

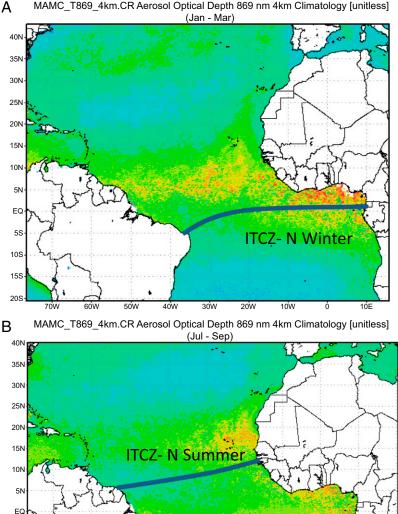


An iron curtain in the Atlantic Ocean forms a biogeochemical divide

Douglas G. Capone¹

Department of Biological Sciences and Wrigley Institute for Environmental Studies, University of Southern California, Los Angeles, CA 90089

the Sea. Longhurst identified distinct oceanic The concept of biogeochemical provinces in the ocean was implicit in Longhurst's (1) zones based on the relationships of oceanic classic monograph, Ecological Geography of biology (using chlorophyll, a proxy for



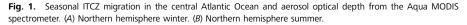
MAMC_T869_4km.CR Aerosol Optical Depth 869 nm 4km Climatology [unitless]

phytoplankton biomass, and primary production) to physical forcing (e.g., surface currents, mixing depth, and upwelling). As we have advanced over the last several decades in our understanding of the nutrient biogeochemistry of the seas, it has become evident that there are also distinct provinces with respect to nutrient dynamics. Many of these zones map directly on Longhurst's eco-geography. For example, Sohm et al. (2) recently proposed regions of the sea with characteristic populations of nitrogen fixers and distinct controls on these populations. In PNAS, Schlosser et al. (3) now provide compelling field evidence of two distinct biogeochemical provinces of the tropical Atlantic Ocean with respect to the distribution of nitrogen fixation. These provinces are primarily defined by another physical phenomenon, the Atlantic InterTropical Convergence Zone (ITCZ). In tandem, Schlosser et al. (3) also firmly establish the importance of iron as a major control on nitrogen fixation in these two ocean basins.

During the late 1990s, analysis of the comprehensive ocean nutrient surveys that had taken place over the previous decades provided evidence of excesses of regenerated nitrate relative to phosphate in subeuphotic waters of the North Atlantic. This process led to the hypothesis that nitrogen fixation in the overlying surface waters was responsible for this excess and, moreover, might be a quantitatively more important process in the marine nitrogen cycle than thought to be at that point (4). Given the concurrent developing recognition of the heightened cell quota of marine nitrogen fixers for iron (5), the substantial flux of aeolian iron into the North Atlantic from northwest African deserts was thought to be a driver of this excess (4-6).

Schlosser et al. (3) undertook two major research expeditions, which sampled the North and South Atlantic across the equator, and have identified a sharp ecological boundary for nitrogen fixation associated with the ITCZ. North of the ITCZ the biomass of

Author contributions: D.G.C. wrote the paper The author declares no conflict of interest See companion article on page 1438 ¹E-mail: capone@usc.edu



30W

20W

0.12

10W

0.16

10E

0.2

0.0

60W

50 W

0.04

40W

0.08

55

105

a predominant nitrogen fixer, the cyanobacterium Trichodesmium spp., and rates of nitrogen fixation are much greater than to the south. In parallel with these biological gradients, dissolved iron concentrations are much higher and phosphate concentrations are much lower to the north (7). Low phosphate is presumably a function of its drawdown by primary production supported by nitrogen fixation. Importantly, the two field campaigns were undertaken during contrasting periods in the annual migration of the ITCZ with its northernmost penetration during the northern summer (centered at about 6° N) compared with the northern winter when it is close to the equator (Fig. 1). The observed boundary in nitrogen fixation and upper ocean chemistry migrated concurrently with the ITCZ [figure 3 in Schlosser et al. (3)].

Dust deposition, the climate of the ITCZ, and surface currents appear to combine to create these two biogeochemical provinces. Dust fluxes from northwest Africa into the North Atlantic are the most significant aeolian fluxes into the global ocean (8, 9). These fluxes vary seasonally, with maxima in the northern spring (April, May, June) and minima in the northern fall (September, October, November) (9, 10). The ITCZ is an area of intense precipitation that washes out much of this dust and its associated iron to the surface waters, in the process making it soluble and available for the marine biota (8, 9). In parallel, the ITCZ also decreases surface salinity. Prevailing surface currents sweep the products of wet deposition predominantly to the west and north into the Sargasso Sea. Hence, the ITCZ forms an "iron curtain" shielding the South Atlantic from the influence of this input, as pointed out by Subramaniam et al. (11).

The ITCZ may have a similar structuring effect throughout the world's oceans. An earlier study suggested that changes in several chemical parameters (pCO₂ and higher levels of surface dissolved organic carbon and nitrogen) in the lower salinity region underlying the central Pacific ITCZ was likely a result of increased nitrogen fixation (12); however, the authors hypothesized that the enhanced nitrogen fixation was the result of stronger upper water column stratification (12). Iron may be a less important factor in this region as it is distal from major terrestrial sources (9). However, volcanic sources can potentially provide substantial soluble iron inputs (9) in this region, although this is less well documented.

These two ecological provinces in the Atlantic Ocean undergo annual variability because of the migration of the ITCZ (Fig. 1; see also ref. 11), making their boundary seasonally dynamic as documented by Schlosser et al. (3). In the Pacific ITCZ, greenhouse warming has been projected to increase extreme ITCZ migration events toward the north (13), resulting in severe weather impacts (e.g., droughts, forest fires, coral bleaching). On somewhat longer timescales,

Schlosser et al. now provide compelling field evidence of two distinct biogeochemical provinces of the tropical Atlantic Ocean.

there is also evidence that the Atlantic ITCZ itself may be on a southward migration (14).

Superimposed on the seasonal variability in the ITZC and aerosol flux is variability driven by natural climate cycles, such as the El Niño southern oscillation (14) and droughts associated with it (15). Human-induced variability in aerosol loads through land-use changes and the expansion of combustion sources are emergent factors in the delivery of iron and other nutrients to the tropical oceans (9). The general temporal trend has been a steady increase in dust fluxes from the Sahara/Sahel (16).

Current evidence suggests the global marine nitrogen cycle is tightly regulated through a series of complex and interacting feedbacks (17). These feedbacks include iron regulation of inputs by nitrogen fixation through aerosol delivery, which is in turn regulated by climate (18). Another level of control involves the degree of temporal and spatial coupling of input and removal processes (e.g., ref. 19) and the role of regional phosphorus excesses in controlling this coupling. Indeed, the sources of phosphorus to support higher nitrogen fixation in the North Atlantic remain an open question.

The details of regulation of the marine nitrogen cycle are still being resolved and actively debated (17), and the global cycle itself is experiencing a substantial human perturbation (20). The work of Schlosser et al. (3) shows that one part of this cycle, nitrogen fixation, is complex and controlled by multiple facets, climatological, chemical, and anthropogenic. Their work provides important new insights into the function of this process in a major ocean ecosystem. Thus, human activities are not just perturbing the nitrogen cycle through direct additions, but also through effects on climate and desertification. In any event, we still have much more to learn about this major biogeochemical cycle.

2 Sohm JA, Webb EA, Capone DG (2011) Emerging patterns of marine nitrogen fixation. *Nat Rev Microbiol* 9(7): 499–508

5 Berman-Frank I, Cullen JT, Shaked Y, Sherrell RM, Falkowski PG (2001) Iron availability, cellular iron quotas, and nitrogen fixation in *Trichodesmium*. *Limnol Oceanogr* 46(6): 1249–1260.

6 Wu J, Sunda W, Boyle EA, Karl DM (2000) Phosphate depletion in the western North Atlantic Ocean. *Science* 289(5480): 759–762.

7 Ussher SJ, et al. (2013) Impact of atmospheric deposition on the contrasting iron biogeochemistry of the North and South Atlantic Ocean. *Global Biogeochem Cycles*, 10.1002/gbc.20056.

8 Jickells TD, et al. (2005) Global iron connections between desert dust, ocean biogeochemistry, and climate. *Science* 308(5718): 67–71.

9 Mahowald NM, et al. (2009) Atmospheric iron deposition: Global distribution, variability, and human perturbations. *Annu Rev Mar Sci* 1:245–278.

10 Husar R, Prospero J, Stowe L (1997) Characterization of tropospheric aerosols over the oceans with the NOAA advanced very high resolution radiometer optical thickness operational product. *J Geophys Res, D, Atmospheres* 102(D14): 16889–16909.

11 Subramaniam A, Mahaffey C, Johns W, Mahowald N (2013) Equatorial upwelling enhances nitrogen fixation in the Atlantic Ocean. *Geophysical Research Letters* 40:1766–

1771.

12 Hansell D, Feely R (2000) Atmospheric intertropical convergence impacts surface ocean carbon and nitrogen biogeochemistry in the western tropical Pacific. *Geophys Res Lett* 27:1013–1016.

13 Cai W, et al. (2012) More extreme swings of the South Pacific convergence zone due to greenhouse warming. *Nature* 488(7411): 365–369.

14 Haug GH, Hughen KA, Sigman DM, Peterson LC, Röhl U (2001) Southward migration of the intertropical convergence zone through the Holocene. *Science* 293(5533):1304–1308.

15 Prospero JM, Lamb PJ (2003) African droughts and dust transport to the Caribbean: Climate change implications. *Science* 302(5647):1024–1027.

16 Mahowald NM, et al. (2010) Observed 20th century desert dust variability: Impact on climate and biogeochemistry. *Atmos Chem Phys* 10(22):10875–10893.

17 Gruber N (2008) The marine nitrogen cycle: Overview and challenges. *Nitrogen in the Marine Environment*, eds Capone DG, Bronk D, Mulholland M, Carpenter EJ (Academic, Amsterdam), 2nd Ed, pp 1–15.

18 Michaels A, Karl D, Capone D (2001) Element stoichiometry, new production and nitrogen fixation. *Oceanography (Wash DC)* 14(4):68–77.

19 Deutsch C, Sarmiento JL, Sigman DM, Gruber N, Dunne JP (2007) Spatial coupling of nitrogen inputs and losses in the ocean. *Nature* 445(7124):163–167.

20 Gruber N, Galloway JN (2008) An Earth-system perspective of the global nitrogen cycle. *Nature* 451(7176):293–296.

¹ Longhurst A (2007) *Ecological Geography of the Sea* (Academic, San Diego), 2nd Ed, p 398.

³ Schlosser C, et al. (2014) Seasonal ITCZ migration dynamically controls the location of the (sub)tropical Atlantic biogeochemical divide. *Proc Natl Acad Sci USA* 111:1438–1442.

⁴ Gruber N, Sarmiento J (1997) Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochem Cycles* 11(2): 235–266.