Vitamins in the sea

Stephen J. Giovannoni[1]
Department of Microbiology, Oregon State University, Corvallis, OR 97331

Nearly half of all photosynthesis happens in the oceans, in communities of microscopic microbial plankton that can vary greatly in time and space. On the one hand these communities are ephemeral, changing with changing ocean conditions, but on the other they can be counted on to cycle in predictable patterns driven by seasons, weather, and ocean currents (1, 2). In PNAS, Sañudo-Wilhelmy et al. (3) explore vitamin concentrations in the oceans, showing that B vitamins are distributed in complex patterns and offering the idea that they might be important factors controlling microbial plankton community composition. The issue considered is not gross ocean productivity but rather the composition of plankton communities, which can impact geochemical cycles.

The search for growth factors that control community composition is an old tradition in oceanography that often appears under the heading "bottom-up control," to differentiate it from predation by viruses, protists, and zooplankton, which can alter community composition by selective cropping (4). Compounds of phosphorus and nitrogen are widely understood to be the major drivers of ocean productivity and plankton community structure, but, famously, in the 1970s iron was recognized as running a close third. Many other elements contend on the list, including silica, which is required by diatoms as a structural component of their frustules, and a number of trace metals that cells use as enzyme cofactors. The distribution of trace metals in the ocean was explored under the auspices of the National Science Foundation in the "Geotracers" program, which revealed striking patterns in many biologically important metals, including Co, Zn, and Cu (5).

Despite recognition of the importance of iron and the success of Geotracers, today only part of the variation in plankton communities can be predicted from chemistry and physics. A thought on many minds is that biological molecules dissolved in the water column might be a missing piece of the puzzle (6). In pursuit of this idea, oceanographers are turning their attention to vitamins. The amount of data directly supporting the hypothesis that vitamins control marine microbial communities remains small. One of the most cited reports demonstrated the stimulation of phytoplankton photosynthesis in the Ross Sea by the addition of both iron and vitamin B_{12} (7). The field is primed for further work aimed at getting to the bottom of this question.

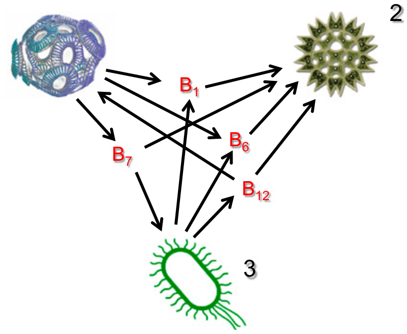

Fig. 1. Simple model for metabolic outsourcing and vitamin traffic in a plankton community where phytoplankton species 1 produces three B vitamins, phytoplankton species 2 produces none, and bacterium species 3 produces three B vitamins. Phytoplankton species 1 is auxotrophic for B_7, which is produced by bacterial species 3, and 3 requires B_{12}, made by A. Phytoplankton species 2, an auxotroph for all four B vitamins, cannot survive without species 1 and 3, but in principle it can be smaller, simpler, and reproduce more efficiently than species 1. Note that none of the species in this example can reproduce without vitamins produced by at least one other community member.

Vitamins are truly "old school," having been topics of extensive research on nutrition and long recognized as requirements for many phytoplankton strains cultured in laboratories (8). Many microbial plankton species are auxotrophic for one or more vitamins—that is, they lack one or more vitamin biosynthetic pathways and therefore must gather essential vitamins from the environment (9). Possession of a vitamin biosynthetic pathway means independence, at the cost of synthesis. It is not difficult to imagine how this might influence the species distributions in plankton communities: a cell that needs a vitamin can only thrive in a community that provides it.

Vitamin traffic may explain some of the network connectedness that has been observed in ocean microbial plankton communities (10). Connectedness has become an important concept in ecology because it can help explain the responses of biological communities to stresses (11). In oceanography connectedness is manifested as correlations in the abundances of species. When two populations are correlated, it could be because they are interacting directly or because they are both controlled by the same environmental factor. Most often connectedness is associated with trophic interactions, for example, in predator–prey relationships. Microbial plankton communities seem to be highly connected, but there is little direct evidence about the nature of the interactions.

Vitamins are perhaps the most well-known and historical examples of biological molecules that are involved in intracellular traffic, but other examples have emerged of metabolic requirements being outsourced to the community (12, 13). In our work with the highly abundant SAR11 clade of marine chemoheterotrophs, we sought to understand how genome streamlining impacted metabolism. Our objectives were both practical—to learn how to grow these enigmatic cells, and theoretical—to understand what metabolic functions were dispensable as selection shrank genome size in these ultra-efficient, small cells. *Pelagibacter sp.*, the main experimental strains of SAR11, have very unusual requirements for reduced sulfur compounds (14) and for glycine or glycine precursors (15). Both requirements were traced to genome reduction.

Our interpretation of these observations is that evolution is a good integrator—in the periodically fluctuating ocean milleau, fluxes of reduced sulfur and glycine compounds are sufficient to meet SAR11 requirements most of the time, so the fitness advantages of smaller genomes and lower cell replication costs offset the potential gain in fitness that would come from autonomy when reduced sulfur and glycine compounds are in short supply. Interestingly, *Pelagibacter* seems to synthesize at least some of its own vitamins (16). This suggests that these compounds, which are just as essential for cell growth as glycine and reduced sulfur, must not be sufficiently available to offset the costs of maintaining biosynthetic pathways for these compounds in the genome. The presence of vitamin biosynthetic pathways in highly streamlined cells suggests that Sañudo-Wilhelmy et al. (3) are on the right track, implicating vitamin distributions in ecology. If vitamins were always available from the environment, why would organisms retain these genes in the

Author contributions: S.J.G. wrote the paper.

The author declares no conflict of interest.

See companion article on page 14041.

[1]E-mail: steve.giovannoni@oregonstate.edu.

face of strong selective pressures for genome reduction?

An important question is, what determines which cells in a community do not make vitamins and instead outsource this function to other community members, creating a vitamin traffic pattern? So far most of the information about vitamin traffic in nature is indirect. Morris et al. (17) coined a clever name for the general phenomenon of some community members relying on others for services: the black queen hypothesis. "Black queen" is a reference to the ace of spades in the card game "hearts," where the objective is to avoid taking the ace of spades. The idea is that within a microbial community some cell populations might supply essential functions that other populations benefit from. In their article describing the black queen hypothesis, Morris et al. examined the theoretical side of this idea. Surprisingly, they did not discuss vitamins, which may be the most widespread and important example of metabolic outsourcing.

Although oceanographers are alert to the potential significance of vitamins, there have not been enough data about vitamin distributions and turnover in the oceans to paint a clear picture. Sañudo-Wilhelmy et al. (3) provide the most comprehensive data to date, showing a latitudinal variation of all five B vitamins along the northeast Pacific margin. Each vitamin showed a different distribution, with drops below detection thresholds over extensive regions. Presumably, in regions where a vitamin was present at picomolar concentrations, cells auxotrophic for that vitamin (requiring it but lacking the necessary biosynthetic pathways for its synthesis) could thrive. The scarceness of the vitamins in some regions and their dynamic variation are a strong argument for further research aimed to determine how vitamin traffic works and when and where it exerts an influence in shaping community structure.

One reason we do not know more about vitamins in the oceans is that they are challenging to measure.

One reason we do not know more about vitamins in the oceans is that they are challenging to measure. Researchers face not only the traditional problems of sampling the oceans but also the difficulty of accurately measuring traces of compounds in a complex, high-salt solution. Advances in mass spectrometry are playing an important role in the development of better methods. Sañudo-Wilhelmy et al. (3) use solid phase extraction coupled with liquid chromatography/tandem mass spectrometry and achieved detection thresholds below 1 pM. It is important to be cognizant that environmental vitamin concentration measurements do not necessarily tell us whether vitamins are available, because it is flux that matters, and vitamin traffic can be happening at concentrations below detection thresholds. With that caveat in mind, it is still a big step forward to begin mapping environmental variation.

There are good reasons for a broad swath of scientists to keep an eye on the question of vitamins and ocean ecology. A recent report described some of the first evidence that iron-fertilized diatom blooms can sink far enough and fast enough to sequester carbon for timescales of centuries (18). Diatom-dominated communities are particularly inclined to cause carbon sequestration because of their rapid rate of sinking. Although ocean fertilization remains controversial (19), it is such an important topic that it is bound to stimulate further inquiry into the role played by organic growth factors in determining plankton community composition and productivity.

ACKNOWLEDGMENTS. This work was supported by a grant from the Marine Microbiology Initiative of the Gordon and Betty Moore Foundation (to S.J.G.) and National Science Foundation Microbial Observatory Grant MCB-0237713.

1. Giovannoni SJ, Vergin KL (2012) Seasonality in ocean microbial communities. *Science* 335:671–676.
2. Gilbert JA, et al. (2012) Defining seasonal marine microbial community dynamics. *ISME J* 6:298–308.
3. Sañudo-Wilhelmy SA, et al. (2012) Multiple B-vitamin depletion in large areas of the coastal ocean. *Proc Natl Acad Sci USA* 109:14041–14045.
4. Thingstad TF (2000) Elements of a theory for the mechanisms controlling abundance, diversity, and biogeochemical role of lytic bacterial viruses in aquatic systems. *Limnol Oceanogr* 45:1320–1328.
5. Aparicio-Gonzalez A, Duarte CM, Tovar-Sanchez A (2012) Trace metals in deep ocean waters: A review. *J Mar Syst* 100:26–33.
6. Panzeca C, et al. (2006) B vitamins as regulators of phytoplankton dynamics. *Eos Trans* 87:593.
7. Bertrand EM, et al. (2007) Vitamin B12 and iron colimitation of phytoplankton growth in the Ross Sea. *Limnol Oceanogr* 52:1079–1093.
8. Provasoli L, Carlucci AF (1974) Vitamins and growth regulators. *Algal Physiology and Biochemistry*, ed Stewart WDP (Blackwell Scientific, Oxford), pp 741–787.
9. Croft MT, Warren MJ, Smith AG (2006) Algae need their vitamins. *Eukaryot Cell* 5:1175–1183.
10. Fuhrman JA, Steele JA (2008) Community structure of marine bacterioplankton: Patterns, networks, and relationships to function. *Aquat Microb Ecol* 53:69–81.
11. Gross T, Rudolf L, Levin SA, Dieckmann U (2009) Generalized models reveal stabilizing factors in food webs. *Science* 325:747–750.
12. Morris JJ, Johnson ZI, Szul MJ, Keller M, Zinser ER (2011) Dependence of the cyanobacterium Prochlorococcus on hydrogen peroxide scavenging microbes for growth at the ocean's surface. *PLoS ONE* 6:e16805.
13. Callanan M, et al. (2008) Genome sequence of *Lactobacillus helveticus*, an organism distinguished by selective gene loss and insertion sequence element expansion. *J Bacteriol* 190:727–735.
14. Tripp HJ, et al. (2008) SAR11 marine bacteria require exogenous reduced sulphur for growth. *Nature* 452:741–744.
15. Tripp HJ, et al. (2009) Unique glycine-activated riboswitch linked to glycine-serine auxotrophy in SAR11. *Environ Microbiol* 11:230–238.
16. Giovannoni SJ, et al. (2005) Genome streamlining in a cosmopolitan oceanic bacterium. *Science* 309:1242–1245.
17. Morris JJ, Lenski RE, Zinser ER (2012) The Black Queen Hypothesis: Evolution of dependencies through adaptive gene loss. *mBio*, 10.1128/mBio.00036-12.
18. Smetacek V, et al. (2012) Deep carbon export from a Southern Ocean iron-fertilized diatom bloom. *Nature* 487:313–319.
19. Buesseler KO, et al. (2008) Environment. Ocean iron fertilization—moving forward in a sea of uncertainty. *Science* 319:162.