



Note added in proof*

The field of marine N₂ fixation has moved forward at a rapid pace since we prepared the final draft of this review article nearly two years ago. It is not possible to summarize all of the data, however, we believe that mention of a few papers will provide the reader with access to new lines of research. In addition, several recent review articles that deal, in part, with marine N₂ fixation have also appeared (Capone 2001, Codispoti et al. 2001; Cullen et al. 2002).

The most important recent publication, in our view, is the discovery of unicellular N₂-fixing cyanobacteria in the subtropical North Pacific Ocean (Zehr et al. 2001). The *in situ* expression of nitrogenase in this diverse, numerically abundant population of phototrophs suggests that environmental rates of N₂ fixation, based on extrapolation of *Trichodesmium* distributions and abundances – which is not a very precise method to begin with (Chang 2000) – may have been systematically underestimated in this environment. Likewise, the discovery of small (<10 μm) coccoid (non-heterocystous) cyanobacteria in the Baltic Sea also requires a recalculation of the impact of N₂ fixation as a source of new nitrogen in that habitat (Wasmund et al. 2001). More discoveries of novel N₂ fixing microorganisms are likely to follow in future years.

Recent studies of the oligotrophic regions of the western North Atlantic Ocean have focused on the dynamics of the dissolved P pools and the N:P stoichiometry of the ambient inorganic and organic substrate pools. Wu et al. (2000) and Cavender-Bares et al. (2001) presented evidence that the bioavailable pool of soluble reactive phosphorus in the western North Atlantic Ocean near Bermuda was <1 nM compared to values that were 1–2 orders of magnitude higher in the oligotrophic North Pacific Ocean near Hawaii. Wu et al. (2000) hypothesized that these regional differences were a result of a larger atmospheric flux of iron in the Atlantic Ocean. The iron-sufficient Atlantic would sustain enhanced N₂ fixation, resulting in the efficient and complete removal of bioavailable phosphorus (Wu et al. 2000). This model

* This note in proof refers to the article “Dinitrogen fixation in the world’s oceans” by Karl et al., pp. 47–98 of this issue.

supports the suggestion that dust-derived iron may control N₂ fixation in the North Pacific Ocean, as discussed in the body of our review.

Consistent with the suggestion that the western North Atlantic Ocean may be iron-sufficient, Sañudo-Wilhelmy et al. (2001) have recently reported that the activities of field-collected *Trichodesmium* were independent of dissolved iron concentrations or the iron cell quotas of the colonies. They further concluded that the structural iron requirements for the growth of N₂-fixing microorganisms may be lower than previously calculated; a revised iron efficiency metabolic model has now been prepared (Kustka et al. 2002). Sañudo-Wilhelmy et al. (2001) also concluded that the phosphorus cell quota may control N₂-fixation rates in *Trichodesmium*, and at least one recent deterministic model for the control of marine N₂ fixation, has explicitly included both dissolved inorganic phosphorus concentrations and the nitrogen-to-phosphorus ratios in diazotrophs as key environmental controls (Fennel et al. 2002). Ongoing research at two open ocean time-series stations, BATS and HOT, will continue to focus on the rates, mechanisms, controls and ecological consequences of N₂ fixation (Orcutt et al. 2001; Church et al. 2002; Dore et al. 2002) during the next decade.

References

- Capone DG (2001) Marine nitrogen fixation: what's the fuss? *Curr. Opin. Microbiol.* 4: 341–348
- Cavender-Bares KK, Karl DM & Chisholm SW (2001) Nutrient gradients in the western North Atlantic Ocean: Relationship to microbial community structure and comparison to patterns in the Pacific Ocean. *Deep-Sea Res.* I 48: 2373–2395
- Chang J (2000) Precision of different methods used for estimating the abundance of the nitrogen-fixing marine cyanobacterium, *Trichodesmium* Ehrenberg. *J. Exp. Mar. Biol. Ecol.* 245: 215–224
- Church MJ, Ducklow HW & Karl DM (2002) Multiyear increases in dissolved organic matter inventories at Station ALOHA in the North Pacific Subtropical Gyre. *Limnol. Oceanogr.* 47: 1–10
- Codispoti LA, Brandes JA, Christensen JP, Devol AH, Naqvi SWA, Paerl HW & Yoshinari T (2001) The oceanic fixed nitrogen and nitrous oxide budgets: Moving targets as we enter the anthropocene? *Sci. Mar.* 65 (Suppl. 2): 85–105
- Cullen JJ, Franks PJS, Karl DM & Longhurst A (2002) Physical influences on marine ecosystem dynamics. In: Robinson AR, McCarthy JJ & Rothschild BJ (Eds) *The Sea*, Volume 12 (pp 297–336). John Wiley & Sons, Inc., New York
- Dore JE, Brum JR, Tupas LM & Karl DM (2002) Seasonal and interannual variability in sources of nitrogen supporting export in the oligotrophic subtropical North Pacific Ocean. *Limnol. Oceanogr.*, in press
- Fennel K, Spitz YH, Letelier RM, Abbott MR & Karl DM (2002) A deterministic model for N₂ fixation at stn. ALOHA in the subtropical North Pacific Ocean. *Deep-Sea Res.* II 49: 149–174

- Kustka A, Sañudo-Wilhelmy S, Carpenter EJ, Capone DG & Raven JA (2002) A revised iron use efficiency model of nitrogen fixation, with special reference to the marine N_2 fixing cyanobacterium, *Trichodesmium* spp. (Cyanophyta). J. Phycol., in press
- Orcutt KM, Lipschultz F, Gundersen K, Arimoto R, Michaels AF, Knap AH & Gallon JR (2001) A seasonal study of the significance of N_2 fixation by *Trichodesmium* spp. at the Bermuda Atlantic Time-series Study (BATS) site. Deep-Sea Res. II 48: 1583–1608
- Sañudo-Wilhelmy SA, Kustka AB, Gobler CJ, Hutchins DA, Yang M, Lwiza K, Burns J, Capone DG, Raven JA & Carpenter EJ (2001) Phosphorus limitation of nitrogen fixation by *Trichodesmium* in the central Atlantic Ocean. Nature 411: 66–69
- Wasmund N, Voss M & Lochte K (2001) Evidence of nitrogen fixation by non-heterocystous cyanobacteria in the Baltic Sea and re-calculation of a budget of nitrogen fixation. Mar. Ecol. Prog. Ser. 214: 1–14
- Wu J, Sunda W, Boyle EA & Karl DM (2000) Phosphate depletion in the western North Atlantic Ocean. Science 289: 759–762
- Zehr JP, Waterbury JB, Turner PJ, Montoya JP, Omoregie E, Steward GF, Hansen A & Karl DM (2001) Unicellular cyanobacteria fix N_2 in the subtropical North Pacific Ocean. Nature 412: 635–638