ATP transfers the energy conserved from catabolic reactions to energy-requiring reactions that support anabolism (Figure 1).

However, cells expend energy in ways that are independent of cell biomass production via processes such as overflow metabolism, futile cycles, and maintenance metabolism (see Russell and Cook, 1995) (Figure 1). Thus, efficiency of energy use with regard to biomass production (growth efficiency) can vary significantly depending on the physical-chemical state of the environment.

Overflow Metabolism

Laboratory cultures of bacteria grown in energy and substrate-rich media often display an uncoupling of catabolism from anabolism, resulting in nongrowth energy dissipation rather than maintenance energy expenditure (see Teixeira-de-Mattos and Neijssel, 1997; Liu, 1998, and citations therein). Under this scenario, energy generated from catabolism is in excess of that needed for anabolism; thus, the cell wastes ATP via extracellular release of DOM. It is not known to what extent energy dissipation via overflow metabolism occurs in natural systems, but several studies have demonstrated production of recalcitrant DOM in cultures of natural assemblages of bacterioplankton (Brophy and Carlson, 1989; Heissenberger and Herndl, 1994; Ogawa et al., 2001; Kawasaki and Benner, 2006). Little is known about why free-living bacterioplankton would actively release DOM extracellularly in substrate-limited systems like the open ocean. It has been shown that highly metabolically active bacterioplankton are engulfed by a polysaccharide envelope (Heissenberger et al., 1996) (Figure 2) in which a major part of the cell's ectoenzymes is embedded (Martinez and Azam, 1993). This

polysaccharide capsule might act as sorption/scavenging site for organic molecules for subsequent cleavage by ectoenzymes and is constantly renewed (Stoderegger and Herndl, 1998). Hence, heterotrophic microbial processes might be important sources of recalcitrant DOM (Tanoue et al., 1995; McCarthy et al., 1998). The pool of recalcitrant or semi-labile DOM is biologically reactive. However, its production and subsequent remineralization are uncoupled for time scales of months to decades resulting in accumulation (Carlson, 2002).

Maintenance Metabolism

A more ecologically important mechanism in natural systems is the free energy allocated to nongrowth reactions. Known as maintenance energy, it serves to keep entropy low by fixing what breaks within the cell; thus, it helps a cell to maintain its molecular, cellular, and functional integrity (Hoehler, 2004). The larger the partitioning of energy into maintenance processes, the lower the energetic efficiency of the cell. Studies of bacterial growth in pure bacterial cultures demonstrate that rates of catabo-

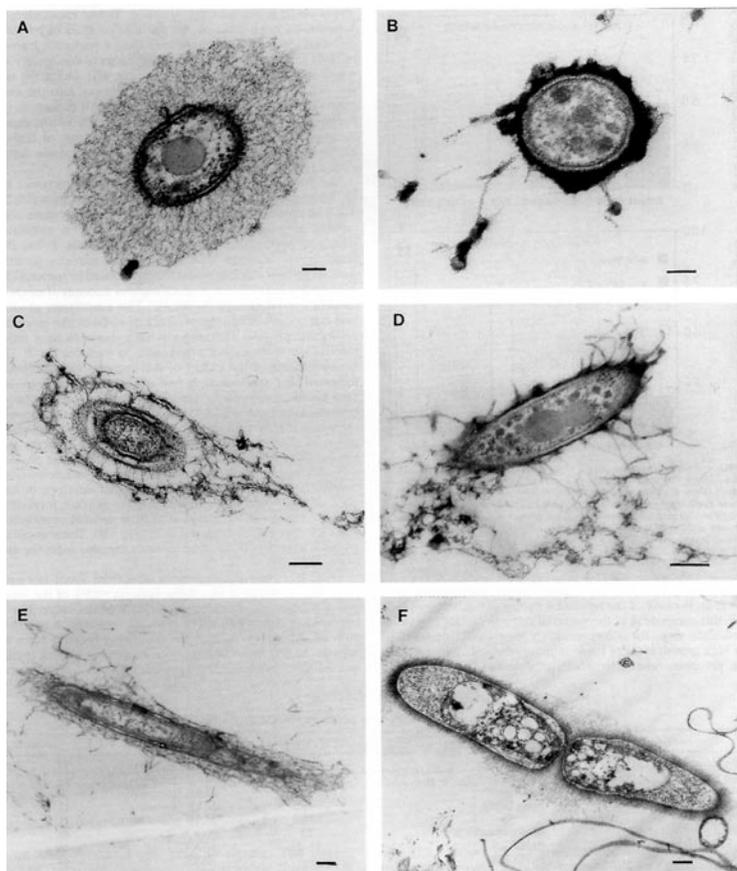


Figure 2. TEM images of the most common types of capsules found in free-living marine bacteria. Note that the morphology of the capsules varies considerably. D and F (a dividing cell) were observed near marine snow particles. Scale bars: A and B—100 nm, C to F—200 nm. TEM pictures adapted from Heissenberger et al. (1996)

lism are independent of anabolism and proceed at maximal rates (Russell and Cook, 1995). Maintaining maximal rates of energy flow within a cell keeps cellular membranes energized and the active transport system functional. This “energized” physiological state is advantageous for cell growth, leaving cells poised to exploit transient but favorable environmental conditions associated with patchiness of available organic and inorganic nutrients (del Giorgio and Cole, 1998). Thus, while cells sacrifice thermodynamic efficiency, their BGE appears to be optimal to support maximal growth rates (Westernhoff et al., 1983).

Factors That Can Affect BGE

Abiotic Factors

Physical factors that hasten biochemical breakdown within a cell will affect the maintenance energy requirement and lower BGE. In a comprehensive review of BGE, Rivkin and Legendre (2001) suggest a significant inverse relationship between temperature and BGE, based on observations that the fraction of respired assimilated carbon is greater at lower latitudes compared to higher latitudes. Because there are major environmental gradients superimposed on this latitudinal range, it is possible that the pattern reported by Rivkin and Legendre (2001) may result from factors other than temperature. However, Apple et al. (2006) also observed a negative relationship between temperature and BGE in estuarine and coastal sites, and experimentally confirmed the temperature effect on BGE. The influence of temperature on bacterial carbon metabolism is complex, and not all reports agree with the patterns described above. Although trends

appear to hold across large temperature ranges, the relationship is weak at any given site in which temperature range is $< 10^{\circ}\text{C}$. For example, a large systematic increase in BGE (i.e., $< 10\%$ to $> 35\%$) was observed throughout the course of a phytoplankton bloom in the Ross Sea, Antarctica, despite little change in temperature (-2°C to $+2^{\circ}\text{C}$) (Carlson and Hansell, 2003). In the southern North Sea, Reinthaler and Herndl (2005) observed the opposite trend in which BGE increased from winter through spring as temperatures warmed. The rise in BGE observed in these studies suggests that other factors, such as DOM bioavailability during a phytoplankton bloom, had a greater effect relative to temperature.

Additionally, abiotic factors may affect bacterial energetic constraints. For example, ultraviolet irradiation, exposure to toxic substances, or osmotic shock may result in large increases in cell respiration associated with protection and repair, and consequent declines in BGE and growth (Koch, 1997). Although these effects have been difficult to document for marine bacterioplankton in situ, there is some evidence of large declines in BGE in freshwater to saltwater transition zones in estuaries (del Giorgio and Bouvier, 2002).

Nutrient Limitation

The stoichiometry of bacterioplankton is relatively constant (i.e., C:N ratio $\approx 4-6$) (Goldman et al., 1987). The C:N and C:P ratios of oceanic DOM range from 9–18 and 180–570, respectively (Benner, 2002). If the substrate supporting bacterial growth is relatively C-rich, one might expect to observe

greater catabolism of DOC in order to balance elemental requirements of the cell. Studies of natural assemblages grown on media enriched with single C or N compounds generally support this trend (Goldman et al., 1987). However, in culture studies where multiple C or N sources were available, no trend between BGE and substrate stoichiometry was observed (Goldman and Dennett, 2000). In natural systems, no discernible trend is observed between BGE and DOM stoichiometry largely because the actual stoichiometric ratio of the available DOM is unknown. In addition, natural assemblages of prokaryotes likely use multiple sources of organic C, N, and P as well as inorganic N and P, making understanding the relationship among substrate stoichiometry, BGE, and microbial growth extremely complex in natural systems (Vallino et al., 1996). Other studies demonstrate a more direct relationship between nutrient limitation and BGE. Tortell et al. (1999) show that under iron deficiency, electron-transport activities associated with respiration decrease, resulting in a significant reduction in BGE. Addition of inorganic phosphorus has been reported to increase microbial respiration in oligotrophic waters (Obernosterer et al., 2003).

Lability (Availability) of DOM

Not all microbes can break down all DOM (Floodgate, 1995). The oceanic DOM pool represents a continuum of biological lability, ranging from refractory material that turns over on time scales of centuries to millennia (Williams and Druffel, 1987; Bauer et al., 1992) to more available material turning over on time scales of minutes to days

(Cherrier et al., 1996; Carlson, 2002). The bulk DOM pool is often conceptually partitioned into broad pools of lability, increasing in concentration from a “labile,” to a “semi-labile,” to a “refractory” pool (see Carlson, 2002, and

to maintain high electrochemical potential and support transport systems for other limiting nutrients.

Although LMW monomers are more easily taken up relative to polymeric material, not all LMW DOM is available

and Cole, 1998, and citations therein). Bacteria consume a wide range of organic compounds simultaneously, and although the nature of the organic matter consumed in the oceans is not well known, there is evidence that very different pools are used. For example, Cherrier et al. (1999) demonstrated that at least a portion of the carbon used by oceanic bacteria is old (> 500 years), and thus probably differs in its energetic contents from recently fixed carbon. The relative importance of these different pools of DOM lability likely plays a major role in shaping oceanic BGE patterns.

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citations therein). Bacteria are limited to transporting low molecular weight DOM (LMW DOM < 700 Da [dalton = atomic mass unit]) via permeases (enzymes that transport other substances across cell membranes); thus, labile compounds such as dissolved free neutral sugars or dissolved free amino acids are assimilated easily by the cell's uptake mechanisms (Keil and Kirchman, 1999). However, efficient DOM uptake does not always equate to increased BGE. For example, in experiments where natural assemblages of oligotrophic bacterioplankton were amended with labile carbon in the form of glucose, Carlson et al. (2002) observed that as much as 85% of the glucose carbon was respired as CO₂ within a few days. The rapid uptake and subsequent remineralization of this labile DOC resulted in only a small increase in cell production, suggesting that most of available DOC was utilized

for uptake. Indeed, the greater majority of oceanic DOM is uncharacterized LMW material that is resistant to microbial attack (Benner, 2002). Amon and Benner (1994, 1996) propose the size-continuum model in which the high molecular weight DOM is more bioactive and available to microbial utilization than the majority of the LMW DOM. However, enhanced bioavailability does not necessarily equate to enhanced BGE. Hydrolysis of large polymeric molecules and subsequent DOM uptake can be energetically costly and offset the nutritional advantage resulting in low BGE.

Energetic Quality

DOM quality can also refer to the biologically available energy from DOM oxidation. Growth efficiency and biomass production of organisms grown on a relatively oxidized substrate will be low even if the supply is high (del Giorgio

Viral Activity

Phage infection can contribute up to 50% of bacterial mortality. Upon lytic infection, cells burst, spilling viruses and organic matter into their environment. As the viral-mediated DOM release is reincorporated into bacterioplankton, bacterial respiration increases by as much as 30% (Fuhrman, 1999). Viral infection can also decrease the BGE of noninfected bacteria as a result of the increased energy demands associated with the degradation of polymeric organic nitrogen and phosphorus lysates (Middelboe et al., 1996).

Bacterial Diversity

Significant diversity of prokaryotic communities exists in oceanic systems. Vertical stratification of major prokaryotic groups between the oceanic euphotic and aphotic zones has been observed (Giovannoni et al., 1996; Karner et al., 2001; Moeseneder et al., 2001; Morris et al., 2002). The mechanisms responsible for spatial variability of specific prokaryotic groups or phylotypes over

depth are not well understood. However, conceptual models provide compelling reasons to believe that the growth of specific heterotrophic microbial populations in planktonic ecosystems is linked to the composition and amount of DOM, as well as to the availability of inorganic nutrients.

Recent work in the North Sea indicates bacterial diversity can affect the BGE of the overall bacterial assemblage. Reinthaler et al. (2005) demonstrate that while the function of DOM remineralization to CO₂ remains stable despite shifts in bacterial assemblage structure, the BGE is inversely related to bacterioplankton richness. This inverse relation between BGE and bacterial richness is largely mediated by bacterial production, which is generally more variable than respiration.

Interaction with Other Metabolic Pathways

The recent discovery of the widespread occurrence of rhodopsin-like pigments in a variety of heterotrophic marine bacterial groups (see Kolber et al., this issue) suggests that nonphotosynthetic light utilization may be a common feature among marine heterotrophs in surface waters. These light-harvesting pathways, which result in energy fixation but are not necessarily coupled to carbon or oxygen dynamics, could play a significant role in shaping microbial biogenergetics and thus influence the patterns in BGE. Gómez-Consarnau et al. (2007) demonstrate that proteorhodopsin-mediated photoheterotrophy significantly stimulates production of some marine Flavobacteria under oligotrophic conditions, thus supporting

energy for respiration, maintenance, and active growth. However, other laboratory studies with the alpha-Proteobacteria *Candidatus Pelagibacter ubique* were unable to resolve differences in growth response between cultures incubated in the light versus the dark using nutrient-enriched cultures (Giovannoni et al., 2005). Thus, light-mediated energy fixation could potentially increase the baseline BGE in the illuminated layers of the oceans under oligotrophic conditions by supplying additional energy to that derived from organic substrates, but the factors that control photoheterotrophy and its impact on the ocean carbon cycle are not yet fully understood.

ECOSYSTEM AND BIOGEOCHEMICAL IMPLICATIONS

As discussed above, the allocation of carbon and energy in marine bacteria depends on many factors, and it is difficult, if not impossible, to place the variation of BGE as a function of a single variable. In general terms, however, BGE will tend to be low in situations of either insufficient supply of energy and nutrients, of inappropriate stoichiometry of resource supply, or under increased maintenance and repair requirements of the cells. These environmental factors may be summarized as the level of environmental “hostility” (Figure 3). This hostility may result from extreme lack of resources (i.e., organic matter or nutrients), overabundance of others (i.e., pollutants, allelopathic substances), physical or chemical stresses (i.e., salinity and temperature gradients, UV radiation, extreme pH gradients), or a combination of these. Regardless of its

origin, increased overall environmental hostility will result in an increase in the proportion of the total flux of energy that is devoted to cell maintenance (EM). Associated with this increase in cell maintenance, it is expected that cell-specific respiration (SP) (standardized for differences in cell size among systems) should also increase to fuel the increased maintenance and repair. BGE will therefore decrease along this gradient of increasing environmental hostility. Figure 3 is hypothetical and the exact shapes of these curves are not known, but the ranges of BGE shown in the figure are realistic and are within what has been reported for marine systems, suggesting that marine bacterioplankton may experience a wide range in overall environmental hostility.

On the ecosystem level, microbial oceanographers are interested in how the hostility of the marine environment affects microbial energy partitioning and respiration and how the integration of all these individual cell processes affects the magnitude and efficiency by which organic matter flows through heterotrophic bacterioplankton. In practice, researchers have taken various approaches to determine the magnitude of organic matter flux through the oceanic bacterial component, including measurements of growth, biomass production, respiration, or a combination of the latter.

Indirect Estimates of Bacterial Carbon Demand

Estimates of BP via uptake of radioactive tracers are by far the most common measurements of bacterial metabolism and are routinely carried out in marine studies. There is thus a wealth of data

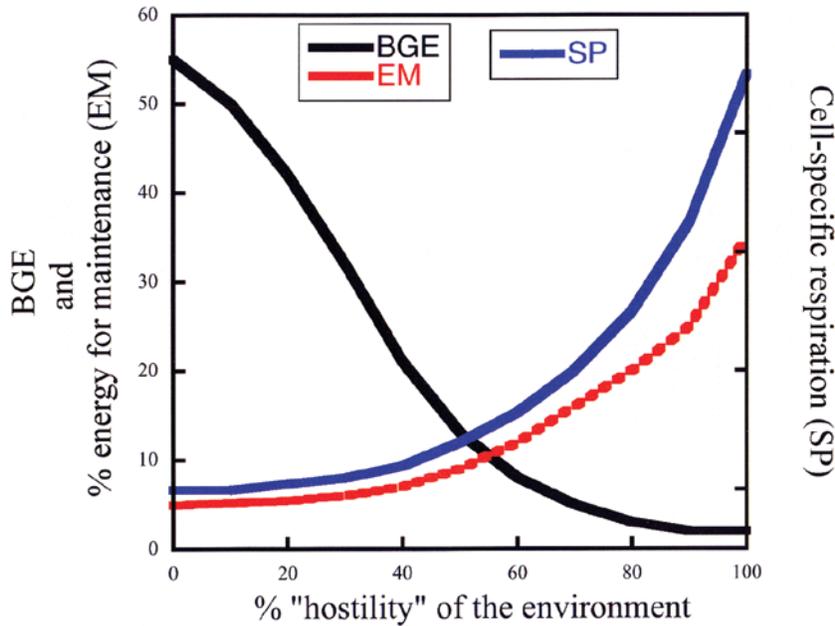


Figure 3. Conceptual diagram demonstrating the relationship between environmental stressors or environmental "hostility" and the partitioning of energy within a bacterial cell, the resulting bacterial growth efficiency (BGE), and cell specific respiration. As environmental hostility increases, more energy is partitioned into maintenance energy (EM). Thus, bacterial growth efficiency decreases and cell-specific respiration (SP) increases. Some combination of both physical (temperature, pH, salinity) and chemical (toxins, substrate availability) factors contribute to environmental hostility

from a wide range of oceanic regions (Ducklow and Carlson, 1992; Ducklow, 1999). Cole et al. (1988) first reported that, in the euphotic zone, BP was positively and significantly correlated to primary production (PP) across a wide range of aquatic ecosystems, and concluded that net BP averaged about 30% of PP. In similar analyses of seven oceanic sites, Ducklow (1999) concluded that BP was < 20% of PP.

Although the magnitude of net BP appears modest compared to PP, one must consider the efficiency by which bacterioplankton convert DOC into bacterial biomass. The flux of carbon needed to support a given estimate of BP is referred to as bacterial carbon demand (BCD). It is possible to derive BCD, and

thus total carbon consumption (BR plus BP), by combining measurements of BP with estimates of BGE, such that,

$$BCD = BP / BGE \quad [2]$$

One of the main findings in the past decade is that marine BGE is both far more variable and much lower than what was traditionally assumed in models of bacterial carbon consumption, as hypothesized by Jahnke and Craven (1995) over a decade ago. For example, there is growing evidence from field experiments that BGE generally increases along trophic gradients, from < 10% in oligotrophic oceanic water to > 20% in the most productive environments (Ducklow and Carlson, 1992; del Giorgio and Cole, 1998; Biddanda et al., 2001).

Further, a recent quantitative review of published marine BGE measurements concludes that the median BGE for the surface open ocean is 8% and for the coastal ocean is 16% (Robinson, in press). Within the ocean interior, estimates of BGE are even lower. Carlson et al. (2004) estimate BGE to be $8 \pm 4\%$ for bacterioplankton in the upper mesopelagic zone after convective overturn, and Reinthaler et al. (2006) find BGE to be < 2% in the bathypelagic zone deeper than 1000 m.

The finding that BGE is generally low but highly variable has both conceptual and practical consequences. From a conceptual point of view, these field observations support the hypothesis that, in dynamic environments under condition of low nutrient supply, microbes have evolved versatile metabolic machinery to take advantage of multiple nutrient, carbon, and energy sources. By increasing the capacity of enzymes in the uptake/assimilation systems, a larger percentage of energy is funneled into maintenance processes to safeguard metabolic flexibility at the cost of energetic efficiency (Teixeira-de-Mattos and Neijssel, 1997). From a practical point of view, a lower BGE implies a relatively larger flux of carbon to support an observed BP; thus, BCD can be a greater percentage of PP in low-productivity systems.

Interestingly, this approach generally leads to estimates of BCD in the open-ocean euphotic zone that are often similar to or greater than the estimates of local PP (Ducklow, 1999; del Giorgio et al., 1997) when PP values are low (Figure 4). Figure 4 shows integrated euphotic zone BCD estimates in relation to integrated PP. These data dem-

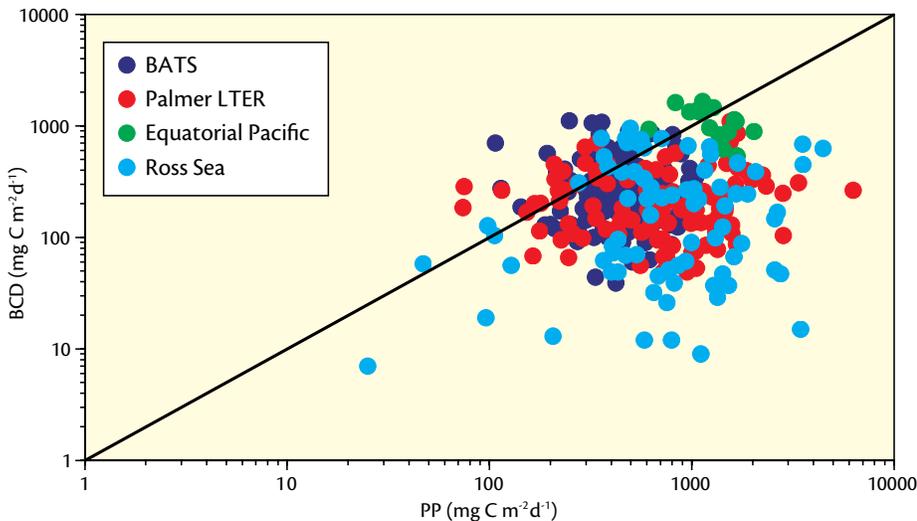


Figure 4. Relationship between integrated bacterial carbon demand (BCD) and primary production (PP) within the euphotic zone of representative ocean sites. All data are derived from paired measurements of bacterial production and PP integrated within the euphotic zone from each study site. A common bacterial growth energy of 0.1 was used to estimate BCD. The black line represents the 1:1 line. Data points that lie above this line indicate that bacterial carbon demand was greater than local primary production at the time of sample collection. The Bermuda Atlantic Time-series Study (BATS) data represent monthly values from 1991–2003 ($n = 155$; see Steinberg et al., 2001 for details; data available at <http://bats.bbsr.edu/>). Paired BP and PP from the Equatorial Pacific ($n=16$) and Ross Sea, Antarctica, ($n=77$) were calculated according to Ducklow (1999) (data available at <http://usjgofs.whoi.edu/jg/dir/jgofs/>). All data from the Palmer Peninsula, Antarctica, ($n=112$) provided by H. Ducklow and the Palmer LTER program.

onstrate that when PP is $> 1 \text{ g m}^{-2} \text{ d}^{-1}$, BCD was significantly less than local PP. However, when PP is $< 1 \text{ g m}^{-2} \text{ d}^{-1}$, BCD can be similar to or greater than local estimates of PP, indicating an apparent mismatch between what bacteria consume and what appears to be available for consumption.

Waters deeper than 200 m comprise $\approx 75\%$ of the volume of the global ocean, yet little is known about the microbial processes that persist at depth. Recent studies demonstrate enhanced prokaryotic activity and BCD within the ocean's mesopelagic and bathypelagic zones (Aristegui et al., 2005; Reinthaler et al., 2006). Reinthaler et al. (2006) compare BCD with particulate organic carbon

(POC) flux into the interior. They find that the gap between BCD and POC supply lead to a deficiency of as much as an order of magnitude at depths greater than 1000 m.

The apparent imbalance that results from combining current measurements of BP and BGE and comparing the resulting carbon consumption with primary production or POC flux (in the case of deeper waters) may be either a real feature of oceanic systems or the result of current uncertainties in the metabolic measurements. Routine measurements of BP via the thymidine or leucine uptake methods are only a proxy for bacterial production; accurate estimates are confounded by variability in

the conversion factors needed to estimate cell or carbon production (Ducklow and Carlson, 1992; Ducklow, 2000). Measurements of BGE also have their own set of shortcomings due to technical difficulties (Robinson and Williams, 2005). Thus, it is clear that our understanding of BGE and, consequently, estimates of BCD in the oceans is still very uncertain, and that direct measurements of BR and total community respiration are required to better constrain the flux of energy and organic matter in oceanic systems.

Direct Measurements of Bacterial Respiration

Bacterial respiration still represents a major technical challenge and in spite of its obvious importance, there is a paucity of direct BR measurements. The available oceanic BR data set is extremely modest, especially compared to existing measurements of other carbon fluxes, such as bacterial and algal production. A recent synthesis concluded that there are fewer than 500 individual measurements for the global euphotic ocean, which result in a median (mean \pm standard deviation) BR of $0.5 \text{ mmol C m}^{-3} \text{ d}^{-1}$ ($1.3 \pm 2.3 \text{ mmol C m}^{-3} \text{ d}^{-1}$, $n=105$) and $3.1 \text{ mmol C m}^{-3} \text{ d}^{-1}$ ($10.5 \pm 20.9 \text{ mmol C m}^{-3} \text{ d}^{-1}$, $n=332$) for the open ocean and coastal regions, respectively (Robinson in press). These rates are very significant relative to other major carbon fluxes, such as primary production and carbon export, as we discuss below.

Despite the modest size of the available database, these direct measurements of BR tend to support the patterns obtained by combining BP and BGE: bacterial carbon consumption is high,

particularly in oligotrophic systems, and often exceeds local estimates of primary production. The existing data further suggest that bacteria are the largest contributors to community respiration in the oceanic system. Within the euphotic zone of marine systems, BR represents a large fraction ($\approx 50\%$ to $> 90\%$) of community respiration (Sherr and Sherr, 1996; Biddanda et al., 2001; Rivkin and Legendre, 2001; Robinson and Williams, 2005).

Other studies using estimates of respiration from changes in O_2 in bottle experiments also report that portions of the surface oligotrophic open ocean appear to be net heterotrophic (Duarte and Agusti, 1998). But, what about metabolic balance in the open sea? The apparent discrepancy is interesting and controversial (Geider, 1997; Williams, 1998; Williams and Bowers, 1999; Goldman and Dennett, 2000), but perhaps provides insight to better interpret C and energy flow in the open sea. We explore recent findings and evaluations below.

METABOLIC BALANCE

Current evidence suggests that the total carbon consumption by heterotrophic bacteria represents one of the largest components of the marine biological carbon budget, and that much of this carbon is respired by bacteria. Respiration, on the ecosystem level, represents the largest sink of organic matter in the biosphere and accounts for the total amount of organic matter oxidized, oxygen consumed, and CO_2 produced. On a global scale, respiration must be balanced by the input of organic matter via primary production. On the local scale, this relationship can become more

complicated and potentially weakened due to temporal uncoupling between respiration and primary production (Billen, 1990) or large transport of organic matter between ocean sectors (Hansell et al., 2004), and can result in an unbalance between respiration and local production sources. Better understanding of oceanic respiration will ultimately help oceanographers assess the magnitude of organic carbon input and help interpret measurements of primary production (Williams et al., 2004).

Neither bacterial nor community respiration within any ecosystem can exceed the supply of organic carbon. In circumstances where bacteria or the net community respire more than is produced by local photosynthesis (net heterotrophy), there must be an allochthonous (outside the system) input of organic matter. Because all ecosystems are open to exchange of organic matter, local environments may not be in metabolic balance. It is easy to envision how external input of organic matter from

otrophy is counter intuitive and controversial (Williams et al., 2004).

To test the hypothesis of net heterotrophy within the euphotic zone of the oligotrophic gyres and address some criticism of temporal- and spatial-scale problems from previous studies, Williams et al. (2004) designed a year-long investigation of metabolic balance at the Hawaiian Ocean Time-series (HOT) site (Station ALOHA) in the oligotrophic North Pacific. They directly measured respiration and primary production by monitoring O_2 changes in light/dark bottles incubated for 24 hours in vitro over six depths within the euphotic zone. Their integrated results indicate a metabolic deficit equivalent to 40% of measured primary production.

Discrepancy with Geochemical Estimates

Evidence from several independent geochemical measures all point to net organic carbon production even in oligotrophic sites (Doney, 1997). For exam-

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terrestrial runoff or advected organic matter from coastal blooms can subsidize respiration in estuarine and coastal systems. But for open-ocean systems like oligotrophic gyres that are physically isolated from allochthonous inputs of labile organic matter, the notion of net heter-

ple, geochemical measurements at the two most intensively studied oligotrophic ocean sites at the Bermuda Atlantic Time-series Study (BATS) and HOT indicate annual patterns of O_2 supersaturation in the euphotic zone (Steinberg et al., 2001; Karl et al., 2003), O_2 efflux to

the atmosphere (Emerson et al., 1997), net export of sinking organic particles from the surface waters (Karl et al., 1996; Steinberg et al., 2001), vertical export of DOC from the surface 100 m (Carlson et al., 1994), and long-term accumulation of DOM in the surface waters (Church et al., 2002). All of these independent observations require net organic carbon production to reconcile the data.

How Do We Explain the Metabolic Imbalance of Aquatic Ecosystems Indicated from These Approaches?

Granted, there are errors associated with the various approaches used to estimate community respiration, including in vitro O₂ rate measurements or microbial respiration from BGE and BP (Robinson and Williams, 2005). Nonetheless, these data are still valuable and provide significant insight to our interpretation of metabolic balance. In their 2005 paper, del Giorgio and Williams state, “In reality there is essentially no imbalance, because aquatic ecosystems consume and respire all but a small amount of organic matter available. The apparent imbalances are artifacts that result from our largely insufficient understanding of the magnitude and regulation of total organic matter flux in aquatic ecosystems.” Perhaps these apparent deficits tell us something about the approach we use to assess carbon and energy flow in oceans and its interpretation.

Geochemical in situ observations provide better spatial and temporal averaging compared to in vivo incubation approaches and are considered to have greater accuracy for estimating net organic carbon production (Williams et al., 2004). Accepting the geochemi-

cal estimates as evidence of net organic matter production in the euphotic zone, Williams et al. (2004) explore alternative possibilities to explain the discrepancy. Rates of respiration are relatively constant compared to the large degree of primary productivity observed in aquatic ecosystems (del Giorgio and Williams, 2005). Part of this constancy is due to the fact that community respiration integrates all components of the food web and the various organic pools each component utilizes. In contrast, autotrophic production is more episodic and can become temporally decoupled from respiration (Karl et al., 2003). These pulses of energy and carbon from episodic events will be dampened as they flow through the heterotrophic component of the food web, thus yielding a more constant respiration signal. As a result, if the system is undersampled through time, the production term would be underestimated relative to consumption, yielding an apparent metabolic deficit (Karl et al., 2003; Williams et al., 2004).

Currently, the oceanographic benchmark for assessing the magnitude of energy and carbon that flows through an oceanic ecosystem is set by measurements of primary production. However, mass balance and inverse modeling approaches suggest that rates of organic matter production may be underestimated by a factor of two or more for ecosystems like the subtropical North Pacific gyre (Williams et al., 2004) or the global ocean (Robinson and Williams, 2005). Respiration is equal to the source of organic input and integrates over greater temporal scales; thus, in an undersampled system, it has the potential to be a more accurate measure of

integrated net organic production than photosynthesis (Williams et al., 2004; del Giorgio and Williams, 2005). Because of its great integrating properties, microbial oceanographers should include more regular measurements of respiration in future studies to better constrain the magnitude of energy flow within the oceans, and to better understand the potential mechanisms that control it. Bacterioplankton are responsible for a large fraction of oceanic respiration, and therefore a better understanding of the controls of bacterial carbon consumption, and of the partition of this carbon between anabolic and catabolic pathways, will help to better understand global ocean respiration.

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