Solar energy capture and transformation in the sea

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“Everything is based on energy. Energy is the source and control of all things, all value, and all the actions of human beings and nature.”

H. T. Odum and E. C. Odum (1976)

Ecological energy flow

Solar energy ultimately drives all biogeochemical cycles and sustains planetary habitability. All life forms and processes on Earth, including human economic and social systems, exist within a complex network of energy flow. In the sea, microorganisms comprise most of the genetic and metabolic diversity, and are responsible for a majority of the system energy flow including solar energy capture, transformation, and dissipation. All of these processes involve conversion of low quality forms of energy into a smaller fraction of higher quality energy plus degraded heat, in accordance with the basic laws of thermodynamics. Energy flow is at the core of ecosystem analysis (Odum 1968).

Sunlight is the most abundant form of energy for marine microorganisms, and biophysical/biochemical mechanisms for solar energy capture have evolved by natural selection during eons of Earth’s history (Brown and Ugliati 2004; Nealson and Rye 2003). Marine ecosystems, especially the expansive subtropical gyres, have an enormous capacity for solar energy capture and transformation. Ecologists often use the term “carbon and energy flow” to describe solar energy capture, organic matter transformation, and heat dissipation through the food web via the coupled processes of photosynthesis and respiration. A number of different methods have been used to track the flow of carbon and associated bioelements (e.g., nitrogen, phosphorus, oxygen, and sulfur), but energy flow is rarely if ever measured in field studies. An untested assumption is that matter and energy flow are inextricably and quantitatively linked in space and time in the open sea.

Howard T. Odum, largely in collaboration with his brother Eugene P. Odum, pioneered the discipline of systems ecology. He observed and studied a variety of aquatic ecosystems and was the first to characterize them as networks of energy circuits (e.g., Silver Springs, Florida; Odum 1956). Odum later developed an explicit energy circuit language and set of symbols that could be used to represent interactive energy capture, transformation, and dissipation in both natural and manmade systems (Odum 1983a). While some scientists have criticized “Odum's conjectures” and his energy-centric approach to the study of ecosystems (e.g., Månsson and McGlade 1993), the debate centers on the formidable obstacles to a comprehensive, quantitative analysis and understanding of ecological energy flow rather than a challenge to its fundamental importance in ecosystem analysis.

In a pioneering essay on the relationship of energy flow to evolution, Alfred Lotka concluded that natural selection will operate to preserve and expand those species “possessing superior energy-capturing and directing devices” (Lotka 1922). Consequently, he reasoned, as long as there is a residue of untapped available energy, “the total organic mass of the system, the rate of circulation of mass through the system, and the total energy flux” will be maximized. This reasoning has since become known as the maximum power principle (Odum and Pinkerton 1955; Odum 1983b), and has led to vigorous debate over the validity and implications of what some have termed the fourth law of thermodynamics (see Sciubba 2011 for a recent assessment).

The Earth is an energetically open system where solar energy input is balanced by radiative heat loss. There are numerous connections among the hydrosphere, lithosphere, and atmosphere such that materials and energy can be easily exchanged. In a thought-provoking commentary, On certain unifying principles in ecology, Ramon Margalef concluded that the energy required to maintain an ecosystem is inversely proportional to energy flow.
Solar energy capture and transformation in marine microbial assemblages. This change has resulted in large part from two independent discoveries of unexpected pathways of phototrophy that supplement the better understood OP pathway (Karl 2002; Figure 1 and Table 1). These two novel pathways differ significantly in the mechanism of solar energy capture and in the quantitative and mechanistic role that light energy plays in cellular metabolism. For example, both aerobic anoxygenic phototrophy (AAP) and proteorhodopsin (PR) phototrophy appear to be facultative solar energy capture processes that supplement an otherwise chemoorganoheterotrophic metabolism (Figure 1). Quantitative analysis of energy flow through these alternate pathways will require the development of new instrumentation and methodology, and will likely lead to a new paradigm of energy flow in the sea.

During the past decade, there has been a "quiet revolution" in our conceptualization of energy flow in marine systems. This change has resulted in large part from two independent discoveries of unexpected pathways of phototrophy that supplement the better understood OP pathway (Karl 2002; Figure 1 and Table 1). These two novel pathways differ significantly in the mechanism of solar energy capture and in the quantitative and mechanistic role that light energy plays in cellular metabolism. For example, both aerobic anoxygenic phototrophy (AAP) and proteorhodopsin (PR) phototrophy appear to be facultative solar energy capture processes that supplement an otherwise chemoorganoheterotrophic metabolism (Figure 1). Quantitative analysis of energy flow through these alternate pathways will require the development of new instrumentation and methodology, and will likely lead to a new paradigm of energy flow in the sea.

Table 1. Solar energy capture in marine microbial assemblages via complementary energy and carbon flow pathways.

| Sample organisms          | Metabolic type                     | Primary (secondary) electron source(s) | Primary (secondary) electron source(s) | Primary (secondary) carbon source(s) | Comments                                      |
|---------------------------|-----------------------------------|----------------------------------------|----------------------------------------|--------------------------------------|----------------------------------------------|
| Diatoms                   | Oxygenic phototroph (OP)          | Light                                  | H2O                                    | CO2                                  | Obligate photolithoautotrophy may not exist in nature |
| Prochlorococcus           | Oxygenic phototroph (OP)          | Light (Org-C)                          | H2O                                    | CO2 (Org-C)                          | Facultative mixotrophy; can also grow photolithoautotrophically |
| Roseobacter, Erythrobacter| Aerobic anoxygenic phototroph (AAP)| Light and Org-C                          | Org-C                                  | Org-C                                | Facultative photoorganoheterotrophy (mixotrophy); can also grow chemoorganoheterotrophically, but not photolithoautotrophically |
| Flavobacter, Pelagibacter, Vibrio | Prochlorophyceae-based phototroph (PR) | Light and Org-C                          | Org-C                                  | Org-C                                | Facultative photoorganoheterotrophy (mixotrophy); can also grow chemoorganoheterotrophically, but not photolithoautotrophically |

*Organic carbon

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Bacteriochlorophyll a-containing marine bacteria were first reported by Shiba et al. (1979) from coastal marine habitats. They were later rediscovered in the oligotrophic waters of the North Pacific Ocean using a
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Solar energy capture processes of OP (oxygenic phototrophy), AAP (aerobic anoxygenic phototrophy), and PR (proteorhodopsin-based phototrophy) convert solar energy into chemical bond energy as ATP plus heat, and in the case of OP a portion of the energy gain is used to reduce carbon dioxide (CO₂) to organic carbon (Org-C). The light-independent heterotrophic (HETERO) flow of carbon and energy ultimately dissipates the potential energy in Org-C to heat.

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Figure 1
Schematic view of the flow of energy (red arrows), carbon (blue arrows), or energy plus carbon (purple arrows) through a hypothetical marine system.

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Quantitative assessments of energy flow

This brief commentary has focused on new pathways for solar energy capture and transformation in the deep blue sea. However, there are also other important aspects to marine system energy flow that need to be considered. These include the cycling of: (1) dissolved organic matter (DOM), especially labile products of photosynthesis; (2) reduced biogenic gases, especially methane and hydrogen; and (3) reduced inorganic derivatives of nitrogen, phosphorus, and sulfur. These reservoirs store and shunt potential energy, and enhance the overall magnitude and efficiency of solar energy capture and transformation in the sea. In the case of DOM, the energy content of the fairly large reservoir (~75–100 mmol C per cubic meter in the euphotic zone) greatly exceeds the daily capture of solar energy and may regulate energy flow in stable oceanic communities. Even the more refractory portion (~30–40%) of the total surface DOM pool, with a mean age of a few thousand years, may represent a longer term potential energy reservoir for the growth of “low-energy” specialists. Any quantitative assessment of ocean system energy flow must be able to measure all possible pathways of energy capture, transformation, and dissipation and needs to integrate over both space and time. Two possible experimental approaches have been employed to estimate total energy flow through marine planktonic assemblages: (1) heat flow via microcalorimetry, and (2) total ATP pool turnover rate, but additional methods need to be devised, calibrated, and field-tested. Future developments in the emergent field of metabolomics, especially energy transduction and energy storage molecules, will likely provide new opportunities for field application.

Microcalorimetry has only rarely been used to estimate heat flow in marine ecosystems (Pamatmat et al. 1981; Pamatmat 1982), primarily in coastal benthic habitats where metabolic activities are relatively high. Comparison of heat flow estimated from dark rates of oxygen uptake using assumptions regarding organic substrate composition and utilization efficiencies can lead to large discrepancies with direct heat flow estimation (Pamatmat 2003). In one of the few published studies of heat flow in marine plankton (Friday Harbor, Washington), the direct calorimetric-based value of 200–300 µW per liter was 4–6 times larger than that derived from extrapolation based on oxygen utilization (Pamatmat 2003). However, calorimetry currently suffers from several limitations. First, the nature of the differential microcalorimeters used for ecological studies cannot be used to assess solar energy for capture directly or to resolve biotic versus abiotic reactions. Second, the specialized nature of differential microcalorimeters limits sample throughput and replication. Finally, the relatively insensitive limits of heat detection preclude measurements in most open ocean planktonic ecosystems and, even for those systems that can be measured, calorimetry requires fairly long incubation periods which may bias estimates of in situ energy flow.

Recently, Djamali et al. (2012) have employed a purpose-built, differential microcalorimeter to measure the heat output of the marine microbial food web with an emphasis on the role of viral lysis. They experimented with aquarium-reared, size-fractionated model systems that were diluted to provide treatments with or without viruses. Their results indicated that approximately 25% of the total heat flow in their artificial planktonic communities could be attributed to viral activities. While the claim is made that their novel instrument is capable of measuring the heat produced from open ocean assemblages of ~10^9 bacterial cells ml^-1 without pre-concentration (Djamali et al. 2012), no such data are presented, or to my knowledge published elsewhere. Nevertheless, recent improvements in technology are very encouraging for possible use in future field studies (see review by Braissant et al. 2010). The three major limitations of calorimetry, however, remain: (1) inability to resolve biotic from abiotic processes, (2) difficulty measuring light versus dark energy heat fluxes, and (3) low sample throughput and lack of sample and reference replication for most commercial microcalorimeters.

An alternative to direct estimation of heat flow is the measurement of the turnover rate of the ATP pool in the microbial community (Karl and Bossard 1985). The central role of ATP in the stoichiometric coupling of all energy transforming metabolic reactions (phototrophic as well as chemotrophic) has been known since the pioneering work of Lipmann (1941). While intracellular ATP concentrations (i.e., the so-called “ATP pool”) are fairly well buffered at 1–3 mM, the turnover rate of the pool tracks metabolic energy flow. ATP pool turnover results from the hydrolysis of one or both “high energy” phosphate bonds, followed by regeneration of ATP via substrate level, oxidative, or photophosphorylation. Because ATP is the common energy currency in all organisms and because the free energy of ATP hydrolysis is well constrained (46 ± 4 kJ per mol; Bridger and Henderson 1983), direct measurements of ATP pool turnover coupled with ATP
concentration should provide a quantitative estimation of biological energy flux (Karl 1993). Both heat flow and ATP pool turnover might be viewed as the epitome of reductionism because neither approach provides explicit information on which organisms or which pathways are most important in natural systems. Clearly in order to be useful, energy flow measurements need to be part of the holistic study of ecosystems and used as a tool in experimental perturbation studies to learn more about the controls on energy capture, transformation, and dissipation in marine systems.

Future research prospectus

As we move further into the anthropocene and continue to alter the sea around us, we need to have the capacity to monitor changes in the most fundamental property of the system, namely energy flow. The future ocean will be warmer, more stratified and nutrient starved, more acidic, and less oxygenated as a consequence of anthropogenic forcing by greenhouse gas emissions (Gruber 2011). These habitat changes will impact solar energy capture and transformation by microbial assemblages, so there is an urgent need to improve our conceptual understanding and quantitative assessments of energy flow in the open sea. I consider this to be one of the greatest contemporary challenges in microbial oceanography and marine ecology. The Center for Microbial Oceanography: Research and Education (C-MORE) is poised to begin a systematic two-year study (2014–2015) of planktonic community energy flow in the NPSG with an emphasis on pathways and controls. Once a comprehensive energy budget is available for the NPSG microbial assemblage, other fundamental properties including the maximum empower selection principle (Odum 1983b; Scibba 2011), net metabolic balance (Ducklow and Doney 2013), the concept of energy equivalents and transformity (Odum 1983a), and the enigma of microbial production of recalcitrant organic matter (Jiao et al. 2010) can be systematically investigated. The development of a new theoretical framework for solar energy capture and energy flow via microorganisms in the sea may also be of practical value for policy makers and society as a whole (Prosser et al. 2007). As our demands for renewable energy continue to increase, a better understanding of the unique evolutionary adaptations of our magnificent marine microbes might improve our standard of living and extend our survival as a species.

References

Béjà O, Aravind L, Koonin EV, Suzuki MT, Hadd A, et al. 2000. Bacterial rhodopsin: Evidence for a new type of phototrophy in the sea. Science 289(5486): 1902–1906.
Béjà O, Spudich EN, Spudich JL, Leclerc M, DeLong EF. 2001. Proteorhodopsin phototrophy in the ocean. Nature 411(6839): 786–789.
Braissant O, Wize D, Gópfert B, Daniels AU. 2010. Use of isothermal microcalorimetry to monitor microbial activities. FEMS Microbiol. Lett 303: 1–8.
Bridger WA, Henderson JF. 1983. Cell ATP. New York: John Wiley & Sons.
Brown MT, Ulgiati S. 2004. Energy quality, energy, and transformity: H. T. Odum's contributions to quantifying and understanding systems. Ecol. Model 178(1–2): 201–213.
DeLong EF, Béjà O. 2010. The light-driven proton pump Proteorhodopsin enhances bacterial survival during tough times. PLoS Biol 8(4): e1000359. doi: 10.1371/journal.pbio.1000359
Djamilé E, Nulton JD, Turner PJ, Rohwer F, Salamon P. 2012. Heat output by marine microbial and viral communities. J. Non-Equil. Thermodyn 37(3): 291–313.
Ducklow HW, Doney SC. 2013. What is the metabolic state of the oligotrophic ocean? A debate. Ann. Rev. Mar. Sci 5: 525–53.
Frigaard NU, Martinez A, Mincer TJ, DeLong EF. 2006. Proteorhodopsin lateral gene transfer between marine planktonic Bacteria and Archaea. Nature 439(7078): 847–850.
Gómez-Consarnau L, González JM, Coll-Lladó M, Gourdon P, Pascher T, et al. 2007. Light stimulates growth of proteorhodopsin-containing marine Flavobacteria. Nature 445(7124): 210–213.
Gómez-Consarnau L, Akram N, Lindell K, Pedersen A, Neutze R, et al. 2010. Proteorhodopsin phototrophy promotes survival of marine bacteria during starvation. PLoS Biol 8(4): e1000358. doi: 10.1371/journal.pbio.1000358
Grande KD, Williams PJLeB, Marra J, Purdie DA, Heinemann K, et al. 1989. Primary production in the North Pacific gyre: a comparison of rates determined by the 14C, O2 concentration and 18O methods. Deep-Sea Res. Part A 36(11): 1621–1634.
Gruber N. 2011. Warming up, turning sour, losing breath: ocean biogeochemistry under global change. Phil. Trans. Royal Soc. A — Math. Phys. Eng. Sci 369(1943): 1980–1996.
Helm-Hansen O, Booth CR. 1966. The measurement of adenosine triphosphate in the ocean and its ecological significance. Limnol. Oceanogr 11(4): 510–519.
Jiao N, Hernal GJ, Hansell DA, Bennet R, Kattner G, et al. 2010. Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean. Nature Rev. Microbiol 8(8): 593–598.
Karl DM. 1993. Adenosine triphosphate (ATP) and total adenine nucleotide (TAN) pool turnover rates as measures of energy flux and specific growth rate in natural populations of microorganisms, in Kemp PF, Sherr BF, Sherr EB, Cole JJ, eds., Current Methods in Aquatic Microbial Ecology. Boca Raton, Florida: Lewis Publishers: p. 483–494.
Karl DM. 2002. Hidden in a sea of microbes. Nature 415(6872): 590–591.
Karl DM, Bossard P. 1985. Measurement and significance of ATP and adenine nucleotide pool turnover in microbial cells and environmental samples. J. Microbiol. Meth 3(3–4): 125–139.
Solar energy capture and transformation in the sea

Karl DM, Bidigare RR, Letelier RM. 2002. Sustained and aperiodic variability in organic matter production and phototrophic microbial community structure in the North Pacific Subtropical Gyre, in Williams Pjell, Thomas DR, Reynolds CS, eds., Phytoplankton Productivity and Carbon Assimilation in Marine and Freshwater Ecosystems. London: Blackwell Publishers: p. 222–264.

Kimura H, Young CR, Martinez A, DeLong EF. 2011. Light-induced transcriptional responses associated with proteorhodopsin-enhanced growth in a marine flavobacterium. ISME J 5(10): 1641–1651.

Kirchman DL, Hanson TE. 2013. Bioenergetics of phototrophetotrophic bacteria in the oceans. Environ. Microbiol. Reports 5(2): 188–199.

Koblicz M, Beja O, Bidigare RR, Christensen S, Benitez-Nelson B, et al. 2003. Isolation and characterization of Erythrobacter sp. Strains from the upper ocean. Arch. Microbiol 180(5): 327–338.

Koblicz M, Mloušková J, Kolber Z, Kopecký J. 2010. On the photosynthetic properties of marine bacterium COL2P belonging to Roseobacter clade. Arch. Microbiol 192(1): 41–49.

Kolber ZA, Van Dover CL, Niederman RA, Falkowski PG. 2000. Bacterial photosynthesis in surface waters of the open ocean. Nature 407(6801): 177–179.

Kolber Z. 2007. Energy cycle in the ocean: Powering the microbial world. Oceanogr 20(2): 79–88.

Kolber ZS, Prasül O, Falkowski PG. 1998. Measurements of variable chlorophyll fluorescence using fast repetition rate techniques: defining methodology and experimental protocols. Biochim. Biophys. Acta 1367(1–3): 88–106.

Kolber ZA, Plumley FG, Lang AS, Beatty JT, Blankenship RE, et al. 2001. Contribution of aerobic phototrophetotrophic bacteria to the carbon cycle of the ocean. Science 292(5526): 2492–2495.

Lipschitz A. 1941. Metabolic generation and utilization of phosphate bond energy. Adv. Enzymol 1: 99–162.

Lotka AJ. 1922. Proc. Natl. Acad. Sci. USA 8(6): 151–154.

Margalef R. 1963. On certain unifying principles in ecology. Amer. Naturalist 97(3): 357–374.

MacKenzie TDB, Burns RA, Campbell DA. 2004. Carbon status constrains light acclimation in the cyanobacterium Synechococcus elongatus. Plant Physiol 136(2): 3301–3312.

Måsson BA, McGlade JM. 1993. Ecology, thermodynamics and H. T. Odum's conjectures. Oecologia 93(4): 582–596.

Marchetti A, Schruth DM, Durkin CA, Parker MS, Kodner RB, et al. 2012. Comparative metatranscriptomics identifies molecular bases for the physiological responses of phytoplankton to varying iron availability. Proc. Natl. Acad. Sci. USA 109(6): E317–E325.

Martinez A, Bradley AS, Walsdauer JR, Summons RE, DeLong EF. 2007. Proteorhodopsin photosystem gene expression enables photophosphorylation in a heterologous host. Proc. Natl. Acad. Sci. USA 104(13): 5590–5595.

Nealson KH, Rye R. 2003. Evolution of metabolism, in Schlesinger WH, ed., Systems Ecology: An Introduction, New York: John Wiley & Sons.

Odum HT. 1956. Primary production in flowing waters. Limnol. Oceanogr 1(2): 102–117.

Odum EP. 1968. Energy flow in ecosystems: A historical review. Am. Zoologist 8(1): 11–18.

Odum HT. 1983a. Systems Ecology: An Introduction. New York: John Wiley & Sons.

Odum HT. 1983b. Maximum power and efficiency: A rebuttal. Ecol. Model 20(1): 71–82.

Odum HT. 1976. Energy Basis for Man and Nature. New York: McGraw-Hill Book Co.

Packard TT. 1971. The measurement of respiratory electron transport activity in marine plankton. J. Mar. Res 29: 235–244.

Pamatmat MM. 1986. Heat production by sediment: ecological significance. Science 235(4531): 395–397.

Pamatmat MM. 2003. Heat-flow measurements in aquatic ecosystems. J. Plankton Res 25(4): 461–464.

Shiba T, Simidu U, Taga N. 1979. Distribution of aerobic bacteria which contain Bacteriochlorophyll a. Appl. Environ. Microbiol 38(1): 43–45.

Shiba T, Simidu U, Taga N. 1979. Distribution of aerobic bacteria which contain Bacteriochlorophyll a. Appl. Environ. Microbiol 38(1): 43–45.

Slamovits CH, Okamoto N, Burri L, James ER, Keeling PJ. 2011. A bacterial proteorhodopsin proton pump in marine eukaryotes. Nature Comm 2(Article 183): doi:10.1038/ncomms1188.

Steindler L, Schwallbach MS, Smith DP, Chan F, Giovannoni SJ. 2011. Energy starved Candidatus Pelagibacter ubique substitutes light-mediated ATP production for endogenous carbon respiration. PLoS One 6(5): e19725. doi: 10.1371/journal.pone.0019725.

Wang Z, O'Shaughnessy TJ, Soto CM, Rahbar AM, Robertson KL, et al. 2012. Function and regulation of Vibrio campbellii proteorhodopsin: Acquired photosynthesis in a classical organoheterotroph. PLoS ONE 7(6): e38749.

Yoshizawa S, Kawanabe A, Ito H, Kandori H, Kogure K. 2012. Diversity and functional analysis of proteorhodopsin in marine Flavobacteria. Environ. Microbiol. doi: 10.1111/j.1462-2920.2012.02702.x

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