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A Century of Phytoplankton Research at Scripps

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Over the past 100 years Scripps Institution of Oceanography has been a center for plankton research. Its reputation has waxed and waned depending largely on the scientists present, and their ability to incorporate new technologies, collect and interpret new data, and synthesize and disseminate their results. The study of marine phytoplankton has always been limited by the technologies available to gather and analyze samples. It is not surprising then that the development of technology and evolution of ideas at Scripps has mirrored, and often driven, the changes in the oceanographic community as a whole.

Here I trace some developments in phytoplankton research at Scripps, concentrating first on the tools, then on the concepts. My review is by no means exhaustive, for I have said embarrassingly little or nothing about the work and lives of many extraordinary scientists. Still, I hope that this review will give a flavor of the changes in the field, from the time of a "sheltered local marine station" to the present.

Tools

Fundamentally, biological oceanographers seek to answer the questions: What organisms are present? Where are they? How many are there? What are they doing? Though seemingly simple, these questions continue to be the essence of thousands of researchers' lifelong careers. The fact that the major primary producers in the ocean (cyanobacteria) were only discovered in the last 10 (*Prochlorococcus*) or 20 (*Synechococcus*) years underscores the relatively primitive state of our field. One of the great barriers to answering these questions is the lack of tools to investigate plankton.

Scripps has a century-long history of developing technologies for ocean exploration, including the study of phytoplankton. The most basic of these tools is the sampling bottle. To obtain an uncontaminated sample of phytoplankton, an open bottle must be lowered to the desired depth, then closed and brought back to the surface for sample processing. The first such bottle associated with Scripps is the Kofoid Bottle (Figure 1). Charles A. Kofoid was the assistant director of the Scripps Institution for Biological Research (later Scripps Institution of Oceanography) from 1903–1924, even though he was based at University of California Berkeley. Kofoid is well known for his studies of dinoflagellates, which he sampled with a bottle of his design, closed by a messenger sent down the wire. The bottle was suspended from the end of the wire, so only a single sample could be obtained on each cast.

The next sample bottle associated with Scripps was developed by Winfred E. Allen, a student of Kofoid's and an assistant professor at Scripps from 1919–1943 (Figure 2). Allen gathered a remarkable 20 year-long data set of weekly phytoplankton samples from the Scripps pier, using a closing bottle he designed. Like the Kofoid bottle, the Allen bottle was suspended from the end of a wire, and closed at depth with a messenger (see Figure 3). Samples were poured out of the bottle through a spigot, and filtered through silk bolting cloth (the standard plankton filter of the time) into a small jar for preservation. Allen (1929) wrote, "*A series of subsurface catches at fifteen depths from surface to one hundred meters has been obtained with it in thirty-two minutes.*" Even by modern standards, this is impressive.

Probably the most famous bottle designed at Scripps is the Van Dorn bottle, patented by William G. Van Dorn in 1956. Van Dorn, a physical oceanographer, was a student at Scripps until 1953 when he obtained his Ph.D. degree. His bottle could be attached at any point along a vertical wire, and was tripped closed by a messenger. The bottle—a long tube—was sealed by two rubber "plungers" joined by a length of rubber tubing running inside the bottle. Bottles of this design are still available today.

Lest I give the impression that Scripps was a hotbed of sample-bottle development, it seems that between the late 1800s and mid-1900s any oceanographer worth his salt had developed a bottle bearing his name. In a haphazard search of the National Oceanic and Atmospheric Administration image archives, I came across more than 100 bottles developed during this time, mainly in Europe and Scandinavia.

As useful as bottle samples were, and are, they have problems, particularly when trying to understand distributions and activities of phytoplankton. In 1943 H. W. Graham of Scripps published a paper in which he noted,

> *"The time-honored method of counting the number of plant cells is not satisfactory. First, it is a slow and tedious procedure. Second, the results must be expressed in numbers of cells when the size of the cells in different species or organisms is very*

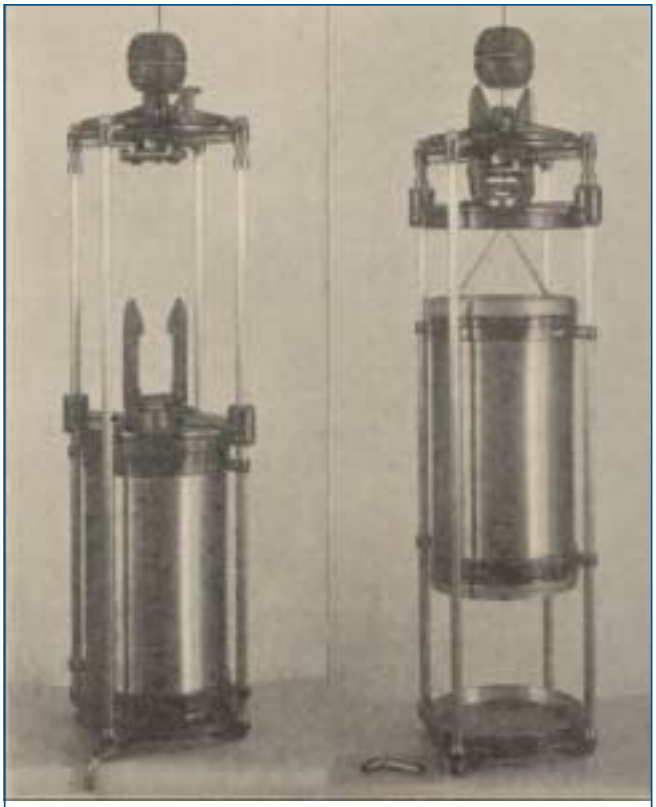


Figure 1. *The Kofoid bottle: open (right panel), and closed (left panel).*

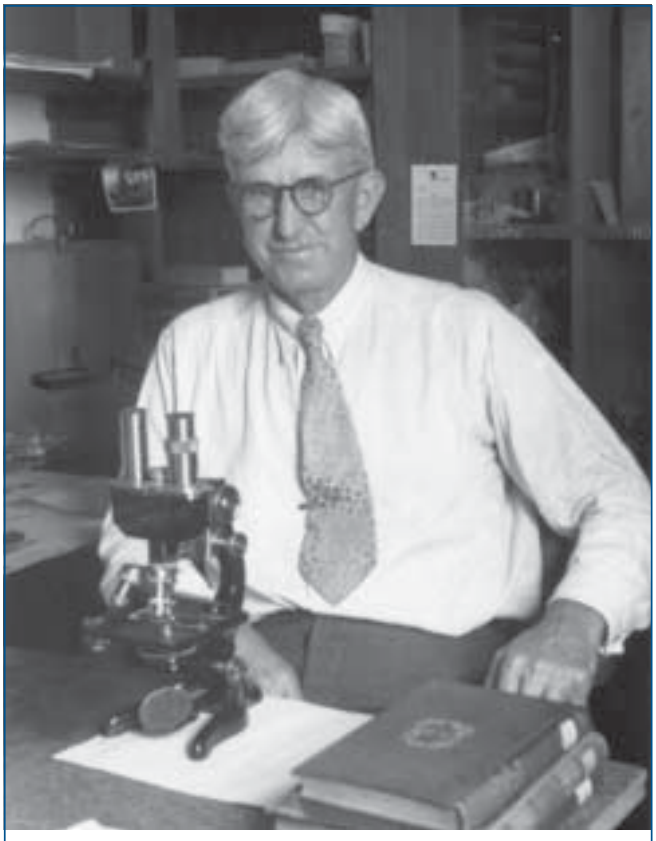


Figure 2. *Winfred E. Allen at his microscope.*

Figure 3. *R.W. Fleming filtering a plankton sample captured with an Allen bottle.*

different. Furthermore, silk bolting cloth which is usually used for collecting the samples on board ship is not a reliable filter."

Graham sought a method of *"determining organic production in the sea"* that obviated the problems he outlined. His solution was to use chlorophyll as a measure of phytoplankton biomass.

This was not original to him; for example, in 1934 H.W. Harvey published a technique of filtering the sample through silk and comparing the extracted plant pigments to a color scale to get a "Harvey Unit" of phytoplankton. Graham found this too qualitative. His technique was to filter a sample onto "chemical filter paper" and extract the chlorophyll from the phytoplankton using acetone. The amount of chlorophyll in the solution was then quantified using a spectrophotometer, which would measure the absorption of red (668 nm) light. This method, while extremely accurate, was somewhat insensitive, so large volumes of water had to be filtered.

The next advance in measuring phytoplankton was the introduction of fluorescence measurements. In 1965 Scripps researcher Osmund Holm-Hansen and colleagues—including John D.H. Strickland, the head of Scripps' Food Chain Research Group—published a method for the fluorometric determination of chlorophyll and its by-product phaeophytin. This method built on an earlier (1963) method of Yentsch and Menzel, again using acetone to extract chlorophyll *a* from a plankton sample that had been filtered. The sample was irradiated with blue light to induce red fluorescence of chlorophyll *a*. Phaeophytin was obtained by adding a few drops of HCl to the extract, and the fluorescence re-measured. This method is now standard and has been codified in the "bible" of oceano-

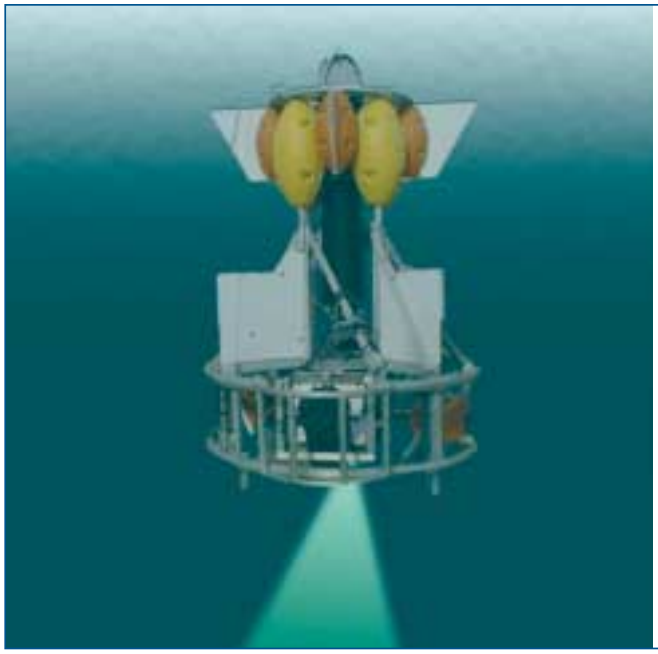


Figure 4. *Artists impression of the FIDO-Φ slowly descending, capturing two-dimensional images of phytoplankton fluorescence stimulated by the green laser sheet.*

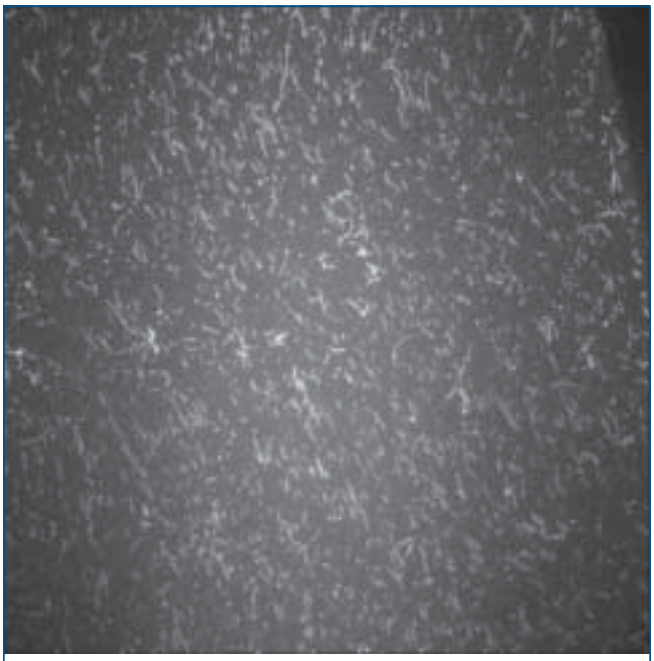


Figure 5. *A 32 ' 32 cm image of phytoplankton fluorescence captured by FIDO-Φ at 35 m depth, about 10 km off the coast of San Diego. The white objects are individual phytoplankton chains, some as long as 2 cm.*

graphic methods, Strickland and Parsons' (1968) "A Practical Handbook of Seawater Analysis." The fluorescence method is not as accurate as the spectrophotometric method; however, it is fast and sensitive, requiring much smaller sample volumes.

One of the co-authors of Holm-Hansen's paper was Scripps colleague Carl J. Lorenzen. Shortly after Holm-Hansen's paper appeared, Lorenzen (1966) published a short but significant paper in the journal *Deep-Sea Research* showing that the fluorescence of *living* phytoplankton could be used as a measure of their chlorophyll content. He designed a flow-through system to obtain continuous measures of chlorophyll fluorescence while a ship was underway. Water pumped from an inlet at the bow passed through a fluorometer, and the signal was recorded on a strip chart recorder. The trace he shows in his publication is one of the first to give a well-resolved picture of the horizontal spatial patchiness of phytoplankton biomass.

Near the end of his paper, Lorenzen (1966) wrote, "*The instrument could also be used for obtaining vertical profiles in conjunction with a pump*." The first profiling *in situ* fluorometers did exactly that: a bench-top fluorometer was fitted into a pressure case, and seawater was pumped through the sample chamber as the apparatus was lowered by winch from a ship. Alternatively, the fluorometer could remain on board ship, while the pump brought water from depth through a length of hose that was raised or lowered to obtain a profile (this is how I obtained fluorescence profiles for my own dissertation research in the late 1980s). The drawbacks to these techniques were numerous, including contamination by bubbles, the high power requirements of the pump and fluorometer, and the large, heavy pressure case for submersible units. With a market identified, many types of mini fluorometers were developed that are now available commercially; they are standard additions to most conductivity-temperature-depth packages.

While fluorometers are indispensable tools for quantifying one aspect of phytoplankton biomass, they still cannot replace microscopic examination of samples (usually obtained by bottles) for identification of the organisms present. In the last decade, technological advances have led to the development of tools that combine the two—microscopes and fluorometers—in a single tool for *in situ* observation. One such tool developed at Scripps is FIDO-Φ (Free-Fall Imaging Device for Observing Phytoplankton) designed and built by Jules S. Jaffe and Peter J.S. Franks. This instrument uses a thin sheet of laser light to stimulate phytoplankton fluorescence, which is then imaged with an extremely sensitive digital camera. A vertical profile of images is obtained as FIDO-Φ descends, allowing an unprecedented view into the undisturbed spatial distributions of the phytoplankton and their relationship with their environment and each other (Figure 5).

The Organism as Tool: Dinoflagellates

In 1902 Harry Beal Torrey published what may have been the first account of a "red tide" in the Southern California Bight. This dark brownish-purple discoloration of the water was caused by extraordinary concentrations of a dinoflagellate that Torrey tentatively put in the genus *Gonyaulax*. It was probably the organism we now call *Lingulodinium polyedrum*, a common bloom-forming dinoflagellate in our coastal waters. In September 1952, Beatrice M. Sweeney, a researcher in the laboratory of Frances Haxo at Scripps, successfully established the first unialgal culture of *Lingulodinium polyedrum* (then named *Gonyaulax polyedra*). Sweeney confirmed that the organism was bioluminescent and made the first quantitative measurements of its light emission, presented in 1954 at the first-ever conference on The Luminescence of Biological Systems. Joined in 1955 and 1956 by J. Woodland Hastings, then at Northwestern University, they demonstrated that the luminescence is controlled by an endogenous rhythm, showing for the first time that single eukaryotic cells were able to maintain circadian rhythms and establishing *L. polyedrum* as a model organism for study of circadian rhythms. Sweeney and Hastings also studied the biochemistry of luminescence, isolating and partially purifying a novel luciferin and luciferase, the molecules involved in light production. A daily rhythm in luciferase was the first demonstration of a biochemical rhythm, providing a means for tracking the biochemistry of the underlying biological clock. The legacy of this work reaches to the present.

The sensitivity of dinoflagellate blooms to wind had been a common observation in Europe, North America, and Asia. Strong winds tended to terminate the blooms, and suggested that the organisms were particularly affected by the water turbulence created by the wind. William Thomas, a phytoplankton ecologist at Scripps, and Carl Gibson, a fluid dynamicist, collaborated on a series of studies published in the early 1990s to attempt to quantify the effects of turbulence on phytoplankton—*L. polyedrum* in particular. In a series of papers, they showed that this dinoflagellate was extremely sensitive to the small-scale shears created by turbulent mixing. Ongoing work in the laboratory of Michael Latz at Scripps has shown that *L. polyedrum* is one of the most sensitive organisms ever tested for its response to shear. Furthermore, it responds to shear with a burst of bioluminescence, which Latz has exploited for visualizing flows around things such as dolphins in the ocean. Thus, the organism has become a tool to investigate both biological and nonbiological phenomena in the sea.

Distribution Patterns and Ecosystem Function

Patterns and Trends

Up to the early 1930s, there was strong disagreement among the European plankton researchers Victor Hensen and Ernst Haeckel concerning the spatial patterns of plankton: Hensen (one of the founding fathers of biological oceanography who coined the term *plankton*) believed that the plankton were distributed evenly; Haeckel (who coined the term *ecology*) believed that plankton were patchily distributed. Technical innovations such as the Hardy Continuous Plankton Recorder helped put the argument to rest: The plankton were clearly unevenly distributed. At Scripps W. E. Allen gathered extensive data on the temporal changes in plankton from the Scripps pier, and horizontal and vertical distribution patterns from cruises. His data remain the most comprehensive sampling of dinoflagellate blooms, though seven decades later we still do not understand the dynamics underlying the formation of "red tides." In a charming paper presented at the Sixth Pacific Science Congress (circa 1939), Allen wrote,

> *"To those who may have thought of conditions in the ocean as being so nearly uniform that the routine of life must be rather monotonous, it may seem somewhat shocking to know that our records show not two years alike in the twenty, no two months alike, and no two weeks alike. Continual change is the order of nature as much in the sea as it is on land, weather and many other influences playing their part in the eternal shifting of relationships."*

In a 1941 paper Allen wrote,

> *"Sometimes many diatoms appear at lower levels though few at the surface, sometimes many appear at the surface when numbers are small below, and sometimes rather large numbers may be found at all seven of the levels sampled at a particular station." He also observed "cloudlike aggregations of diatoms and dinoflagellates."*

While these quotes do not do justice to the important contributions Allen made to our understanding of the phytoplankton of the Southern California Bight and other regions, they illustrate the problem in trying to infer ecosystem function or predictability from isolated bottle samples and little auxiliary data. In 1939, Allen coauthored a paper with Harald U. Sverdrup (later director of Scripps) describing physical and biological patterns in the Southern California Bight during six bimonthly cruises in 1938. Data from these cruises revealed spatial patterns of diatom abundance that bear a remarkable resemblance to the patterns shown by the present-day California Cooperative Fisheries Investigations (CalCOFI) program. They showed that eddies of offshore water were low in diatoms, while eddies of inshore waters often had abundant diatom populations. They also identified an inshore counter current (now known as the Davidson Current), and offshore "southeast-flowing upwelled water" (the California Current System or its inshore boundary) with characteristic diatom populations and abundances.

Following in Allen's footsteps, Elizabeth Venrick has made a career of trying to tease apart the community structure of the diatoms in the North Pacific.

Venrick was a graduate student at Scripps and has remained at Scripps since. Now a co-director of the Integrative Oceanography Division, Venrick is probably best known for her work on the deep chlorophyll maximum. In a series of papers, Venrick enumerated hundreds of species of phytoplankton from vertical bottle casts in the North Pacific gyre taken over a period of a decade. Through careful statistical analysis, she showed that there were distinct, stable, surface and deep communities of phytoplankton, and that these communities rarely mixed. Similar analyses of the horizontal distributions of phytoplankton in the CalCOFI region since 1990 (Venrick, 2002) have shown distinct phytoplankton assemblages associated with distinct water masses and circulation patterns in the area, echoing Allen's earlier work.

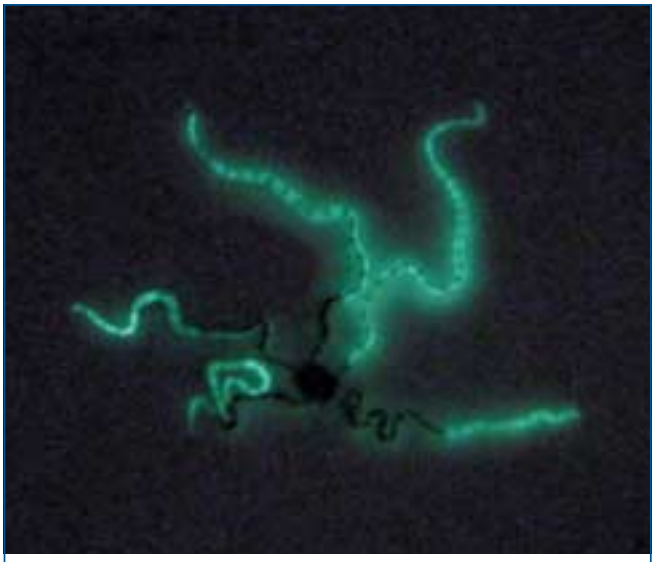
The remarkable stability of the phytoplankton communities recorded by Venrick was superimposed on a background of decadal changes in the total biomass (chlorophyll concentration) of the phytoplankton. Venrick and colleagues from Scripps published a seminal paper in 1987 showing an increase in the concentration of the deep chlorophyll maximum of almost a factor of two from 1966 to 1987. This trend in the phytoplankton biomass of the central North Pacific was probably the first recorded large-scale long-term change in the marine environment, beginning a phase of intense interest in the interactions among global climate, atmospheric carbon dioxide, and marine plankton.

Ecosystem Function: Before the "Biological Pump"

By the early 1900s, the intimate connections between phytoplankton and their physical and chemical environment were well appreciated. In an abstract to a paper presented to the 1929 Fourth Pacific Science Congress, E. C. Moberg of Scripps noted the following: (1) The food of practically all marine animals is derived from the photosynthetic activity of pelagic marine plants (i.e., phytoplankton). (2) The growth of these plants is controlled by certain physical conditions and by the abundance of a number of chemical substances in solution in the water. (3) Some of these substances occur in sea water in exceedingly small quantities and during periods of rapid plant growth may entirely disappear. (4) These substances are restored to the photosynthetic zone chiefly by vertical circulation, the bottom water being rich in nutrient substances derived from the decomposition of organic material.

This is quite a remarkable summary, including as it does the importance of multiple limiting nutrients, vertical water motions (upwelling), mixing, sinking, and remineralization at depth, and spatial and temporal variations in all these processes. The elaboration of these concepts occupied—and continues to occupy—the minds of many phytoplankton researchers.

Even as early as the 1920s, the role of plankton sinking and remineralization at depth was appreciated, as exemplified in Moberg's previously stated quote.



A bioluminescent brittle star.

Still, the dynamics of this process were somewhat obscure even in the 1950s when E. J. Ferguson Wood of Scripps examined samples of mud obtained from 7400 m depth. He found intact diatoms still containing protoplasm, and concluded, "*It is impossible that both cell and protoplasm could have been preserved intact during a slow descent of 7,400 m from the photic zone, so the evidence that these forms are autochthonous is very strong*." Wood was unaware of the tendency of diatom blooms to aggregate and sink intact to the bottom in a matter of days, where they could be found still green and coating the sediments in a layer several centimeters thick.

Iron Limitation

In 1952 Scripps chemist Edward D. Goldberg published a paper exploring the possibility of iron limitation of marine diatoms. The role of iron in phytoplankton growth was well known by that time; however, the details of the iron-phytoplankton relationship were unclear. Goldberg (1952) wrote, "*What is the minimal content of iron per cell needed for further cell division? What constitutes available iron?…Can iron content be one of many possible parameters in the nutrient index of the productivity equation?*" These important questions are still being explored today. At the time, research concentrated on the possibility of iron limiting coastal phytoplankton; there seemed to be no recognition yet of the possibility of iron limitation in the open ocean.

Atmospheric CO_2

While Goldberg and others were investigating the various nutrients that might limit phytoplankton growth, several Scripps researchers were interested in the role of the ocean and its biota in the regulation of gases such as carbon dioxide and oxygen. Allen (1943) wrote, "*We can go so far as to investigate the importance of*

these creatures [phytoplankton] in modifying carbon dioxide and other chemical constitution of waters." He was clearly aware of the influence of phytoplankton on oxygen production, carbon dioxide uptake, and other modifications of their chemical environment. In 1957 Roger Revelle and Hans E. Suess of Scripps published a paper supporting earlier studies suggesting that atmospheric carbon dioxide was increasing, although they concluded the following: "I*t seems therefore quite improbable that an increase in the atmospheric CO_2 concentration…could have been caused by industrial fuel combustion during the last century*." One of their alternate suggestions was that "fluctuations in the amount of organic marine carbon might be an important cause for changes in the atmospheric CO_2 concentration."

Putting the Pieces Together: f Ratios and IRONEX

By the late 1950s, many of the pieces for our modern synthesis of atmosphere-ocean gas exchange, micronutrient limitation of phytoplankton growth, and planktonic ecosystem structure were in place. It was during the mid-1960s that the Food Chain Research Group was formed at Scripps under the directorship of John Strickland. Among many influential biological oceanographers, this group included a young luminary, Richard W. Eppley (see Weiler et al., 1990, for a tribute).

Eppley was a phytoplankton ecologist/physiologist with a remarkable knack for combining insights from laboratory experiments with fieldwork to obtain a broad vision of the workings of the ocean. One of Eppley's best-known papers synthesized much of the published literature on the relationship of phytoplankton growth rate and temperature, from which he derived an empirical curve defining the maximal phytoplankton growth rate for a given temperature. Growth rates falling above this curve were suspect.

This seemingly innocuous paper touched off a firestorm of research attempting to refute everything from the estimates of total production to the relationship of new and total production, and the methods of averaging over time and space.

Probably Eppley's most important contribution was a paper published in 1979 with Bruce J. Peterson. In this paper, Eppley and Peterson (1979) built on an earlier paper by Dugdale and Goering (1967) in which they defined "new" and "recycled" production. New production is primary production supported by nutrients introduced to the euphotic zone by nitrogen fixation, atmospheric deposition, or most important, vertical mixing from the deep pool of nitrate (cf. Moberg quote in previous section). Recycled production was fueled by nutrients released by the activities of heterotrophic organisms and bacteria in the euphotic zone. Eppley and Peterson codified this idea in the *f* ratio—a ratio of new production to total production. The central idea was that new production (the flux of nutrients into the euphotic zone) had to be balanced by export production (the flux of organic material out of the euphotic zone). If there was some predictable relationship between new production (which is difficult to measure) and total production (which is relatively easy to measure), then measurements of total production could be used to estimate new production and export production. Thus one relatively simple measurement could give information on the flux of organic material to the sediments, and the potential for the ocean to sequester atmospheric carbon dioxide.

This was an important conceptual leap: The amount of carbon dioxide that could be sequestered by the ocean was related not to total primary production, but to the fraction of primary production that sank out of the euphotic zone (and was replaced by new nutrients). Eppley and Peterson (1979) suggested that new production was a saturating function of total production (a rectangular hyperbola), estimating new production in the world's oceans to be about 4.7 times 10^9 tons of carbon per year. This seemingly innocuous paper touched off a firestorm of research attempting to refute everything from the estimates of total production to the relationship of new and total production, and the methods of averaging over time and space. Several important fruits were born of this work. Clean techniques were adopted for measurements of primary productivity (previous estimates were low due to toxic bottle effects), and better estimates of global primary production were obtained using alternate methods such as satellite imagery for estimating phytoplankton biomass and growth rates.

Today, the *f* ratio is such a central concept in oceanographic biogeochemical cycling that Eppley and Peterson (1979) are often not cited (though the paper had almost 1,000 citations as of this writing). If new production can be increased, then the export production will be increased, sequestering more atmospheric carbon dioxide. It was about a decade later that ideas of the possibility of iron regulation of phytoplankton growth and new/export production controlling atmospheric CO_2 came together in a most interesting and synergistic way.

Though it was generally accepted that nitrogen was the main nutrient limiting phytoplankton growth, by the 1970s it was recognized that there were vast areas of the equatorial and subequatorial Pacific and the Southern Ocean that had abundant nitrogen at the surface, had sufficient illumination much of the year, but had extremely low phytoplankton biomass—so-called High Nutrient Low Chlorophyll (HNLC) regions.

Two alternate hypotheses were put forward for the existence of HNLC regions: John Martin of the Moss

Landing Marine Laboratories suggested it was iron limitation of phytoplankton growth. Others, including Bruce Frost (a former student at Scripps) held that grazer control of phytoplankton biomass could be the cause. The controversy culminated in the first massive, controlled manipulation experiment in the ocean: IRONEX. The results of the iron enrichment experiment in 1993 off the Galapagos Islands were equivocal: primary production increased, but nitrate was not consumed, and grazing was not measured. John Cullen, a former student of Eppley's, made it clear that unless the hypothesis of grazer control of the phytoplankton biomass was rejected, the iron limitation hypothesis could not be accepted. A second experiment in 1995 was more conclusive: phytoplankton growth rates increased by a factor of two, the biomass of some large diatoms increased by 85 times, and nitrate was drawn down to detection limits—exactly as predicted by the iron limitation hypothesis. Two subsequent enrichment experiments in the Southern Ocean have been similarly successful. But, while the nitrate was drawn down and phytoplankton increased (i.e., an increase in new production), demonstration of an increase in the sinking organic flux was equivocal.

Even though the sinking flux of organic material was not significantly enhanced in all the iron enrichment experiments, the possibility of using iron fertilization to mitigate anthropogenic increases in atmospheric CO_2 has been seized upon by several entrepreneurs—much to the consternation of many oceanographers. Cullen and S. W. "Penny" Chisholm, a former postdoctoral fellow of Eppley's, have been vocal in their criticism of such proposals. The scientific and social/political/economic arguments still rage. However, one of the important spin-offs of the iron fertilization experiments was the insight gained into the workings of the planktonic ecosystem. The role of the smallest phytoplankton, and their control by nutrient limitation and grazing was made clear, while the dominance of phytoplankton blooms by larger phytoplankton could be better understood in the context of their own grazers and nutrient limitation.While no Scripps scientists were directly involved in the iron fertilization experiments, many of the participants were trained at Scripps as students or postdoctoral scholars.

Scripps now has quite a number of scientists studying the phytoplankton, employing tools from imaging fluorometers, satellites, and computer models, to molecular biology and genomics. While the fundamental questions remain unchanged, the detailed questions have been refined and refocused, based on the extraordinary work of scientists over the last century. New organisms have been identified, new dynamics have been uncovered, and new insights have brought the field forward. Scripps and its scientists now look forward to another century of exploration and discovery, fueled by the incorporation of new tools, in the quest to understand our ocean's ecosystems. 

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