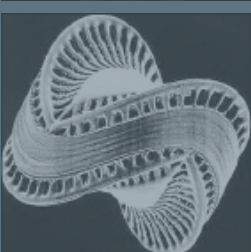
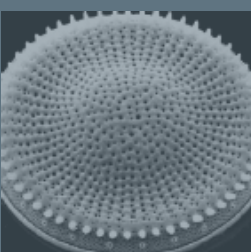
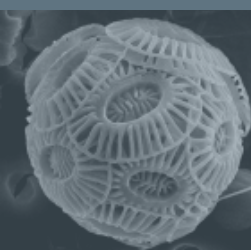
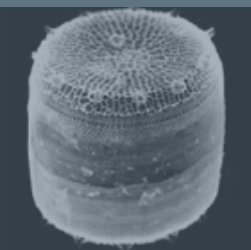
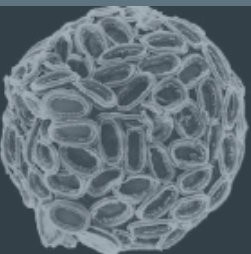




THE LEGACY OF FRANÇOIS M. M. MOREL

# *“What’s New?”*





*Geosciences Chair Bess Ward and Professor Morel caught in one of the many moments of humor and laughter at Guyot Hall, in 2009. Credit: Eva Groves*

## François M. M. Morel

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*On the Cover: (Upper left) François in Florence, Italy, c. 1992. (Left-side) Scanning electron micrographs of diatoms and coccolithophores. (Top-right) François in front of Guyot Hall, c. 2000. (Center-left) Jim Morgan, François and Werner Stumm in Küsnacht, 1983. (Center-right) François' last lecture in Room 10, Guyot Hall, 2018 by Eva Groves. (Bottom-left) Alaskan landscape image by Dalin Shi. (Bottom-center) Cadmium, carbonic anhydrase. (CDCA) (Bottom-right) Sunset on a research cruise by Yeala Shaked.*

# François Morel's Fête

*June 10 & 11, 2018*

Registration Completed Through EventBrite  
Packet Pick-up Sunday Morning at McCosh 50

## SUNDAY, JUNE 10, 2018

8:00 a.m. – 9:30 a.m.	Breakfast & Registration	McCosh 50 (Door #7)
9:30 a.m. – 10:30 a.m.	Plenary Talk	McCosh 50
10:30 a.m.	Break	
10:45 a.m. – 11:45 a.m.	Plenary Talk	McCosh 50
11:45 a.m.	Group Photo	Woodrow Wilson School (WWS) Fountain
12N – 1:30 p.m.	Boxed Lunch	Weickart Atrium
1:30 p.m. – 4:00 p.m.	Poster Session	Weickart Atrium
5:30 p.m. – 6:45 p.m.	Cocktails and Hors d'oeuvres	Prospect House
6:45 p.m. – 10:00 p.m.	Dinner	Prospect House

## MONDAY, JUNE 11, 2018

8:00 a.m. – 9:30 a.m.	Breakfast	McCosh 50 (Door #7)
9:30 a.m. – 10:30 a.m.	Plenary Talk	McCosh 50
10:30 a.m.	Break	
10:45 a.m. – 11:45 a.m.	Plenary Talk	McCosh 50
11:45 a.m.	Group Photo	Front of Nassau Hall
12N – 1:30 p.m.	Boxed Lunch	Chancellor Green Rotunda
1:30 p.m. – 3:00 p.m.	Poster Session (shortened)	Chancellor Green Rotunda
4:00 p.m.	Buses Depart	Ivy Lane (across from Guyot Hall)
6:30 p.m.	Boarding Metro Yacht	Hoboken
7:00 p.m. – 11:00 p.m.	Sailing, Cocktails and Dinner Around Manhattan	
11:00 p.m.–12:30 a.m.	Return to Princeton	

### Activities for early arrivals/ family members

*Sunday tour of Princeton University Art Museum*

*Tour of Princeton University Campus*

*Nature Tour: Institute Woods (Institute for Advanced Study)*





## CAMPUS INFORMATION

Princeton University has a downloadable **mobile app** that contains a **helpful map** and a guide to a free shuttle bus system on campus called **TigerTransit**. You can also navigate to **m.princeton.edu** on any device using an internet browser to view the app. Guyot Hall is located in the heart of campus at Washington Road and Ivy Lane. The University provides public lots at **Lot 23** with a **Central Line** shuttle stop and **Lot 21** with the **East Commuter Line** shuttle stop. It's approximately a **10 minute walk** from Lot 23, yet a little longer from Lot 21. There are Zagster bike rentals at the Princeton train station. In downtown Princeton, parking is available in metered spaces or in public garages.

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### *Then and Now*

**François M. M. Morel** was born and raised in Versailles, France, a propitious place for peripatetic walks in the expansive gardens. He was educated by the Jesuit fathers, learning some Latin and math, a modicum of Greek, and almost no English. He practiced all available sports, with great enthusiasm, good strength, speed and moderate talent. Neither family tradition, nor his education presaged an academic career.

# François M. M. Morel Biography



*François in his laboratory at Guyot Hall, 2015.*

**François Morel** is the Albert G. Blanke, Jr. Professor of Geosciences at Princeton University. He received a B.S. in Mathematics and Engineering from the University of Grenoble, France, and a Ph.D. in Engineering Science from the California Institute of Technology. He was a faculty member at the Massachusetts Institute of Technology (MIT) from 1973 to 1994 and joined the Princeton faculty in 1994. The research in his laboratory focuses on the interaction of trace metals and microorganisms in the environment, with particular emphasis on the role of metals in the global cycles of carbon and nitrogen in marine and terrestrial systems. His research group discovered the only known cadmium enzyme, a cadmium carbonic anhydrase used by marine phytoplankton to acquire inorganic carbon for photosynthesis. At Princeton, François teaches both undergraduate and graduate courses. He co-authored with his student Janet Hering the widely used teaching text: “Principles and Applications of Aquatic Chemistry” (Wiley).

François directed the Ralph M. Parsons laboratory at MIT from 1991 to 1994, the Princeton Environmental Institute (PEI) from 1998 to 2006 and again from 2014 to 2017. He organized and directed the NSF-supported Center for Environmental BioInorganic Chemistry (CEBIC) from 1998 to 2007. This center, which brought together environmental scientists and chemists working on metalloenzymes, aimed to provide a mechanistic molecular understanding of global environmental

processes. It influenced the research careers of many, particularly young, participants. François also served on the Editorial Board of the Princeton University Press from 1999 to 2004.

François is a member of the National Academy of Sciences and of the Istituto Veneto di Scienze, Lettere ed Arti. He is a Fellow of the American Geophysical Union and of the Geochemical Society. He received a Guggenheim Fellowship in 2001, the Patterson Medal from the Geochemical Society in 2001, the Urey Medal from the American Geophysical Union in 2005, the Distinguished Alumni Award from the California Institute of Technology in 2009, and the Award for Creative Advances in Environmental Science and Technology from the American Chemical Society in 2010. He is the recipient of the 2010 Eni Environmental Award from the Eni Foundation and of the 2012 Dickson Prize in the Sciences from Carnegie Mellon University.

## Areas of Research

- Biogeochemistry
- Oceanography
- Environmental chemistry and microbiology of trace elements

## Education

- B.S., Mathematics and Engineering, Université de Grenoble, France
- Ph.D., Engineering Science, California Institute of Technology



# An overview of past research in the Morel group

## Prologue

The research carried out in the Morel group over nearly 45 years focused principally on the chemistry of trace metals in natural waters and their biological effects. This research helped transform the field of biogeochemistry by providing a new focus on the interactions among chemical species, on the challenges that chemical speciation poses for aquatic microorganisms, and on the role played by these organisms in manipulating the chemistry of their external milieu.

This overview is organized in part chronologically. But in several instances closely related topics that are covered here in the same section were addressed at very different times, reflecting the interests of people, progress in experimental techniques, the maturation of concepts, and the whimsical cycle of ideas.

## I. Chemical equilibrium and kinetics in aquatic systems

### *Equilibrium Calculations*

The biogeochemical cycle of elements is governed in large part by their partitioning among gas, liquid and solid phases and by the bioavailability of chemical species to microorganisms. One approach to quantify the chemistry—more precisely the chemical speciation—of metals in natural waters is to assume thermodynamic equilibrium (often a reasonable first approximation) and calculate the resulting concentrations of all chemical species. Early work by Morel and co-workers, including his postdoctoral advisor Jim Morgan, resulted in the development of computer programs to calculate chemical equilibrium in complex systems such as natural waters. These programs, principally MINEQL and derivatives such as EPA's MINTEQA2, have been widely used in industry, government and academia for a variety of applications. The conceptual architecture of these

programs is based on a general algebraic formulation of the chemical equilibrium problem using chemical components as defined by JW Gibbs. The same conceptual approach is also utilized in the teaching text *Principles of Aquatic Chemistry*, Morel, Wiley 1983, and its sequel *Principles and Applications of Aquatic Chemistry*, Morel and Hering, Wiley 1993. The corresponding “tableau method” which

bedeviled many a graduate student was eventually adopted by other authors, including Stumm and Morgan in a later edition of their influential tome, *Aquatic Chemistry*.

### *Metal adsorption on mineral surfaces*

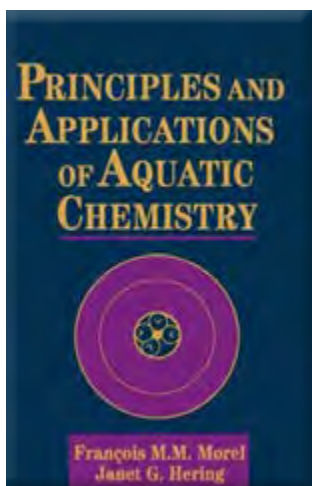
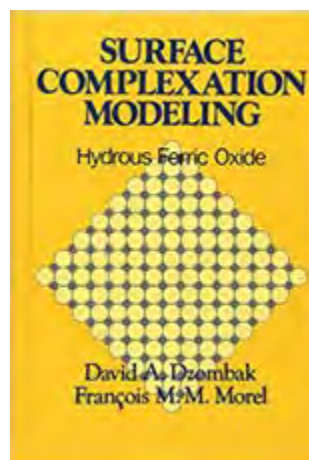
By incorporating solutes into the solid phase, adsorption controls the geochemical cycles of many trace elements and compounds. To include adsorption in chemical equilibrium calculations requires quantifying in a coherent thermodynamic formulation short-range chemical interactions at solid surfaces as well as long-range coulombic interactions, which depend on the electrostatic surface charge and hence on the extent of adsorption of ions. This was achieved through the development of “Surface Complexation Models” which utilize some variation of the Gouy-Chapman theory and were incorporated into MINEQL. The transition between adsorption and surface precipitation at high sorbate concentrations was quantified in the “Surface Precipitation Model” which

treats the surface phase as a solid solution. A further extension of this work allowed the quantification of adsorption on permanently charged minerals such as clays. These models, which were made practically useful by the development of a coherent thermodynamic database for adsorption of metals on hydrous ferric oxide (a dominant adsorbing phase in aquatic systems), have been widely

used by engineers and scientists in a variety of fields.

### *Metal complexation by inorganic and organic compounds*

The net effect of complexation (i.e., the reaction of two solutes to form a dissolved “complex”) on the cycling of trace elements is opposite to that of adsorption since it increases the solubility of elements and compounds. The Morel group carried out theoretical and experimental studies of the complexation of trace metals by inorganic and natural organic compounds in aquatic systems. A simple application of MINEQL entailed the modeling of complexation of trace metals by major anions upon mixing of freshwater with seawater. A more difficult problem is the quantitative description of metal complexation by humic substances, the “yellow stuff”



in natural waters that is composed of a mixture of small molecular weight compounds with carboxylic, alcoholic and phenolic functional groups. A variety of methods to quantify the formation of metal-humate complexes was developed in the Morel group, including one that quantified the “polyelectrolyte effect”, i.e., the long-range coulombic interactions involved in the reaction.

Because the kinetics of reactions among most solutes are relatively fast, it is generally assumed that, on the time scale of hours to days, complexation reactions are at equilibrium in natural waters. But experimental studies of the kinetics of complexation of metals by organic ligands in natural waters demonstrated that some of these reactions are in fact exceedingly slow, despite the inherently fast kinetics of the underlying reaction steps. This counterintuitive result was explained by the rapid formation of intermediate metastable complexes that results in an extremely slow approach to equilibrium.

#### *Photochemical redox cycling of iron*

The absorption of photons by chemical compounds can promote thermodynamically unfavorable or kinetically hindered reactions. The Morel group initiated the study of the photoredox cycle of iron in natural waters, including the photoreductive dissolution of iron oxides in oxygenated surface waters. The photoreduction of Fe(III) oxides is fastest at low pH and enhanced by the presence of organic compounds including fulvic acid. Fe(II) is re-oxidized by the radical  $\text{HO}_2/\text{O}_2^-$  produced via reduction of  $\text{O}_2$  by photo-excited fulvic acid. The net result is a rapid light-driven iron redox cycle, the efficiency of which depends on the ambient pH as well as the light spectrum and intensity. The formation of dissolved Fe(II) from Fe(III) oxides enhances the bioavailability of Fe to aquatic organisms.

## **II The bioavailability of trace metals**

### *A chemically defined medium for studying metal-phytoplankton interactions*

From the beginning, an ambition of the Morel group was to understand how the chemical speciation of metals in natural waters affects their availability to aquatic microbes, particularly phytoplankton. For this purpose, an important initial step was the development of the “chemically defined” Aquil growth medium, now widely used. The preparation of this medium includes the addition of the chelating agent EDTA to maintain constant concentrations of free (bioavailable) metals through an experiment, at levels ranging from limiting to plentiful.

### *Metal bioavailability: the free ion model*

Early biological work in the Morel group resulted in the conceptual development and experimental verification of the “Free Ion Activity Model” (FIAM) for the effects of metals on aquatic organisms, including

Cu and Cd toxicity, as well as Zn, Fe and Ni limitation. This model links quantitatively the biological availability and effects of essential and toxic metals to their chemical speciation, rather than simply their total concentration. It is the basis of most modern work on the interactions of trace metals and aquatic organisms and is also now incorporated in various EPA rules based on the FIAM model, or its extension the Biotic Ligand Model (BLM).

### *Field studies in the Equatorial Pacific*

On the basis of its studies on metal bioavailability, the Morel group was invited to participate in two of the early cruises designed to test the “Iron Hypothesis” according to which High Nutrient Low Chlorophyll (HNLC) regions of the oceans are iron-limited. Ship-board experiments conducted in the Equatorial Pacific showed that the population of small cyanobacteria, which obtain their N supply from the low ambient  $\text{NH}_4^+$  concentration and have low Fe requirements, is controlled by zooplankton grazing. In contrast diatoms need  $\text{NO}_3^-$  to grow and they are indeed limited by the low ambient Fe concentration. This is because  $\text{NO}_3^-$  uptake and assimilation requires additional iron, while the large size of diatoms makes iron uptake relatively less efficient. This limitation results in the high  $\text{NO}_3^-$  concentration observed in the Equatorial Pacific, a region that can be described as an iron-limited ecosystem with a grazer-controlled picoplankton population.

### *Metal bioavailability: a kinetic framework*

Further laboratory and modeling work on trace metal uptake by phytoplankton used a kinetic framework. Molecular and kinetic data generated by the Morel group showed that the uptake of Fe involves a reduction step catalyzed by transmembrane reductases. This finding led to the development of a new kinetic model for iron uptake by phytoplankton. The resulting “Fe(II)s Model” is based on a calculation of the steady state concentration of Fe(II) at the cell surface. New experiments verified the predictions of this model, which, under appropriate conditions, is indistinguishable from the Free Ion Activity Model.

Kinetic considerations also explain the enhancement of metal uptake rates in the presence of weak ligands that can exchange the metal with high affinity cellular transporters. This was shown in experiments in which the addition of cysteine or histidine increased Zn uptake rates to an extent predicted by the concentrations of Zn-Cys and ZnHis complexes. These results were corroborated by electrochemical measurements of labile Zn, the first quantitative demonstration of the correspondence between the bioavailability of a metal and its electrochemical lability.

### *The hypothesis of co-limitation by trace metals*

The work on trace metal uptake by phytoplankton in



the Morel group provided quantitative data that could be analyzed on the basis of chemical kinetics. This led to the notion that the acquisition of essential trace elements by planktonic organisms in oligotrophic oceanic waters should reach the limit imposed by the kinetics of chemical reactions with uptake molecules. As a result, because the geochemical cycling of these elements is itself controlled by biological uptake, many trace elements should be co-limiting over appropriate time and space scales.

### III The biogeochemistry of mercury and arsenic

#### *The mercury cycle*

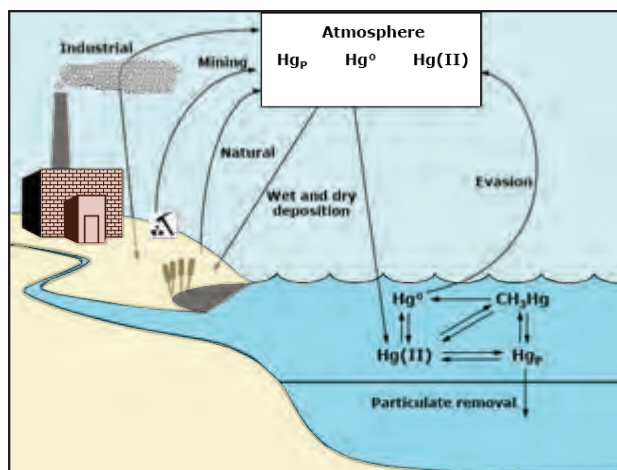
The Morel group modeled the global cycle of mercury and studied some key mercury transformations. Over the last century, anthropogenic emissions have tripled the concentrations of mercury in the atmosphere and surface ocean. The biological and photochemical reduction of  $\text{Hg(II)}$  leads to the volatilization of  $\text{Hg}^0$  from the oceans, which balances the oceanic deposition of  $\text{Hg(II)}$  from the atmosphere. As a result, deposition on land is the dominant sink for atmospheric Hg. The absence of change in mercury concentration in Pacific tuna over a span of thirty years led to the hypothesis that the concentration of methylmercury, which is the form that accumulates through the marine food chain, is not responding to global atmospheric mercury pollution. Unfortunately, the mechanism responsible for mercury methylation in the ocean is still unknown and the marine biogeochemical cycle of mercury is still a controversial topic.

In freshwater systems, the lipophilic chloro complexes of mercury and methylmercury ( $\text{HgCl}_2$  and  $\text{CH}_3\text{HgCl}$ ) accumulate at high concentrations in phytoplankton. But only methylmercury which is concentrated in the cytoplasm (while  $\text{Hg}^{2+}$  is membrane-bound) is assimilated by zooplankton and further accumulated up the foodchain. The mercury concentration in fish is thus determined primarily by methylmercury accumulation in phytoplankton, which is governed by pH and the chloride ion concentration.

It is now known that, in anoxic sediments, mercury methylation is effected by microbes that possess the *hgcA* gene. Work in the Morel group demonstrated that mercury is taken up by anaerobic bacteria via an active transport system (likely one used for zinc uptake), that  $\text{Hg}$ -thiol complexes play a key role in uptake and methylation, and that methylmercury is rapidly exported by the cells. Field studies of the *hgcA* gene, demonstrated that different bacterial phyla —methanogens, sulfate reducers, iron reducers— are involved in mercury methylation in various wetlands in Sweden and Florida.

#### *Arsenate respiration*

The Morel group discovered and studied in cultures and in the field the respiration of arsenate by bacteria.



*The global mercury cycle. Image from John Reinfeldler, adapted from his figure in Mason et al, 1994.*

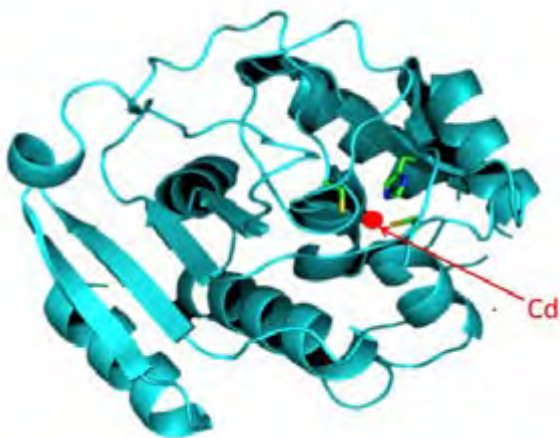
Although arsenic is highly toxic to many organisms,  $\text{As(V)}$  is a reasonably good electron acceptor —better than  $\text{S(VI)}$ — and it is perhaps not surprising that it should be used for respiration by some anaerobic microbes. The ability to use  $\text{As(V)}$  as an electron acceptor is in fact shared by a number of bacterial isolates. One such organism, which reduces both  $\text{As(V)}$  and  $\text{S(VI)}$ , forms arsenic trisulfide, a striking gold colored precipitate. Recent work in another lab has now uncovered the genetic basis for  $\text{As(V)}$  respiration.

### IV Mechanisms of carbon, nitrogen and phosphorus acquisition by microbes

#### *Inorganic carbon acquisition by phytoplankton*

Phytoplankton use a Carbon Concentrating Mechanism (CCM) to acquire  $\text{CO}_2$  for the dark reaction of photosynthesis. The CCM is necessary to nearly saturate the excruciatingly slow carbon fixation enzyme Rubisco, which, having evolved when atmospheric  $\text{CO}_2$  was very high, has a low affinity for its  $\text{CO}_2$  substrate. (Paradoxically, the low  $\text{CO}_2$  concentrations in the modern atmosphere and surface ocean result in part from the export of  $\text{CO}_2$  to deep seawater by sinking phytoplankton.) The Morel group quantified Rubisco, along with its  $\text{CO}_2$  affinity and turnover rate, in a variety of marine phytoplankton species, and developed a kinetic model of the CCM in diatoms, based on measurements of passive and active cellular carbon fluxes. The cellular and chloroplast membranes of diatoms are highly permeable to  $\text{CO}_2$ , which is recycled in the cell via the activity of carbonic anhydrases (*see below*). Under low  $\text{CO}_2$  conditions, the CCM architecture of some diatoms resembles that of  $\text{C}_4$  higher plants such as corn and grasses.

The laboratory work on inorganic carbon acquisition by phytoplankton provided critical insight for field work at the Western Antarctic Peninsula. A deployment at Palmer Station in early spring coincided with a massive



The structure of CDCA, the cadmium carbonic anhydrase. Adapted from a figure in Xu et al, 2008.

diatom bloom. Measurements of carbon fixation rates and protein content demonstrated that the very high rates of primary production were supported by unusually large cellular concentrations of Rubisco and other proteins in the extant phytoplankton. These high protein concentrations, which likely reached a physiological limit, are necessitated by the slow turnover rate of Rubisco and other enzymes at the ambient temperature of  $-1^{\circ}\text{C}$ .

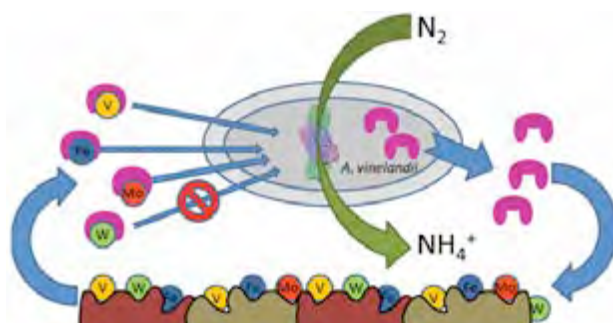
Carbonic anhydrase (CA) is an enzyme that catalyzes the reversible transformation of  $\text{CO}_2$  into bicarbonate and is important in inorganic carbon acquisition for photosynthesis by phytoplankton. Early experiments in the Morel group demonstrated that cobalt and cadmium can partially replace zinc as essential elements for the growth of marine diatoms. This led eventually to the discovery and characterization of two novel classes of CA, one that uses either zinc or cobalt as its metal center and the other zinc or cadmium. “CDCA”, the only known cadmium enzyme, is ubiquitous in marine waters. Despite the extremely fast kinetics of CAs, these enzymes are needed at high cellular concentration because of their low affinity for their inorganic carbon substrate. As a result, CAs represent a major metal requirement in marine phytoplankton. This work provides an explanation for the “nutrient-like” vertical profiles of cadmium in seawater. Interestingly the silica frustule of diatoms serves as a proton buffer for their external CA, thus establishing a biochemical role for silica in phytoplankton. There are likely other Cd enzymes to be discovered; for example, in the ubiquitous coccolithophore *Emiliana huxleyi* (which does not have the *cdca* gene), half of the zinc requirement can be replaced by cadmium (and all of it by cobalt). Complexation by phytochelatin,  $(\gamma\text{-Glu-Cys})_n$ , which can exchange  $\text{Cd}^{2+}$  with CDCA, buffers the intracellular concentration of cadmium (and of some other metals). At high concentrations that are toxic to phytoplankton, the Cd-phytochelatin complex is exported from the cell.

### Extracellular enzymes: acquisition of Nitrogen and Phosphorus from organic compounds

A number of enzymes on the surface of phytoplankton are used for the acquisition of major nutrients such as nitrogen and phosphorus from organic compounds. Early work in the Morel group discovered extracellular amine reductases and amino-acid reductases that provide  $\text{NH}_4^+$  for uptake and produce  $\text{H}_2\text{O}_2$  extracellularly. Other work demonstrated that the acquisition of nitrogen from urea can be limited by the bioavailability of nickel, a metal cofactor in urease which hydrolyzes urea into ammonium. A study of the acquisition of phosphorus from organic compounds in the coccolithophore *Emiliana huxleyi* led to the discovery of a novel alkaline phosphatase, a zinc enzyme that hydrolyses the phosphate group from organic moieties.

### Trace metals, $\text{N}_2$ -fixation and siderophores

Work directed by Anne Kraepiel in the Morel lab has focused on the interaction between trace metal bioavailability and nitrogen fixation—the transformation of  $\text{N}_2$  gas into biologically available ammonia which is catalyzed by the nitrogenase enzyme in specialized bacteria. The development and application of a new technique, the Isotope Acetylene Reduction Assay (ISARA), demonstrated that in most field samples, including those from environments with high molybdenum concentrations, 15-20% of  $\text{N}_2$  fixation was catalyzed by alternative nitrogenases—which contain vanadium+iron or iron-only instead of molybdenum+iron as metal co-factors. Gene sequencing confirmed that these enzymes accounted for a similar fraction of the nitrogenase in the samples. Alternative nitrogenases were found to impart a larger isotopic fractionation of nitrogen during fixation than the Mo-nitrogenase, a result that provides an explanation for the low  $^{15}\text{N}$  content of organic matter in some ancient sedimentary rocks.



Metallophores are produced and excreted into the soil by the bacterium *Azotobacter vinelandii*, resulting in the increased bioavailability of essential metals such as iron (Fe), molybdenum (Mo) and vanadium (V) and detoxification of toxic metals such as tungsten (W). Credit: Kraepiel et al, 2009

Laboratory studies with model  $N_2$ -fixers demonstrated that the uptake of molybdenum and vanadium is effected by siderophores, extracellular metabolites previously known for their role in iron acquisition. At high concentrations of molybdenum and vanadium, as well as tungsten, binding of these metals by siderophores stops uptake and avoids toxicity. Under low iron conditions, the export of large quantities of siderophores with low  $^{15}N$  content leads to a modest increase in biomass  $^{15}N$ , possibly explaining previous reports of variability in the isotopic signature of  $N_2$  fixation. New software for analyzing high precision mass spectrometry data allows the identification of all the siderophores produced by an organism using the isotopic fingerprint of iron. A new study examined the regulation of siderophore production by quorum sensing, QS, a mechanism through which bacteria sense their population density. QS allows organisms to match siderophore concentrations to their uptake capacity.

## V Ocean acidification

A large fraction of the  $CO_2$  produced by fossil fuel burning ends up in the ocean, leading to both an increase in the dissolved  $CO_2$  concentration and an acidification of surface seawater (which varies with latitude and water depth). This ongoing "Ocean Acidification" (OA), may affect marine phytoplankton in four ways: i) the high  $CO_2$  may increase the rate of photosynthesis; ii) the low ambient pH may make it difficult (or energetically expensive) to maintain a constant cellular pH; iii) indirect effects of low pH on the chemistry of seawater, for example on the chemical form and bioavailability of nutrients, may elicit physiological responses; and iv) the low carbonate ion concentration resulting from acidification may lead to dissolution of the  $CaCO_3$  shells of calcifying organisms, including coccolithophores. These possibilities have been studied by the Morel group in a number of laboratory and field experiments, several of which were designed to test separately the effects of  $CO_2$  and pH changes on model organisms. In many instances, the effects of OA over the range predicted for the next century were found to be relatively small. This is a reflection of the fact that, for many phytoplankton species, maintaining constant  $CO_2$  concentration and pH in cellular compartments (where  $CO_2$  is fixed and  $CaCO_3$  is precipitated) is energetically inexpensive compared to photosynthesis and respiration. Nonetheless, a high  $CO_2$  concentration is likely to lead to a change in the phytoplankton assemblage, as demonstrated in some field experiments.

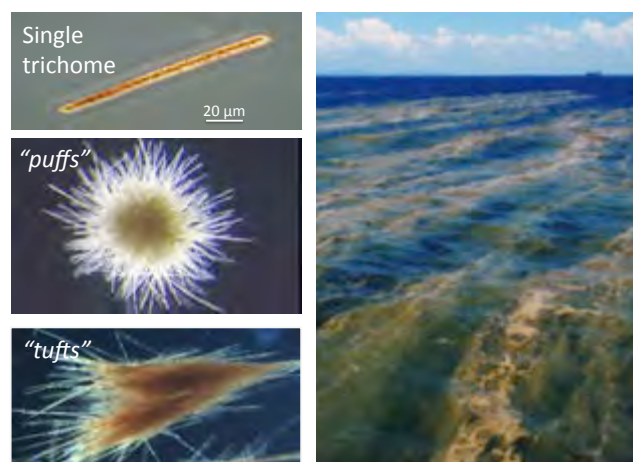
There is, however, at least one important phytoplankton genus that will be negatively affected by acidification: the cosmopolitan cyanobacterium *Trichodesmium* (in which the Morel group previously characterized a "Dps" iron storage protein). OA decreases significantly the growth and  $N_2$  fixation rates of *Trichodesmium*, which is

responsible for a large fraction of new bioavailable nitrogen inputs to the nutrient-poor tropical and subtropical ocean. This deleterious effect, which is magnified under conditions of Fe limitation, is observed despite a beneficial effect of high  $CO_2$  on carbon fixation and is caused by the organism's inability to maintain constant cellular pH and a resulting decrease in the rate of  $N_2$ -fixation. However, when *Trichodesmium* is organized in large colonies (the "puffs" and "tufts" that are sometimes seen at the surface of the Sargasso-Sea and other regions), the supply of  $CO_2$  becomes limiting, and the positive effect of increasing  $CO_2$  can dominate over the negative effect of low pH, resulting in increased growth and  $N_2$  fixation rates, as observed in some field experiments.

As expected, the bioavailability of trace metals responds to acidification in accordance with the changes in their chemical speciation. The uptake rate of dissolved Fe(III) generally decreases at low pH, reflecting the lower concentration of bioavailable inorganic  $Fe(OH)_n$  species. In contrast, the uptake rate of dissolved zinc (and likely that of other divalent metals) can increase or decrease upon acidification depending on the acid-base properties of ambient complexing agents and the bioavailability of their metal complexes. The pH-induced changes in the rate of zinc uptake by model species match quantitatively the changes in lability measured by electrochemistry.

## Epilogue

Serendipity played a large role in the research outlined above. The taste and background of individual students and postdocs, luck in the laboratory and the availability of new experimental techniques, opportunities for fieldwork or collaborations, all influenced the research critically. This work launched the scientific careers of many gifted young people in a variety of fields, including environmental science and engineering, oceanography, chemistry and biology.



*Trichodesmium colonies under the microscope and in the surface ocean. Credit: Dalin Shi and Sven Kranz.*



## What's new?

It is difficult for me to distinguish François' and Anne's influence on my career for I spent almost nine years under the supervision of the Morel-Kraepiel team, first as a PhD candidate with Anne in Strasbourg, then as a Postdoc with both at Princeton. But, today we celebrate François, so I will focus on him.

I thought a long time about what to say about François. I could have talked about his impressive career, his ground-breaking contributions, but his record speaks for itself. I could have talked about the memorable BBQ / Pool parties and other dinner (i.e., super bowl, Chinese New Year) gatherings at his home, that reflect his true kindness, but I am sure we will have loads of pictures to remind us of these. I could have talked about his incredible and inspiring energy, by sharing some of my personal experiences like the time we took a bike ride and I almost got lost

because I could barely keep up with him. In my defense, he lent me a mountain bike that was no match for his ultra fancy road bike, but I am making half-excuses.

Instead, I decided to talk about the one thing that always reminds me of François and one of the first things that pop into my mind when I think of him; a short and powerful question: "What's new?"

This short question was, and hopefully still is, the first one students heard when François stepped into the lab or our offices. When



Anne Kraepiel

I say "stepped" I should say "rammed," as we all know François' peculiar fast paced and energetic way of walking. To me, and I am sure to many others, "what's new?" became the unofficial motto of the Morel lab. And what a powerful motto it was. These few words were at the same time a question that demands to be answered, a challenge that needs to be met and an incentive that has defined my time at Princeton and contributed to shape my career.

As a question, it was very open and broad in scope. Of course, it referred to progresses in individual research projects, but it was also an invitation to simply share with him what was on our mind. It was a short version for "Hey JP, I have time right now, do you want to talk about your project or anything else?" I remember monopolising large amount of



Jean-Philippe Bellenger and daughter Enola.

*"To me, and I am sure to many others, 'what's new?' became the unofficial motto of the Morel lab."*

François' time in discussions of various science related topics after one of his "what's new?" question, paradoxically often receiving answers instead of providing one. It was also the opportunity to engage in more trivial discussions about e.g., sport. These many discussions have largely contributed to my training as an independent researcher and accessorially turned me into a NFL fan (Go Pats!).

As a challenge, it was a stimulating scientific game; try to find an idea or introduce a new set of data that would truly catch François' interest, because succeeding to do so was a solid validation of the potential of the idea or the quality of the data. Feeding François' voracious scientific mind with a new idea was always rewarded by an even better version of the idea once processed through his restless brain. But more importantly, the improved idea was coming back with a plethora of questions challenging the robustness and relevance of the idea as well as advice that would set the course of the research project for weeks toward new challenging horizons. François' "what's new?" taught



*J.P. Bellenger hung this comic on François' door years ago to signify his "What's new" greeting whenever entering the laboratory.*

me that there is not a better way to do science than by challenging preconceived ideas, your colleagues and yourself.

As an incentive, it was not only the question "what's new?" that was stimulating it was the peculiar way François asked it. With his curiosity-sparkling eyes and energetic demeanor that made us feel that he truly cared about our research but also about us as young scientists and individuals. As a mentor myself now, I realise how important it is to show students that we care and we are present for

*—J.P. Bellenger (Postdoc 2005-2010)*



*Yeala Shaked*

I was privileged to be mentored by François during my post-doc and was blessed to gain a life-long mentor and an invaluable friend. I chose "Life" as the theme of my testimonial, since one of the projects I worked on, examining the biochemical roles of liths in the physiology of Cocoliths, was termed by François—"Life is Hard."

My experience at the Morel lab was a lot of Hard work, but was also full of Life with all its flavors. It was broadening, stimulating, challenging, exciting, inspiring and had highs & lows, undercurrents and high pitch waves. Let me take you through a typical day in the Life of the Morel lab at Guyot hall in the years 2002-2005:

At 11:00 or so, a wave of energy flooded the common computer room in the form of François who already completed a proposal or a paper at home (working since 5am) and was overflowing with ideas, which he joyfully developed out loud and distributed among students and post-docs. This recurrent scene termed by Allen Milligan as the "Idea of the Day" was a blessing for some and a source of anxiety for others, as was evident by the rapid personal exchange in the room when the distant voice of François was heard, completing his other daily routine of loudly criticizing the world's politicians while reading

them and that was François' way to efficiently do it. It is in this sense that I always considered this "what's new?" to be our research team motto.

Thus, to summarise, this emblematic question "what's new?", to me, truly personifies François as a mentor and as an individual. It is simple and straight to the point but at the same time it is open, challenging and above all highly stimulating.

At the dawn of François' retirement, which I do not expect to be quiet or inactive, it is my turn to return the favour:

So, François, what's new?

*"I chose 'Life' as the theme of my testimonial, since one of the projects I worked on, examining the biochemical roles of liths in the physiology of Cocoliths, was termed by François –'Life is Hard.'"*

the newspapers at the PEI table next to the Dinosaur. The bravest, who survived the deluge of ideas (and tasks), then headed to lunch at the Frist campus center, where François recharged himself

with a super-greasy pizza. Armed with these saturated fats François used to surge back to his office and fill the board with equations. These exciting equation solving afternoons were somewhat intimidating for us salad-eaters, since it required much more than a salad to keep up with François' train of thought. I have many heart-warming images of sun-filled afternoons in François' office, typified by somewhat contradicting scenarios: the energetic mode, where he would frantically develop kinetic terms, raise questions, solve them and raise new ones before we even grasped the original problem; and the quiet mode, where he was caught in deepest thoughts with his eyes closed, and that often resulted in a true breakthrough (rather than a short afternoon nap). Evenings were less predictable, although the weekly mind-broadening environmental course where nice wine and a full course dinner were served, stand out as an example of François' special gift of enjoying Life.

Back to the "Life is Hard" theme, I actually think it describes François, with his explosion of Life, energy, ideas, curiosity, mischief, inspiration and vision. These treasures were often covered with Hard liths of sheer determination (or stubbornness), non-conformism, slight snobbishness, and lack of tolerance towards stupidity (which, according to François, is quite vast). But, luckily the cover was easily shed, like the liths, and François' great heart, that is second only to his great mind, was revealed.

My encounter with François enriched my personal Life and has shaped my academic Life (both of which are Hard by definition). François

was, and still is, a role model and a source of inspiration. I remember writing our first joint paper, where François shuffled my discussion to the results and urged me to think deeper. In fact I have never met a deeper thinker than François and would like to thank you —François— for stretching my limits and convincing me to always search deeper for "fundamentals".

I am also in debt to François for tirelessly convincing me to believe in myself. While initially his attempts to inspire me with examples from his own career resulted in an utter state of panic, his persistence was fruitful —thank you again, François, for providing a strong enough uplift that allowed me to spread my wings.

—*Yeala Shaked (Postdoc 2002-2005)*



*Janet Hering*

been a pleasure throughout my career to stay in touch with François and other members of his research group.

Being a member of François' research group at MIT was a tremendous preparation for my own career as a professor. François always treated his students as junior colleagues, giving us opportunities to develop our own ideas and expecting us to develop as independent scientists. I also benefited greatly from François' diverse interests, which were represented by the range of projects that his students and postdocs carried out. In group meetings, there was always a chance to learn from the other group members. It has

*François always treated his students as junior colleagues, giving us opportunities to develop our own ideas and expecting us to develop as independent scientists.*

—*Janet Hering (Ph.D. 1988, MIT)*





*Not only did you encourage me to become a professor (a career I never had considered before meeting you), more importantly, you taught me what it meant to be a great mentor.*

Dear FM3,

While I realized how fortunate I was to be in your lab back in 1993-1997, I appreciate you now even more. Not only did you encourage me to become a professor (a career I never had considered before meeting you), more importantly, you taught me what it means to be a great mentor. You have given me the benefit of the doubt and have supported me at every stage since we first met, in many different ways I from not ridiculing my German Studies major to giving me free reign to follow my curiosity within your lab and encouraging and enabling me to seek help outside of it, to teaching me how to think and write clearly as a scientist, to building my self confidence by making me feel my brain was bigger than it actually was, to being a true friend and wise counselor during periods of stress and uncertainty. I am deeply grateful for everything you have done for me. But above all: thank you for being a role model for what really counts in life and science: facing with joy, creativity, high standards and generosity. I can only hope that one day, the people who have passed through my lab will view me with as much warmth and gratitude as I feel towards you.

I love and respect you very much, FM3! You are an exceptional person, and I wish you many more years of happiness in your retirement.

with love, Dianne



← Often the best things in life we encounter by chance and if we're wise, we take note. I didn't apply to MIT thinking I'd become a molecular geomembranologist but I sure realized I'd found the best possible PhD mentor for me when I met you!

—Dianne K. Newman (Ph.D. 1997, MIT)



*Jennifer Grant Lee and husband Glenn Moglen, honorary Morel Group member, on the Maryland Heights trail in Harpers Ferry.*

I was one of François' students during his last years at Parson's Lab at MIT. I first heard about François from KC Swallow, my supervisor at Gradient, a consulting firm in Cambridge that employed many Parson's grads. KC was one of François' first students. When I was applying to graduate school, she suggested I talk with François, and I am very glad I did.

When I think of my years in graduate school, the first thing I think about is François' generosity. He was generous in providing his students with opportunities to grow professionally, and he was generous in hosting many memorable gatherings at his house. I'll start with the professional opportunities he provided his students. Every other year, François funded his students to attend the Gordon Research Conference, Environmental Sciences: Water. I got to attend two GRC conferences. The talks were inspiring, but even better was

*“When I think of my years in graduate school, the first thing I think about is François' generosity.”*

meeting the leaders of the field—many of whom were former students of François—in an informal setting. We went whitewater canoeing, hiking, and swimming together. It was great fun. I also had an opportunity to serve as a teaching assistant for Aquatic Chemistry. I fondly remember all those tableaux. “Think logs!” François would tell his students. Finally, all François' students learned about each other's research during weekly group meetings. We had the best pizza of any group, usually from Bertucci's. I remember Sarah Green's “potatoes under a blanket” 3-D spectra of humic acid and Samantha Brown's magical touch with the finicky carbonic anhydrase assay.

François was a great host. Every Friday the group got together for happy hours at the Cambridge Brewing Company. We also had

many multi-course, French-style dinners at his house in Lexington with lots of wine. We got to know his children and his first wife, Nicole, who co-hosted with François. The best gatherings were down at the Cape at his house on Herring Pond. In the winter, François built bonfires in the woods from the brush he had cleared in an effort to make his woods like the “gardens of Versailles.” We would sit around the fire, drinking more wine. In the summer we would swim in the pond and drink still more wine. François' summer favorite was Portuguese vinho verde. François and Nicole even hosted a party for the whole lab to celebrate the wedding of me and my husband, Glenn Moglen, also a Parson's grad. Guests got to sail, water ski, and canoe. François knew how to have fun.

I will tell one story on François. He was a brilliant thinker and collaborator, but we never saw him actually in the lab himself except for once. He was hired as an expert witness by Arm

& Hammer. A man was suing the company because his stomach had ruptured after taking baking soda for indigestion. François conceived a simple but effective experiment of adding baking soda to hydrochloric acid in a graduated cylinder. He also mixed in dish detergent, using the volume of the bubbles generated to estimate the amount of carbon dioxide generated. It wasn't high-tech, but it worked. The man lost his suit. So François really can do lab work.

François' official retirement can't help but be a loss to the field of

aquatic chemistry, although I suspect he will continue to work almost as hard as an emeritus professor. Hopefully, he will have more time to enjoy his family and his wife Anne. I wish him all the best in this new phase in life.

—Jennifer Grant Lee (Ph.D. 1995, MIT)



Eva Groves

From a unique vantage point in my adjoining office, “Kommen Sie Bitte” are the words I hear all day long. The moment François arrives at his office at 153 Guyot Hall, it seems there are non-stop visitors knocking at his door. In sixteen years, I have never witnessed anyone being turned away. No matter how busy François may be, he always has time. After a welcoming “Kommen Sie Bitte” he stops whatever he is doing and gives the visitor his undivided attention. Hence, afternoons are productive

for students and staff alike as issues are addressed, questions are answered, and manuscripts are edited. I am constantly amazed by his unflagging energy and have felt exhausted by merely witnessing his busy days.

François has high standards and demands a lot of his students, but no more than he demands of himself. He cares deeply for his students and wants them to excel. Years ago, a student mentioned to me that she had trouble keeping up with François' mental math even with a calculator. When François had gone for the day, there was a knock at my door asking for permission to photograph the whiteboard before the evening janitors could wipe away the notes. I am sure hours were spent trying to

recreate what François had done in only a matter of minutes.

The hard work put in by these students is noticed and “repaid” by the thoughtfully written reference letters which unfailingly land jobs in prestigious institutions around the globe.

François refers to me as “The Boss”... but of course we all know differently! I am happy to serve as “Mom” of the Morel Group. This feels very natural to me after raising three children before joining Princeton as François' assistant.

I feel blessed to have been part of the Morel Lab all these years. François is truly one of a kind!

—Eva Groves, Assistant



Kevin Farley '84 with his wife Bea Farley.

François,

To this day, I am still amazed by all the seminal ideas that you gave us to start our research careers. My most wonderful memories of MIT remain Friday afternoon research meetings in the Ippen Room, Friday evenings at the Paradise, and méchouis and dance parties in Lexington. But most of all, thank you for bringing me together with Bea, my spouse of now 35 years!

All the best,

—Kevin Farley (Ph.D. 1984, MIT)





*Sheryl Robas*

In 1996 I was assigned to work for Prof. François Morel, and Prof. Michael Bender (talk about two heavy hitters). I would do François' work in the morning and Michael's in the afternoon. Luckily, in 1998, CEBIC was born and I became François' fulltime assistant. In the beginning, it was rough. He was very fair but also very demanding. Learning a new vocabulary in science and learning French. François' French accent was very heavy and his handwriting was awful. I would leave blanks for the words I could not make out because I was afraid to ask. But, in time, I got used to the accent and would joke with him regarding his pronunciation. He never took offense, and often joked himself. Over the years that I worked for François, he was my boss, my mentor, but most of all he was a good friend. He was very supportive, caring, and would help you in any way that he could. At one time I was having personal difficulties, and he was always there trying to help. I will never forget the kind-

ness he showed to my children when I would have to bring them in because they were off from school. I will also never forget a comment that Philippe Tortell made when François and I were working on a proposal, and he dictated to me while I typed. As I argued with him to scroll down instead of jumping all over the paper, Phil stated "you both sound like an old married couple." In 2002, I had the occasion to take on a new position, working with the students and academics. François encouraged me to chase my dreams even if it meant to be an inconvenience to him. Merci François d'être un ami et un super patron.

—*Sheryl Robas, Academic Coordinator*

Hi François,

It's so good to hear from you. You're lucky and caught me during one of Connor's few 5 min naps!

I am very sorry that I can't join in June, it sounds like a great occasion and I would very much like to celebrate with you and catch up with old friends.

I also wanted to write and thank you for providing such wonderful mentorship (which I hope will continue!). You have really helped me develop professionally from a student to an assistant professor! I especially want to thank you for your wonderful references letters that have helped my success. I've recently been awarded 3 grants as PI: a Simons Early Career Award for Marine Microbes (to study marine Rubiscos), a NSF Antarctica Grant (to study the physiological effects of salinity and temperature on sea ice algae) and a UW Innovation Award (to develop a lab system to grow sea ice with algae and bacteria). So you can imagine I'm quite busy, my days are spent bouncing Connor while planning a field trip to Palmer in October!

Ok, I hear Connor stirring so I need to run. Hopefully I will be able to skype in sometime to say hi to you all. And I hope Ashley is doing well with Xinning, I'm sure they'll make a great team.

Best wishes,

—*Jodi Young (Postdoc 2011-2015)*



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