

An iron curtain in the Atlantic Ocean forms a biogeochemical divide

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

0.0 0.04 0.08 0.12 0.16 0.2

 $20W$

 0.12

 $10M$

 0.16

 $10F$

 $\overline{0.2}$

Fig. 1. Seasonal ITCZ migration in the central Atlantic Ocean and aerosol optical depth from the Aqua MODIS

30W

40W

 $\frac{1}{0.08}$

A 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

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1 E-mail: capone@usc.edu.

 0.0

60_W

 10_S

spectrometer. (A) Northern hemisphere winter. (B) Northern hemisphere summer.

 $50W$

 $\frac{1}{0.04}$

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,

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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.
- 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.

5 Berman-Frank L, 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.