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CHASING NUTRIENTS AND ALGAL BLOOMS IN GULF AND CARIBBEAN WATERS: A PERSONAL STORY

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ABSTRACT: Over the past 5 decades, coastal waters have experienced unprecedented global change, including widespread eutrophication, harmful algal blooms (HAB), dead zones, and loss of biodiversity. During this period, I have studied the effects of nutrients (N, P) on HAB dynamics in tropical seagrass and coral reef ecosystems. Important findings that emerged from my research include: 1) a primary role of anthropogenic nitrogen (N) relative to phosphorus (P) as a driving factor in algal blooms and coastal eutrophication; 2) altered N:P stoichiometry that results in greater P—limitation and metabolic stress in reef corals; 3) recognition that macroalgal blooms be considered as a type of HAB because of their increasingly negative impacts on oceans and human health; and 4) mitigation of anthropogenic N inputs can increase resiliency of seagrass and coral reef ecosystems relative to population growth and climate change. Major developments during the research involved the use of computers and software; EAN NITROX, dive computers, and high resolution underwater video to make SCUBA surveys safer and more effective; analysis of stable nitrogen isotopes, sucralose, and other human tracers to discriminate between natural and anthropogenic N sources; and satellite remote sensing to better monitor the large—scale HAB phenomena. My research sparked considerable debate about the root cause(s) of algal blooms on Caribbean coral reefs, as several senior coral reef biologists had concluded this problem was caused solely by the reduction of reef grazers. Since 2011, the massive *Sargassum* influx to the Caribbean region appears to be a eutrophication response to increasing nutrients in the tropical Atlantic Ocean and is now considered the largest HAB on the planet. Going forward, early career scientists need to extend research on declining coastal ecosystem health to upland watersheds to better understand and mitigate nutrient pollution at its source(s) to enhance resilience of seagrass and coral reef ecosystems to climate change.

KEY WORDS: *Sargassum*, nitrogen, phosphorus, eutrophication, stoichiometry

> *"It is the sea that holds the great mysteries. There is still much to be learned from land, to be sure, but it is the third dimension of the oceans that hides the answers to the broad elemental problems of natural history"* Archie Carr, *The Windward Road.*

INTRODUCTION

Over the past 5 decades, there has been a growing awareness that tropical and subtropical marine ecosystems have experienced a variety of environmental problems that can be attributed to excess nutrients. While many of these diverse problems may seem unrelated and their causes often not readily apparent, evidence now clearly shows that increasing harmful algal blooms (HAB), wildlife mortalities, fish kills, seagrass die—off, coral reef degradation, and "dead zones" have more in common than previously thought. All of these events are linked by the common thread of excess nutrients, which cause slow, subtle shifts in the abundance of organisms at the base of the food web (Howarth et al. 2000).

All living organisms require nutrients to grow. Primary producers at the base of the food web use carbon (C), nitrogen (N), and phosphorus (P) in specific ratios and concentrations, in combination with certain wavelengths of light, to produce organic matter through the process of photosynthesis (Redfield 1958). When a necessary nutrient for growth is not available in sufficient quantity, that nutrient is considered "limiting" to algal growth (Droop 1983). A fundamental challenge for scientists and resource managers has been to understand how natural and human modification of watersheds and airsheds affects the overall quantity and relative abundance of N and P, which are the two most common limiting nutrients for primary producers and HAB in coastal ecosystems (Ryther and Dustan 1971, Howarth et al. 2000, Glibert et al. 2005).

Human activities have already more than doubled the amount of biologically reactive N on our planet (Vitousek et al. 1997), which is having profound effects on HAB and the biodiversity and sustainability of coastal ecosystems on which human populations depend (Rockström et al. 2009). This article describes my personal experience over the past 5 decades into the study of anthropogenic nutrient enrichment, HAB, and how the process commonly referred to as *cultural eutrophication* has contributed to the alteration of coral reef and seagrass ecosystems in the Gulf of Mexico (GOM) and the wider Caribbean region. The essay will also highlight how some scientists and resource managers have responded to my findings, which is especially useful to early career scientists to fully understand how this "mysterious" problem accelerated so quickly in the Florida Keys and throughout the wider Caribbean region.

WHERE IT ALL BEGAN: MENTORS AND MACROALGAE

My fascination with marine science began as a teenager growing up in West Palm Beach, FL during the 1960s. In addition to watching *Sea Hunt* and *The Undersea World of Jacques Cousteau* on television, I began snorkeling and fishing in the coastal waters of south Florida and the Florida Keys. The more time I spent on and under the water, the deeper my interest grew. In particular, the "gin clear" water and amazing biodiversity on coral reefs in the Florida Keys aroused my curiosity as to not only what these organisms were (e.g., taxonomy of different species of corals, seagrasses and seaweeds), but more importantly how they functioned. It seemed paradoxical to me that such productive fisheries, including lobster, grouper, snapper, and conch, could thrive in such clean, clear waters of the Florida Keys.

That fascination led me to leave Florida and attend Boston University (BU) as an undergraduate student where I received a B.A. degree in Biology. While my primary interest was basic marine science, the growing environmental awareness in the 1960s and 1970s expanded my interest to include the general field of conservation biology. After reading a paper entitled "Nitrogen, phosphorus, and eutrophication in the coastal marine environment" (Ryther and Dustan 1971) in *Science* for a Conservation Biology class, I was hooked. The conclusion of the paper was that the ongoing replacement of P compounds with N compounds in detergents to protect P limited freshwater rivers and lakes would exacerbate eutrophication in the downstream marine environment that was N limited. I realized that the residential population of Florida was growing fast, as was tourism. Nutrients, especially N, associated with increasing sewage, fertilizers, and fossil fuel emissions, would surely become an important research and management issue for Florida's water future.

My dream at that time was to graduate from BU and gain employment at Woods Hole Oceanographic Institution (WHOI) on Cape Cod, and, in particular, work for John Ryther. Following my application with WHOI and a waiting period that seemed like forever, I was eventually contacted by the WHOI personnel department and urged to compete through a written exam for a research assistant position with John. As luck would have it, I did very well on the exam, largely due to my experience with seaweeds along New England's coastline via a field course in Marine Botany at BU. I was offered the job and worked for John between 1973 and 1977 growing the commercially valuable red seaweeds such as *Gracilaria* and *Agardhiella* as part of an integrated multi—trophic wastewater—recycling aquaculture system. Today, these are referred to as Integrated Multi—Trophic Aquaculture (IMTA) systems. After some exploratory research, John had raised enough money to build a moderately—sized pilot—scale system of ponds and raceways—the WHOI Environmental Systems Laboratory (Figure 1A, B). The testing of this system was supported by a new program at NSF called RANN (Research Applied to National Needs). Although initial trials were encouraging, especially with the mass culture of fast—growing seaweeds, the RANN program was discontinued and no other source of funding was available. Meanwhile, Ed Link and Seward Johnson, Sr., directors at the Harbor Branch Foundation (later Harbor Branch Oceangraphic Institution, HBOI) in Ft. Pierce, FL, became interested in the wastewater—recycling aquaculture system and several of us at WHOI moved to HBOI in the winter of 1974 to set up a small experimental system at Linkport (Figure 1C, D). I published my first 3 peer—reviewed papers on seaweed research conducted using an outdoor, flowing seawater culture system at HBOI (Figure 1E) in the journals *Aquaculture* (Lapointe et al. 1976, Lapointe and Ryther 1978) and *Botanica Marina* (Lapointe and Ryther 1979) while having only a B.A. degree from BU.

Mussel Aquaculture, Macroalgal Blooms and Graduate School

By 1977 and after 4 gap years at WHOI and HBOI, I returned to college for graduate degrees. That decision was inspired by an offer of financial support from Ken Tenore (Figure 2A), a benthic ecologist who also worked on John Ryther's aquaculture project at WHOI. Ken had accepted a position at Skidaway Institute of Oceanography (SKIO) in Savannah, GA, and was the Principal Investigator of a cooperative research program on mussel aquaculture in the Rias Bajas, NW Spain. My graduate support involved travel to Spain to participate in the "Spanish—American Rias Study (SARS)," which involved SCUBA to

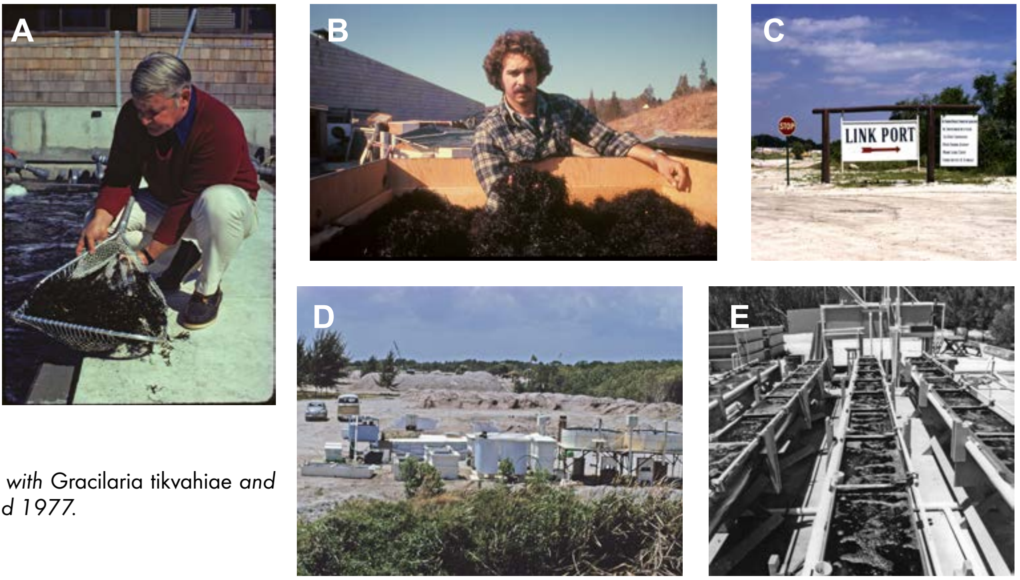

FIGURE 1. *Early work with the red seaweed Gracilaria. A. Dr. John Ryther holding a net of Gracilaria tikvahiae grown on sewage/seawater mixtures at the Environmental Systems Laboratory (ESL), Woods Hole Oceanographic Institution (WHOI), Woods Hole, MA. B. Lapointe holding a sample of Gracilaria tikvahiae at ESL that was being placed in a large outdoor drying oven. C. The entrance to Linkport in 1974, known today as Florida Atlantic University-Harbor Branch Oceanographic Institute (HBOI). D. The original wastewater-recycling aquaculture system at HBOI in 1974. E. Experimental flowing seawater culture system used for research on nutrient-growth rate relationships with Gracilaria tikvahiae and other macroalgae at HBOI between 1974 and 1977.*

FIGURE 2. *Early career work: graduate school and studies in Spain. A. Dr. Ken Tenore, Head of the Chesapeake Biological Laboratory, Solomons, MD. B. Mussel rafts in the Ria de Arosa, Galicia, NW Spain. C. The temperature-controlled, flowing seawater culture chambers at Skidaway Institute of Oceanography (SKIO) used to culture Ulva and Gracilaria under different levels of light, temperature, and nutrients.*

track the seasonal productivity, nutrient contents, and species succession of macroalgae that grew on the mussel ropes (Figure 2B). Working with Spanish collaborators was a very enriching experience for me, especially the amazing meals and lively conversation that extended for hours. With support from SKIO, I began an M.S. program in Environmental Sciences at the University of Florida, graduating in 1979. My M.S. thesis research involved the use of temperature—controlled, outdoor flowing seawater cultures to examine the interactive effects of light and nutrients on growth of the green sea lettuce *Ulva fasciata* (Figure 2C). My M.S. program provided me with a strong background in aquatic chemistry, water quality management, and eutrophication of Florida's lakes. But, I missed the more biodiverse marine environment and decided to apply to the University of South Florida in Tampa for a Ph.D. program with Clinton Dawes in the Biology Department.

During the 1960s and 1970s, the population of Tampa was growing and the shallow waters of Tampa Bay were experiencing eutrophication where thick extensive mats of *Gracilaria* and *Ulva* overgrew and smothered seagrasses. This created a big stink (literally!) for stakeholders around Tampa Bay, and led to an N reduction program in the wastewater treatment plant at Hooker's Point. Realizing that blooms of *Gracilaria* and other macroalgae were ecological indicators of excess nutrients from sewage discharges into Tampa Bay, I decided to study the interaction of light, temperature, and N on growth, physiology and biochemistry of *Gracilaria tikvahiae* for my dissertation, which was completed using a typewriter in the winter and spring of 1982. The work involved outdoor studies in the same flowing—seawater culture system at SKIO that I used for my M. S. research with *Ulva* (Figure 2C) and rate measurements of growth, photosynthesis, respiration, nutrient uptake, and biochemical composition (C, N, and P; protein, carbohydrates, lipids, pigments). Although I already appreciated the importance of nutrients and elemental stoichiometry from working with John Ryther at WHOI, my experience with Clinton Dawes gave me a whole new appreciation for the beauty of seaweeds, as well as broader aspects of seaweed physiology and ecology. I even adopted a cat and named him Sargassum! Seaweeds became the organism of choice for me and I have since used them as indicator organisms to assess the type and degree of nutrient pollution and identify N sources.

Early Career Nutrient and Macroalgae Research in the Florida Keys

When I finished my Ph.D. program at USF in late spring of 1982, John Ryther was retiring from WHOI and moving to Florida. John had just received a grant from the Gas Research Institute (GRI) through the Institute of Food and Agricultural Sciences (IFAS) at University of Florida in Gainesville. John offered me a post—doctoral position to expand my dissertation research on productivity and nutrition of seaweeds. The job involved directing field aquaculture research with seaweeds on Big Pine Key in the lower Florida Keys. Being an avid SCUBA diver and fisherman, I recognized the incredible opportunity and dove right in. Meanwhile, Bob Jones at HBOI in Ft. Pierce enticed John with a position as Director of the new "Division of Applied Biology" and in January 1983, both John and I became employed by HBOI. This was my first real job, and I began as an Assistant Research Scientist. Some 37 years later, I am still with HBOI, although now a Research Professor and employee of Florida Atlantic University.

My field research on Big Pine Key involved nutrient dosing studies with *Gracilaria* and the brown pelagic seaweed *Sargassum* in land—based flowing seawater cultures and moored cage cultures in South Pine Channel (Figure 3A). The research required purchase of a small research vessel (Figure 3B) and going offshore into blue water to collect the two species of pelagic *Sargassum*; *S. fluitans* and *S. natans*. This research turned out to be the first demonstration that *both* N and P were limiting nutrients to algal photosynthesis and growth in coastal waters of the Florida Keys, but the pattern of nutrient limitation varied seasonally. Both N and P limited growth in the dry season (December to May) compared to the wet season (June to November), when only P was limiting (Lapointe 1987). This seasonality was the result of higher dissolved inorganic N (DIN, ammonium and nitrate) concentrations in coastal waters in the wet season, a phenomenon that would become increasingly important throughout my career. Although the GRI project ended in 1984 under the new Reagan administration, my findings led to the far—reaching question: where is the elevated seawater DIN coming from in the wet season?

Being a full—time resident on Big Pine Key since 1982, I witnessed first—hand the worsening water quality and expanding algal blooms in Florida Bay and the Florida Keys following heavy El Niño rainfall in winter 1983 and water management policies to send more water south to Everglades National Park. I realized that a monitoring study was needed to document changes in nutrients on the offshore coral reefs. In October 1984, I began a long—term nutrient monitoring program in the Sanctuary Preservation Area (SPA) at Looe Key reef (Figure 3C), which has continued for 35 years. By the mid—1980s, it was apparent that

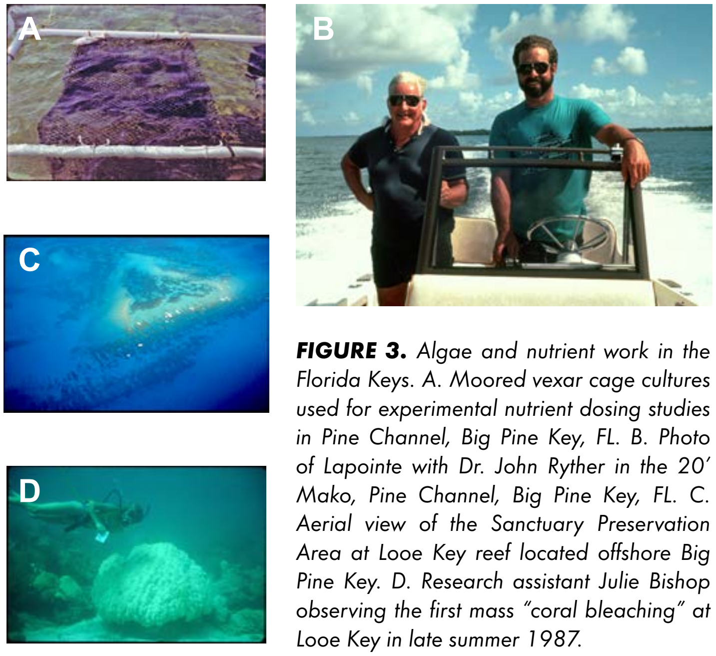

FIGURE 3. *Algae and nutrient work in the Florida Keys. A. Moored vexar cage cultures used for experimental nutrient dosing studies in Pine Channel, Big Pine Key, FL. B. Photo of Lapointe with Dr. John Ryther in the 20′ Mako, Pine Channel, Big Pine Key, FL. C. Aerial view of the Sanctuary Preservation Area at Looe Key reef located offshore Big Pine Key. D. Research assistant Julie Bishop observing the first mass "coral bleaching" at Looe Key in late summer 1987.*

coral diseases and die—off at Looe Key were worsening, and this emerging "coral crisis" was underscored by the first mass bleaching event in summer of 1987 (Figure 3D). Fortunately, funding from the MacArthur Foundation and Monroe County (Florida Keys) allowed me to expand my water quality research beyond Big Pine Key and Looe Key to include the entire Florida Keys and Florida Bay region in 1989/1990. By 1990, these studies clearly showed a gradient in DIN concentrations from Florida Bay and nearshore waters of the Florida Keys to offshore waters at Looe Key, which were approaching the DIN thresholds already known to cause eutrophication and decline of coral reefs in Kaneohe Bay, Hawaii, Barbados, and the Great Barrier Reef in Australia (Smith et al. 1981, Bell 1992).

Backyard Science: Septic Systems as a Nitrogen Source

To identify local sources of DIN enrichment from the Florida Keys, I began a project to assess the effects of septic systems on nutrients in groundwaters and surface waters. When I moved to Big Pine Key in 1982 and built a new home, I was dismayed to find that all residential development outside of Key West relied on either cesspits or septic systems for on—site wastewater treatment and disposal. It seemed obvious to me at the time that the porous limestone substrata in the Florida Keys could not possibly provide adequate treatment of septic tank effluent, especially given the high groundwater tables and close proximity to sensitive surface waters. This project, funded by the Florida Department of Environmental Regulation Coastal Zone Management Program, involved collaboration with the Monroe County Planning Department for installation of groundwater monitor wells, and seasonal sampling of the wells and adjacent surface waters for nutrients, salinity, and temperature. The grant provided funds to purchase my first computer, an Apple IIe, which ultimately led to a series of MacBooks and iPhones. I also purchased a KV Associates heat—pulsing groundwater flowmeter to quantify lateral groundwater flow and effects of tidal pumping and rainfall on nutrient transport (Figure 4A). The research showed a high degree of DIN enrichment and relatively less enrichment of soluble reactive phosphorus (SRP) in groundwaters due to adsorption of P onto the limestone substrata (Lapointe et al. 1990). Ebbing tides resulted in accelerated groundwater discharge, and rainfall caused transient surge flow of groundwaters into adjacent surface waters. The resulting septic system discharges had high DIN:SRP ratios (100:1) that fueled P limited eutrophication in nearshore waters (Lapointe and Clark 1992). This was the first project in Florida to document the failure of septic systems to protect coastal water quality, which combined with subsequent viral tracer studies (Paul et al. 1995), led to a state mandate for central wastewater collection and advanced treatment (nutrient removal) throughout the Florida Keys.

The worsening water quality, algal blooms, coral bleaching, and diseases were driving factors in the establishment of the Florida Keys National Marine Sanctuary (FKNMS) in 1990. My findings of nutrient pollution from septic systems were not well received by some of the public, nor by the new officials and scientists supported by the FKNMS program. A senior seagrass biologist from the University of Virginia who was involved in developing the FKNMS Management Plan disputed the conclusions of my peer—reviewed research that had been published in the journals *Biogeochemistry* (Lapointe et al. 1990) and *Estuaries* (Lapointe and Clark 1992). At a tumultuous Sanctuary Advisory Council (SAC) Meeting in August 1992 led by SAC Chairman George Barley (co—founder of the Everglades Foundation), Jay Zieman stated that the evidence for septic impacts were "poorly filtered white papers" and conclusions were nothing more than an "allegation." The senior seagrass biologist blamed the degraded local water quality on a lack of hurricanes and hypersalinity as a result of reduced freshwater flow from the Everglades to Florida Bay. This new alternative hypothesis was published as a conceptual model in the Proceedings of the Gulf of Mexico Symposium (McIvor et al. 1994) but contained no supporting data for the key model elements such as "salinity stress," "temperature stress," "overdeveloped *Thalassia*," and internal "nutrient efflux" in Florida Bay. There was also no mention of external nutrient inputs, such as the significant nitrogen inputs from the Florida Keys or Everglades watersheds (Rudnick et al. 1999). Nonetheless, the "hypersalinity hypothesis" was widely embraced by politicians, FKNMS officials, environmental activists, state and federal agencies, and scientists receiving grant funding from the FKNMS. All agreed, without scientific evidence, that hypersalinity was the putative cause of the worsening algal blooms and seagrass die—off in Florida Bay that was impacting downstream waters of the FKNMS (Stevens 1997).

The "hypersalinity hypothesis" was attractive politically as it could be "fixed" relatively cheaply and quickly. FKNMS officials, activists, and politicians all implored the US Army Corp of Engineers to increase freshwater flows from Lake Okeechobee into the Florida Bay and Florida Keys region. The lesson here is to be careful what you ask for, because you might just get it. Water managers responded with major increases in flows that resulted in brackish, buoyant plumes of turbid, green water to

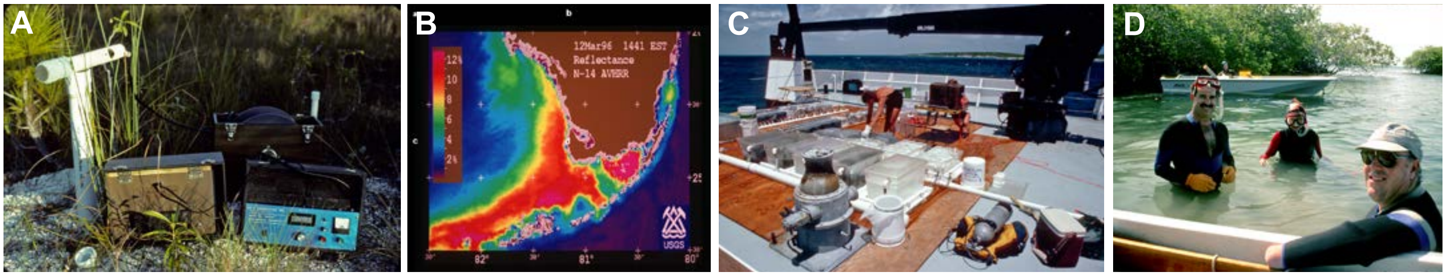

FIGURE 4. *Assessing land-based nutrient sources and their effects on coastal waters. A. KV Associates Model 30 GeoFlo groundwater flow meter used to monitor flow rates of nutrient plumes from septic systems in the Florida Keys. B. USGS AVHRR satellite image showing turbidity plume from Shark River Slough resulting from increased water deliveries to western Florida Bay and heavy rainfall in 1995. C. The experimental, flowing seawater culture system used for Sargassum research on the fantail of the RV Columbus Iselin. D. Lapointe with Drs. Mark and Diane Litter and assistant Barrett Brooks (background) in mangrove channel at Twin Cays, Belize.*

flow from Florida Bay through the tidal channels of the Florida Keys towards the outer bank reefs. The increased N loads from Shark River Slough and Taylor Slough caused unprecedented cyanobacterial blooms in Florida Bay, as well as sponge and seagrass die—off (Lapointe et al. 2004), but not the water quality improvements that scientists, activists, and agency officials predicted (Stevens 1997). Recent analysis of 3 decades of nutrient data, along with satellite imagery (Figure 4B), showed how these increased flows between 1991 and 1995 coincided with a breakpoint in DIN enrichment and phytoplankton blooms at Looe Key; to date, the DIN and chlorophyll *a* concentrations have not returned to their previous baseline levels of the 1980s (Lapointe et al. 2019a). Because the N:P ratio of Everglades water is 260:1 (Rudnick et al. 1999), the regional—scale freshet and DIN enrichment caused a significant increase in the water column DIN: SRP ratio and the molar N:P ratio of benthic macroalgae in the 1990s (Lapointe et al. 2019a).

Nutrient Research Expands to the Caribbean and Great Barrier Reef, Australia

To continue the *Sargassum* research that I began on Big Pine Key in the early 1980s, I submitted a research proposal to the National Science Foundation to investigate the productivity and nutrition of pelagic *Sargassum* over broad areas of the North Atlantic Ocean and Caribbean region. The project involved several research cruises on the *RV Columbus Iselin* and *RV Calanus* to collect *Sargassum* and make comparative rate measurements of photosynthesis, respiration, and alkaline phosphatase activity, as well as tissue analysis for C:N:P (Figure 4C). The research showed the importance of seasonal transport of *Sargassum* through neritic areas where it had access to elevated nutrients from river discharges, upwelling, and atmospheric deposition that supported higher rates of photosynthesis and growth (Lapointe 1995). The research also showed the importance of nutrient cycling from associated fishes and invertebrates to sustaining *Sargassum* growth in oligotrophic waters of the Sargasso Sea, an area John Ryther described as "a biological desert" (Lapointe et al. 2014). As it turned out, these early measurements of productivity and C:N:P ratios in *Sargassum* provided an important planetary baseline. Similar measurements since 2010 indicate that the %N and N:P ratio of *Sargassum* in the Florida Current off Looe Key and in the GOM are significantly greater than the baseline values of the 1980s, indicating that coastal N enrichment as a factor related to the ongoing *Sargassum* blooms in the North Atlantic basin and Caribbean Sea (Wang et al. 2019).

The NSF—sponsored research cruises also provided an opportunity for comparative research on benthic *Sargassum* species and other macroalgae that were beginning to overgrow Caribbean coral reefs. I invited Drs. Mark and Diane Littler from the Smithsonian Institution to participate in the research cruises, which turned out to be one of the most productive collaborations of my career, extending over 2.5 decades. Our research sought to better understand the interactive roles of bottom—up (nutrients) and top—down (grazing) effects in driving macroalgal blooms that were becoming evident on fringing coral reefs in Jamaica and Martinique in the 1980s (Lapointe et al. 1992, 1993). Research along nutrient gradients extending from mangrove habitats to coral reefs near Carrie Bow Cay, Belize in the 1980s (Figure 4D) showed how DIN and SRP enrichment led to macroalgal blooms and eutrophication. This suggested ecological nutrient thresholds for coral reefs of 0.5 — 1.0 µM (7—14 ppb) for DIN and 0.1 µM (3.1 ppb) for SRP (Lapointe et al. 1993). During this same time period, cattails were overgrowing areas of the Everglades in South Florida that were experiencing P—enrichment from farms and urban areas. As a result, the Everglades Lawsuit was filed and eventually mandated that P concentrations no higher than 10 ppb, a concentration very similar to our proposed DIN threshold for coral reefs, would be allowed in water entering the Everglades Protection Area. Research on the southwest coast of Martinique was the first case study in the Caribbean to document how low level DIN enrichment of 0.8 µM and SRP > 0.1 µM from sewage pollution in urbanized areas around Fort—de—France was causing phase—shifts from coral to macroalgal dominated reefs (Littler et al. 1993). Long—term nutrient monitoring at Looe Key reef from 1984 to 2014 has since shown rapid coral decline and expanding algal turf and macroalgae as DIN exceeded this threshold in the early 1990s (Lapointe et al. 2019a).

In the summer of 1990, extensive blooms of the green seaweed *Codium isthmocladum* developed on deep (30 m) coral reefs in northern Broward and Palm Beach counties in southeast Florida, forming thick accumulations on reefs and adjacent

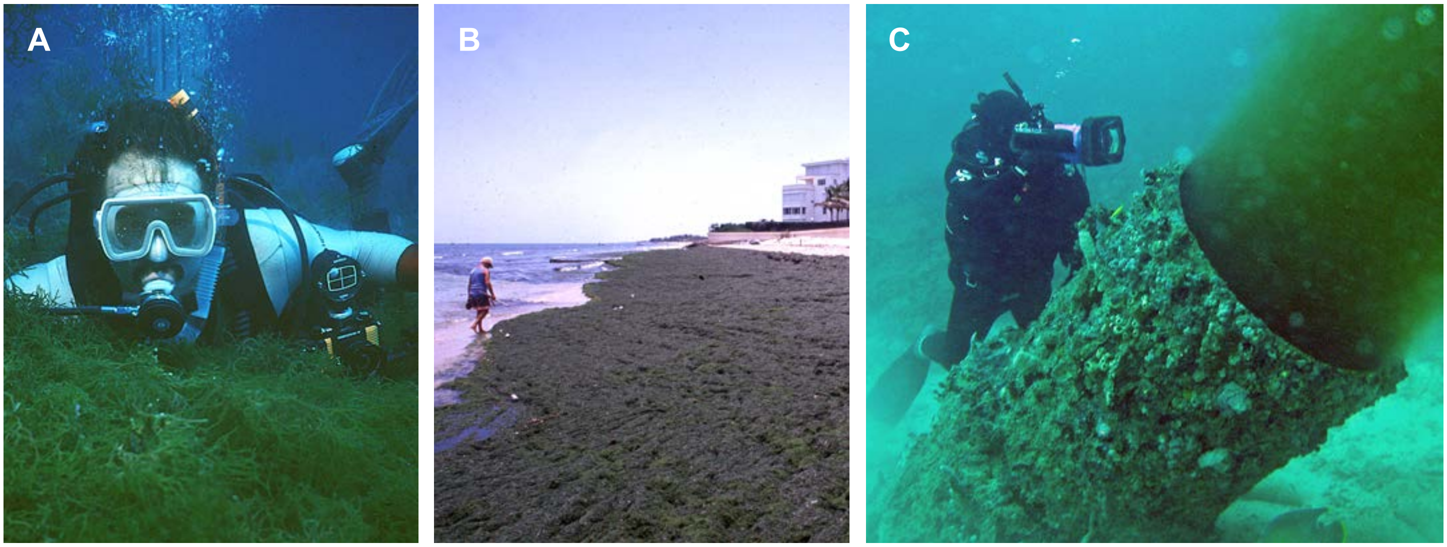

FIGURE 5. *Algae blooms off the southeast coast of Florida. A. Lapointe underwater in bloom of* Codium isthmocladum *smothering the "Football Field" coral reef off Lake Worth Beach, FL. B. Mass stranding of* C. isthmocladum *on beach at Boynton Beach, FL. C. Lapointe shooting video footage of the Delray Beach sewage outfall (which is now shut down).*

beaches (Figure 5A, B). At this time, we began using dive computers, EAN NITROX, and high–resolution underwater video to better document the blooms and quantify biota on affected reefs. *Codium isthmocladum*, as well as several species of *Caulerpa*, were known as opportunistic invaders and formed blooms in nutrient–enriched tropical and subtropical waters, such as around guano–enriched mangrove islands and the Mediterranean Sea. Workshops were organized by the Florida Wildlife Research Institute to determine research priorities. Some scientists questioned the role of land–based nutrient pollution in driving the blooms and alternatively suggested that the blooms were more related to natural, summertime upwelling. To better understand the ecological connectivity and nutrient dynamics of these blooms, I submitted (along with Co–PI Dennis Hanisak) a SeaGrant proposal to address effects of nutrient enrichment and characterize nutrient sources available to the blooms. We found that ammonium, the N form preferred by *C. isthmocladum* and discharged from upstream sewage outfalls (Figure 5C), was ~1 µM on the reefs, high enough to sustain the blooms without the need for the naturally–occurring nitrate from upwelling. We also analyzed the *C. isthmocladum* for stable N isotopes, which increased in the summer wet season to values characteristic of sewage N (Lapointe 1997). This explained why these blooms were recent phenomena associated with population growth in southeast Florida and not upwelling that was part of the natural history of these reefs.

The notion that expanding blooms of *Codium* and *Caulerpa* were bioindicators of nutrient enrichment on Florida's coral reefs was apparent in the summer 1987 when I visited the Discovery Bay Marine Lab (DBML) on the north coast of Jamaica (Figure 6A). My colleague Tom Goreau, Jr., a professor in the Geology Department at University of Miami at the time, had invited me to teach a summer course in Tropical Marine Botany at DBML. It did not take much to convince me to visit the birthplace of reggae and jerk chicken in the heart of the Caribbean. Furthermore, the DBML was the perfect place to examine the role of land–based N in driving macroalgal blooms on coral reefs. The lab was situated on the north coast of Jamaica, providing immediate SCUBA access to fringing reefs described in detail in the seminal research of T. F. Goreau (Goreau 1959). Most importantly, the coral reefs at Discovery Bay in 1987 were being overgrown by macroalgae since Hurricane Allen made landfall in 1980. Hurricane Allen caused major physical disturbance to the reef, especially the reef crest (0–6 m) that was dominated by the elkhorn coral *Acropora palmata*. Although the physical damage to the elkhorn coral reduced it to rubble, the reef was expected to recover "in a few years" (Woodley 1980). However, D'Elia et al. (1981) reported very high nitrate (~125 µM) and low SRP concentrations (0.2 µM; N:P of 625) in groundwaters discharging into the back reef and fore reef at Discovery Bay, indicating very strong P–limitation of the fringing reefs (Lapointe 1997). They concluded that even modest inputs of P from sewage or other sources could cause eutrophication problems, given the existence of widespread nitrate enrichment from submarine groundwater discharges.

My first observations of the lush macroalgal communities around the nitrate–enriched springs, grottos, back and fore reef habitats at Discovery Bay in June 1987 were impressive. Well–known genera of red, green, and brown macroalgae known to respond to nutrients, including *Laurencia*, *Caulerpa*, and *Sargassum*, were blooming in close proximity to the high nitrate groundwater discharges in the grottos and back reef (Figures 6B, 6C, 6D). Further offshore on the fore reef, luxuriant growths of the brown seaweeds *Sargassum*, *Turbinaria*, *Dictyota* and *Lobophora* formed extensive brown meadows. Based on my previous experience on coral reefs in the Florida Keys and Belize, the species composition, spatial zonation and overall biomass of macroalgae suggested N–fueled eutrophication on fringing reefs at Discovery Bay.

In June 1992, I attended the International Coral Reef Symposium (ICRS) in Guam with my colleagues Mark and Diane Littler. We presented 2 talks on the issues of eutrophication on

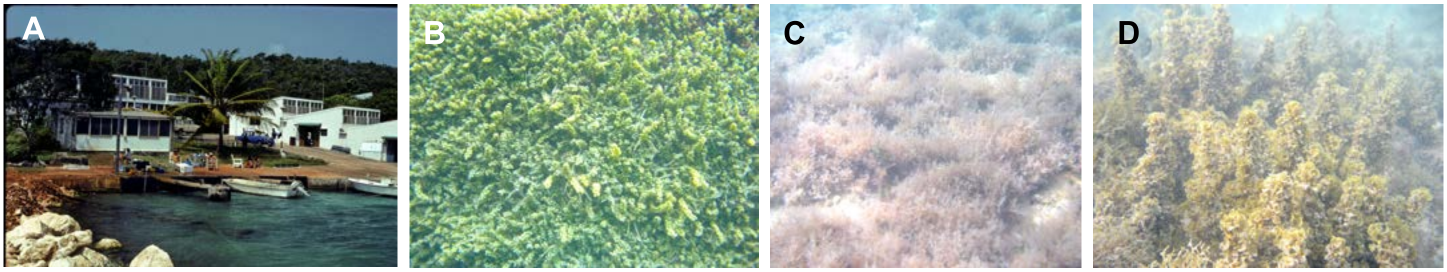

FIGURE 6. *Images from the Discovery Bay Marine Laboratory (DBML) A. The DBML on the north coast of Jamaica in June 1987. B. Thick mat of the green coenocytic macroalga* Caulerpa racemosa *growing in high nitrate waters of a spring-fed grotto. C. Drift blooms of the red macroalga* Laurencia sp. *in the back reef at DBML. D. High biomass meadows of* Sargassum hystrix *grow in the back and fore reef at DBML.*

coral reefs, one on our nutrient threshold research on the Belize Barrier Reef (Lapointe et al. 1993) and another on macroalgal overgrowth of Martinique's coral reefs (Littler et al. 1993). This was my first ICRS and it was very exciting to see the world's senior coral reef scientists discussing effects of nutrients on coral reefs. Another speaker in the eutrophication session, Peter Bell from the University of Queensland (Figure 7A), also spoke to the issue of nutrient thresholds on coral reefs in the Great Barrier Reef lagoon. Surprisingly, from "down—under" on the other side of the world, Peter had arrived at almost identical N and P thresholds (Bell 1992) to those we suggested based on our research on the Belize Barrier Reef. This encounter with Peter Bell led to another very productive collaboration (Bell et al. 2007, 2013) and included several trips to collaborate with Peter at Low Isles and Heron Island in Australia.

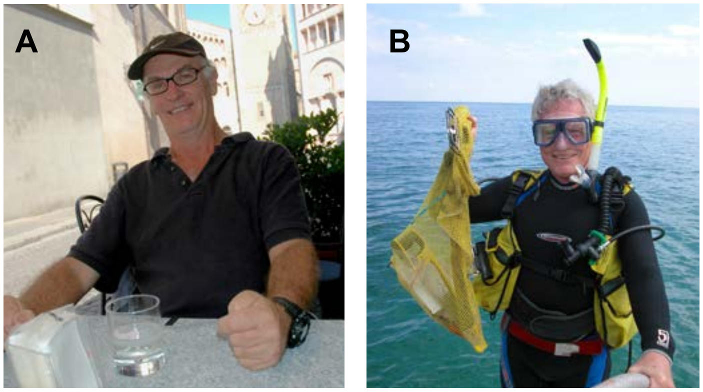

FIGURE 7. *Influential colleagues. A. Dr. Peter Bell enjoying a drink with the author in Venice, Italy. B. Dr. Mike Risk ready to dive for gorgonian samples in southeast Florida.*

ECOHAB and Coral Reef Controversy

In summer of 1994, I was invited to participate in a national meeting of algae experts at Snow Mountain Ranch, CO, to help develop a national plan for HAB research. HAB were on the rise nationally and globally, with negative consequences for the health of the oceans and humans, as well as economies of affected coastal areas. The participants included experts on toxic phytoplankton blooms, such as red tides, as well as non—toxic blooms, such as brown tides. While most attendees were phytoplankton experts, I was one of the few (along with Ivan Valiela from the Marine Biological Laboratory, Woods Hole, MA) to represent macroalgae. By this time, it was clear that macroalgal blooms were also increasing, impacting seagrass meadows and coral reefs in south Florida. The frequency and extent of macroalgal HAB have increased in estuaries and coastal waters throughout North America during the past 5 decades and now include all coastal states as well as Hawaii; in addition, macroalgal HAB have become common in inland freshwater systems, including lakes, streams, rivers, springs, and reservoirs (Lapointe et al. 2018).

The outcome of the Snow Mountain Ranch meeting was the first national research agenda to guide future HAB research — the *Ecology and Oceanography of Harmful Algal Blooms* program (ECOHAB 1995). Participants from the meeting published research papers in a special issue of *Limnology & Oceanography* dedicated to HAB case studies. I contributed a paper based on comparative research of macroalgal blooms on coral reefs in southeast Florida and Jamaica, which addressed the synergistic effects of nutrient enrichment and reduced grazing (Lapointe 1997). That was the first paper to quantify nutrient threshold concentrations for macroalgal blooms on coral reefs in the Caribbean region and challenged the popular view that the "phase—shift" from corals to macroalgae on Jamaican reefs was caused exclusively by reduction of herbivores from overfishing and the die—off of the long—spined sea urchin *Diadema antillarum* (Hughes 1994). There was considerable push—back from Hughes and his colleagues from the Editorial Board of the journal *Coral Reefs*, who attempted to stop publication of my paper in *Limnology & Oceanography*, to no avail. However, they submitted a rebuttal stressing again that only top—down (grazing) forces control algal blooms and coral reef health (Hughes et al. 1999). My reply was the last word and reiterated exactly what I wrote in the original paper, that a multiple stressor model that included both top—down and bottom—up effects operating simultaneously was a much more robust conclusion (Lapointe 1999). As it turned out, my original contribution to the HAB special issue in *Limnology & Oceanography* (Lapointe 1997) has been by far the most popular paper of my career with 773 citations (Google Scholar).

By the year 2000, increasing sewage pollution from the growing residential and tourist population in the Keys, combined with increased flows of N—rich water from the South Florida mainland between 1991 and 1995, caused increased DIN and altered N:P ratios, taking a toll on the health of the FKNMS (Lapointe et al. 2019a). Between 1996 and 2000, coral diseases and bleaching had caused a 40% decline of living coral cover, with a parallel expansion of turf algae, macroalgae, and sponges. Tourist brochures were now describing the water as "emerald green" rather than "gin clear" as a result of phytoplankton blooms, and warning tourists to come to the Florida Keys sooner rather than later if they want to see living coral reefs. Scientists supported by the FKNMS still argued that sewage was not affecting the coral reefs of the Florida Keys, but rather that it was offshore upwelling that was causing the algae blooms and increasingly green, turbid water (Szmant and Forrester 1996). Despite my peer—reviewed papers (and those of others) on the role of land—based nutrient enrichment to phytoplankton and macroalgae blooms on coral reefs in Bermuda, southeast Florida, the Florida Keys and Jamaica, others disputed a role for land—based nutrients. Szmant (2002) concluded that levels of nutrient enrichment reported for human—impacted coastal waters do not affect corals in a harmful way, nor do they alter the balance in coral—algal abundance. Similarly, Furman and Heck (2008) concluded that nutrient enrichment was an unlikely explanation for algal overgrowth of coral reefs in the Florida Keys.

Discriminating Nitrogen Sources in Jamaica, Tobago, and South Florida

While coral reef biologists were denying a role of anthropogenic nutrient pollution supporting HAB, blooms were expanding in areas experiencing rapid population growth and tourism such as Jamaica, and both coasts of South Florida. Based on my earlier research and experience at DBML in 1987 (Lapointe 1997), I was invited to design and implement an integrated water quality—coral reef monitoring program in the Negril Marine Park (NMP) at the west end of Jamaica's north coast. Coral reefs in the NMP had been increasingly impacted by nutrient pollution and macroalgal blooms following decades of intensive development as a major tourist destination. A baseline survey of DIN and SRP concentrations, as well as C:N:P and stable nitrogen isotope ratios (δ^{15}N) of abundant reef macroalgae on shallow and deep reefs of the NMP in 1998 showed strong P—limitation and evidence of increasing sewage pollution. Fertilizers, N_2 fixation, upwelling, and fossil fuel emissions all have low δ^{15}N values (< +2‰); in contrast, septic tank effluent and processed human wastewater have more enriched values ranging from +3—15‰ (Lapointe et al. 2017). The δ^{15}N of reef macroalgae in 1998 indicated sewage N on shallow (+4.9‰) but not deep reefs (+2.0‰) on the West End. However, when sampled again in 2002 the values were significantly higher than in 1998, and both shallow (+8.2‰) and deep (+5.8‰) reefs had been increasingly impacted by sewage N over this timeframe (Lapointe et al. 2011). The escalating δ^{15}N enrichment of reef macroalgae correlated with expanding blooms of the chlorophyte *Chaetomorpha linum* in shallow waters of Long Bay and *Codium isthmocladum* and *Caulerpa cupressoides* on deep reefs of the West End. These blooms in Negril confirmed the role of sewage in driving the *Codium* blooms in southeast Florida and reaffirmed our conclusions that sewage treatment systems adjacent to coral reefs must include nutrient removal.

Measuring δ^{15}N in samples of water, macroalgae, particulate organic matter (POM), and reef organisms to discriminate N sources between upwelling, fertilizers, and sewage was a major advancement in my research program. We used this method in a seasonal study of southeast Florida in 2001, along with seawater nutrient analysis, to address the worsening invasion of *C. isthmocladum* and the non—native Pacific invader *Caulerpa brachypus* on reefs between Jupiter and Deerfield Beach. Multiple lines of evidence supported the hypothesis that land—based sewage N was more important than upwelling as a N source to these HAB: (1) δ^{15}N values were highest on shallow reefs (+8.1‰) and decreased with increasing depth, indicating land—based sources of enrichment; (2) elevated δ^{15}N values occurred in these HAB during the dry season, prior to the onset of the summer upwelling; (3) elevated NH_4^+ concentrations occurred on these reefs during both upwelling and non—upwelling periods and are kinetically preferred by macroalgae compared to upwelled NO_3^-. In collaboration with Mike Risk (Figure 7B), we published a review paper in *Marine Pollution Bulletin* on the use of δ^{15}N to assess sewage stress on coral reefs (Risk et al. 2009), which received the "Best Paper" award from the journal editorial board that year. We had just used δ^{15}N analysis of annual growth rings in gorgonian corals from reefs in highly populated southeast Florida compared to relatively clean waters in the Abacos, Bahamas. The results clearly showed the impact of larger sewage loads discharged into Florida's coastal waters (Sherwood et al. 2010). We also used this approach with reef macroalgae in Tobago, where we documented how sewage pollution was causing macroalgal blooms and coral reef decline in the Buccoo Reef Complex, which was impacted by urban development and use of cesspits and septic systems (Lapointe et al. 2010; Figures 8A, 8B).

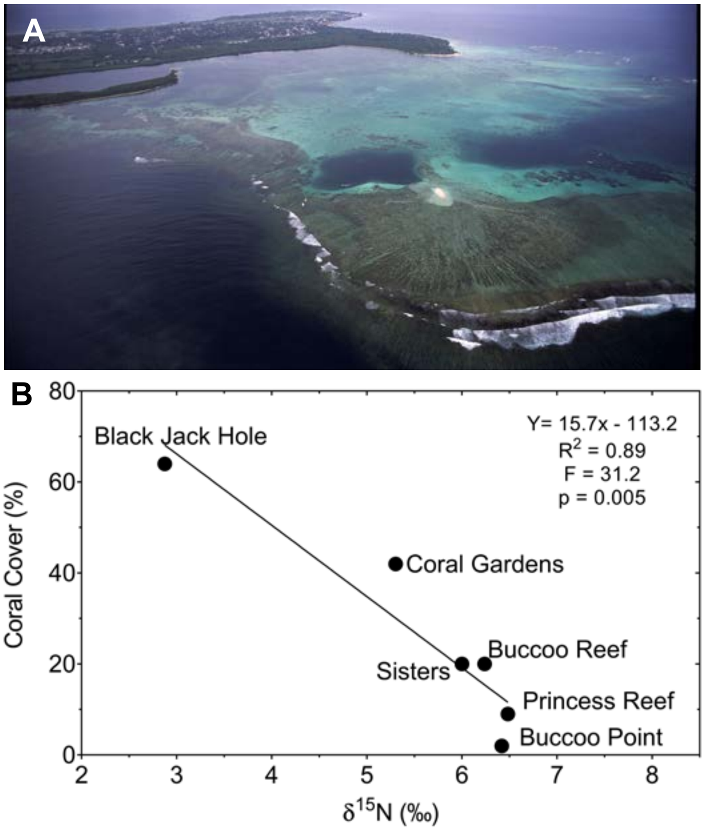

FIGURE 8. *Research in Tobago, West Indies. A. Aerial view of the Buccoo Reef Complex in Tobago. B. Linear regression of* ^{15}*N versus coral cover of various fringing reefs in the Tobago study.*

Unprecedented blooms of red drift macroalgae were also beginning to develop in southwest Florida's coastal waters and strand on beaches. This problem had developed in Tampa Bay in the 1970s, but this reached a critical stage in open coastal waters of Lee County in 2003/2004 when massive blooms washed ashore, making beaches unsuitable for recreation and requiring an expensive removal program (Figure 9A). With support from Lee County government, we sampled along a transect extending from the Caloosahatchee basin through San Carlos Bay and Charlotte Harbor to a network of artificial and natural reefs extending 26 km from shore. Macroalgal δ^{15}N values increased from the Ortona Lock (+8–9‰) west to the Franklin Lock (+12–15‰) during both samplings, and were within the sewage nitrogen range, decreasing with increasing distance from shore to +3.0‰ at the most offshore reef. Macroalgae (*Gracilaria, Hypnea, Botryocladia, Eucheuma, Sargassum*) collected in July 2004 from Lee County beaches had mean δ^{15}N values > +6.0‰, similar to macroalgae values on inshore reefs and within the range of sewage N (Lapointe and Bedford 2007).

The 2004 Lee County study was performed during a very active hurricane year in Florida, with paths of 3 hurricanes (Charley, Frances, and Jeanne) overlapping in the Kissimmee River basin north of Lake Okeechobee. I was asked by Lee County staff to also investigate the role of land–based nutrient runoff on red tides, which had also become a controversial issue. Years earlier in Key West, I had met Charlie Yentsch, the founder of the Bigelow Laboratory in Boothbay Harbor, ME, who had worked with John Ryther at WHOI back in the 1950s and 1960s. Charlie was a pillar in the development of NASA's ocean color program, and we collaborated on several projects addressing optical properties of coral reef environments (Fig. 9B; Yentsch et al. 2002). Charlie was well acquainted with the ecology of red tides and introduced me to the early literature, such as Ketchum and Keen (1948) that related Florida red tide to high P availability. The geology of southwest Florida contains rich hydroxyapatite deposits (Bone Formation) that is mined for P and long known to be a source of P enrichment to local waters (Odum 1953). The mining operations are concentrated in the Peace River basin, which flows into Charlotte Harbor and adjacent coastal waters. Extensive hurricane runoff from north of Lake Okeechobee, the Peace River, Myakka River, and Caloosahatchee basin mixed in a buoyant, stratified plume that extended some 70 km offshore in October 2004. Our 2004 study, which involved sampling before and after the 2004 hurricanes, showed significantly increased DIN concentrations and lowered N:P ratio in the stratified plume water to 26 km offshore (Lapointe and Bedford 2007). This buoyant plume phenomenon has long been considered a prerequisite for Florida red tide (Slobodkin 1953) and has been used worldwide to model the initiation of various red tide phenomena. By late 2004, a massive red tide (*Karenia brevis*) developed in coastal waters of southwest Florida, which persisted through fall of 2005. The mean δ^{15}N value of the *K. brevis* bloom sampled off Sanibel Island in September 2005 was +7.83‰, a value that closely matched the 2004 macroalgae blooms and was within the sewage N range (Yentsch et al. 2008). Brand and Compton (2007), using 50 years of Florida red tide data, found that cell concentrations were highest in nearshore rather than offshore coastal waters and have increased some 15–fold since the 1950s. Coincidentally, the population of Lee County has also grown about 15–fold since the 1950s.

Eutrophication of the Indian River Lagoon

Since 1990, the human population on Indian River Lagoon (IRL) watersheds has grown to ~2 million people and has correlated with increasing fecal bacterial contamination, phytoplankton blooms, HABs, seagrass die–off, and wildlife mortalities (Lapointe et al. 2015, 2017). My research on watersheds of the IRL began in 1994/1995 with 2 studies assessing impacts of septic systems on groundwaters and surface waters of the Loxahatchee River in Jupiter, FL. The studies were funded by the Loxahatchee River District and involved installation of monitor wells and seasonal measurements of groundwater levels and flow to track nutrient and bacterial pollution from septic effluent through groundwaters, tidal creeks, and into the Loxahatchee River. Steve Krupa, a hydrogeologist with the South Florida Water Management District, collaborated on the project. This project was followed by a similar project in Martin County following an active hurricane year in 2004, when health advisories were posted to avoid contact with the waters of the St. Lucie Estuary because of high levels of fecal bacteria. Environmental activists pointed to wet season discharges from Lake Okeechobee and farms as the cause, but our research showed that it was more related to the tens of thousands of septic systems in the local basin of the estuary (Lapointe et al. 2012). Additional studies funded by Martin County in 2015, using monitor wells and multiple sewage tracers, including aqueous and particulate δ^{15}N, sucralose, and microbial source tracking, confirmed the role of septic effluent to fecal contamination and high biomass blooms of the toxic blue–green alga *Microcystis aeruginosa* (Lapointe et al. 2017).

FIGURE 9. *Macroalgae blooms worsen off South Florida. A. Red drift macroalgae blooms stranded on beaches in Lee County, FL in 2003 and 2004. B. Charlie Yentsch making optical measurements of pelagic Sargassum offshore Key West, FL.*

The problems of nutrient pollution were also beginning to worsen throughout the IRL. With Save Our Seas speciality license plate funding granted through the Harbor Branch Oceanographic Institute Foundation, I began the first IRL–wide nutrient monitoring program in 2011, and the timing was serendipitous. This year the northern IRL region experienced an unprecedented phytoplankton "super bloom," which was followed by recurrent brown tides in 2012/2013, 2016, and 2018. Like the St. Lucie Estuary, environmental activists quickly pointed to farm runoff and urban fertilizers as the cause of the blooms. However, our research showed otherwise. Using seawater nutrient monitoring combined with elemental C:N:P and δ15N and δ13C analyses of macroalgae, phytoplankton, and seagrasses, it was clear that N loading from increasing human wastewater was a major driving factor in these blooms and seagrass decline (Lapointe et al. 2015; Figure 10). As a result of severe light limitation from the escalating HAB, 95% of the seagrasses have now been lost from the IRL region north of the Ft. Pierce inlet (Lapointe et al. 2019b). The IRL is in dire need of a Master Wastewater Plan, which includes not only septic–to–sewer projects but also upgrading municipal wastewater treatment plants for advanced wastewater treatment (nutrient removal). In Tampa Bay and other estuaries in southwest Florida, excess N from wastewater was recognized early on in the 1970s as the driving factor in algal blooms and seagrass loss, and decisions were made for N removal from wastewater. Those decisions jump–started the recovery of Tampa Bay, which now has the same areal coverage of seagrasses that it had in the 1950s (Greening et al. 2014).

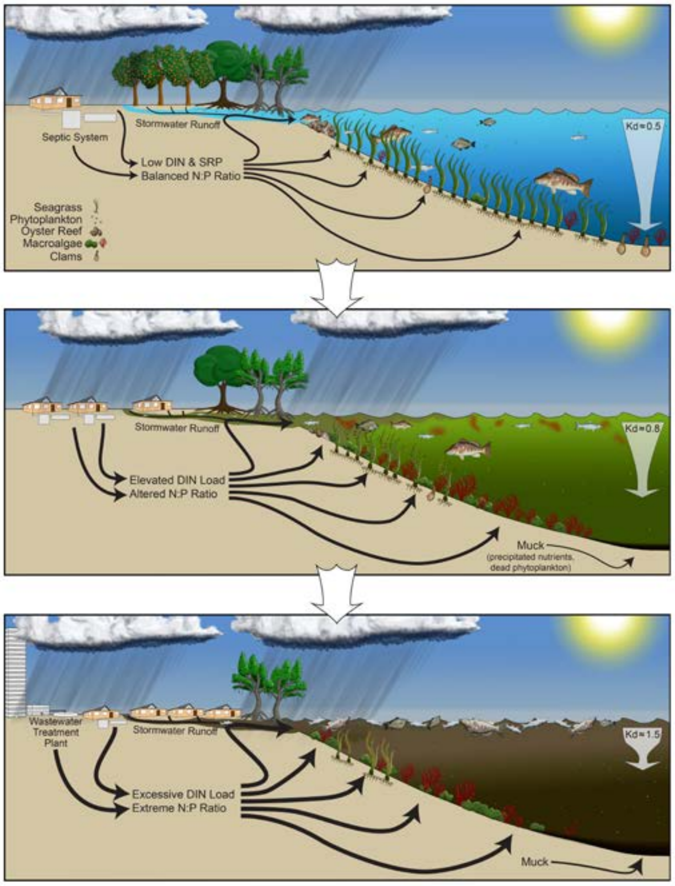

FIGURE 10. *Graphic visualization of land-based nutrient enrichment, including dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP), from human population growth, brown tides, and seagrass decline in the Indian River Lagoon, east-central Florida. Reproduced with permission from Elsevier (Lapointe et al. 2019b).*

Coming Full Circle: The Rise of Pelagic *Sargassum*

The findings from my NSF–sponsored research in the 1980s became key to understanding the ecology and oceanography of the massive *Sargassum* influx to the Caribbean region since 2011. The early research showed the importance of nutrient cycling from associated fishes to the growth and productivity of *Sargassum* in nutrient–poor oceanic waters (Lapointe et al. 2014). The research also showed the importance of nutrient enrichment from river discharges and land–based runoff, as neritic *Sargassum* had much lower C:N, C:P, and N:P ratios and much higher productivity than those in nutrient poor oceanic waters of the Sargasso Sea (Lapointe 1995). This explained why *Sargassum* began forming blooms in the GOM in the 1980s, when it was experiencing increasing N inputs from Mississippi River discharges. Using satellite remote sensing, my colleagues from University of South Florida developed a floating algae index that could be used to track *Sargassum* from space, which greatly advanced our ability to understand the spatial distribution and abundance of *Sargassum* (Hu et al. 2016). Recently, we showed the development of a new massive bloom area in the tropical Atlantic Ocean. The Great Atlantic *Sargassum* Belt, which has developed since 2011, stretched for some 8,850 km from the west coast of Africa, across the tropical Atlantic Ocean, and through the Caribbean basin into the GOM in July 2018 (Wang et al. 2019). The new tropical Atlantic *Sargassum* bloom represents the first oceanic–scale eutrophication involving macroalgae and the largest HAB on earth. The blooms appear to result from increasing nutrient inputs from the Amazon River basin, as well as coastal upwelling off Africa and possibly African dust as well. The excessive *Sargassum* influx is having severe effects on ecosystem and human health in the wider Caribbean region, as well as widespread impacts on tourism–related economies (Lapointe et al. 2018; Figures 11A–D).

Unraveling the Complexity of Nitrogen and Climate Change on Coral Reefs

A strong consensus has developed in recent decades that solving problems of eutrophication and seagrass decline in estuaries will require controls on N inputs (Howarth et al. 2000, Howarth and Marino 2006, Greening et al. 2014). There has also long been evidence that nutrients are a primary factor influencing algal communities and the structure of coral reefs (Smith et al. 1981, Littler and Littler 1984, Tomascik and Sander 1985, Bell 1992, Lapointe and Clark 1992). In 1988, 50 coral reef experts met at a National Oceanographic and Atmospheric Administration (NOAA)–sponsored workshop in Key Largo, FL and ranked various problems affecting the health of coral reefs of the Florida Keys. The primary conclusion was "excessive amounts of nutrients invading the Florida Reef Tract from the Keys and from Florida Bay are a serious and widespread problem" (NOAA 1988). However, recognition of the importance of nutrient controls for coral reefs has not been as widely accepted for coral

FIGURE 11. *Recent* Sargassum *influx in the Caribbean and Florida. A. Lapointe with Christine Finney and Andre Miller observing influx of pelagic* Sargassum *on beaches in Barbados, June 2015. B. Aerial view of large* Sargassum *windrows near Grand Cayman in July 2018. C.* Sargassum *on beaches in Palm Beach, FL in August 2018. D.* Sargassum *floating over Carysfort Reef, Key Largo, FL in August 2015.*

reefs as in estuaries, as some coral reef biologists have strongly favored overfishing and reduced grazing as an exclusive factor explaining the widespread algal overgrowth of coral reefs globally (Hughes 1994, Jackson et al. 2001, Szmant 2002). The recent 30—year study of coral reef decline at Looe Key in the lower Florida Keys (Lapointe et al. 2019a) provides a unique long—term data set showing how increased DIN, chlorophyll *a*, seawater DIN:SRP ratios and N:P ratios in macroalgae are related to increasing P—limitation and coral die—off at Looe Key.

As the problems of coral bleaching, coral diseases, elevated sea surface temperatures (SSTs), and widespread coral reef decline have worsened globally in the past decades, the effects of increasing anthropogenic N are now recognized to be more complicated than just increasing the growth and success of algal competitors in oligotrophic coral reef environments. Wooldridge (2009) was first to quantify the connection between terrestrially—sourced DIN loading and the upper thermal bleaching thresholds for inshore reefs on the Great Barrier Reef, Australia. The stress mechanism involves an increase in the DIN:SRP ratio in the water column of coral reefs, which leads to P starvation of the coral symbiosis (evidenced by the buildup of sulpholipids on the algal lipodome, Wiedenmann et al. 2013). Rossett et al. (2017) concluded that SRP can be critically limiting at concentrations < 0.18 µM, especially if algal tissue N:P ratios exceed 22:1. My research has shown SRP concentrations < 0.18 µM and algal tissue N:P ratios in the range of 33—72 for declining coral reefs at DBML (Lapointe 1997), the Florida Keys (Lapointe et al. 2019b), and the Belize Barrier Reef (Lapointe and Tewfik 2019), supporting a role of P starvation and metabolic stress for coral bleaching and diseases in the Caribbean region. This research highlights the important role of P to endosymbiont photosynthesis and the functioning of symbiotic corals (Ferrier—Pages et al. 2016).

Future research needs to address the growing effects of global N enrichment in altering the N:P stoichiometry on coral reefs, especially remote coral reefs. Research has shown that land—based N loading is a driver of regional algal blooms and coral reef decline in the Florida Keys (Lapointe and Clark 1992, Lapointe et al. 2019a) and the Great Barrier Reef (Bell 1992, D'Eath and Fabricius 2010), a process that involves phytoplankton blooms and turbidity that increase light attenuation (Yentsch et al. 2002). On remote coral reefs, atmospheric N deposition in optically clear waters can enhance macroalgal blooms, even in the absence of terrestrial runoff (Barile and Lapointe 2005, Chen et al. 2019). Consequently, such atmospheric N deposition could also be altering the DIN:SRP ratio on remote reefs, causing metabolic stress that makes corals more vulnerable to coral disease and bleaching (Wooldridge 2009, Lapointe et al. 2019a). In particular, measurement of seawater DIN:SRP ratios, as well as C:N:P ratios and alkaline phosphatase activity of macroalgae and endosymbiotic zooxanthellae would elucidate the degree of P stress and potential for increased bleaching and disease. Ultrastructural biomarkers in endosymbiotic zooxanthellae also hold promise to indicate nutrient stress in a variety of reef settings and should become part of the tool kit for future coral reef studies (Rosset et al. 2017).

CLOSING COMMENTS

My "life's work" in marine science would not have been possible without the inspiration from several amazing mentors. In chronological order, these included John Ryther, Ken Tenore, Clinton Dawes, and Charlie Yentsch. All contributed in different ways to my academic and scientific development by providing their particular insights to my nutrient and algae research. Graduate students and early career scientists need to fully understand the importance of this crucial first step and seek out the best mentors they can find to pursue their particular research interest. This could include, as in my case, several gap years between undergraduate school and graduate school to find that particular mentor and work with that person to build a solid foundation for a career. During this time of exploration, it is also important for graduate students to reflect upon the type of career they envision. Mentors can guide students in making the decision to pursue studies and opportunities which will prepare them for research positions or for professorial teaching roles in academia.

Choosing key collaborators along the way is also an important step. I'm grateful to several colleagues who throughout my career provided opportunities to advance my research by performing comparative research in different environments. These include Mark and Diane Littler, who first introduced me to coral reef ecology on the Belize Barrier Reef. Tom Goreau introduced me to the coral reefs of Jamaica and Peter Bell brought me "down—under" to the Great Barrier Reef, Australia. Mike Risk and I began a productive collaboration using N isotopes in macroalgae and gorgonians to assess sewage stress on coral reefs in Florida, Bahamas, Cuba, and Barbados. Chuanmin Hu and I worked together to track land—based runoff and HAB with satellite remote sensing, which led to major advances in our understanding of the *Sargassum* influx to the Caribbean Sea (Wang et al. 2019). Currently, I'm working with Alex Tewfik on the role of terrestrial nutrient inputs, eutrophication, and altered N:P stoichiometry on the Belize Barrier Reef. At present, I have no plans to retire.

Thinking back, the ways in which we design, conduct, and carry out scientific research have changed dramatically in the 5 decades since I studied at BU. Today I am able to collaborate with colleagues instantaneously using the internet and mobile telephones to communicate and share data. Oceanographic satellite imagery and on—site instrumentation allow us to use real—time data and synthesize our findings in a manner I might have considered science fiction back when beginning my career. The development of social media has revolutionized the ability to share our findings with the public at large, expanding our ability for broader impacts and outreach of our research. For example, following publication of my recent 30—year Looe Key study (Lapointe et al. 2019a), the findings were tweeted and re—tweeted, and picked up by some 300 media outlets globally, including the *NBC Nightly News*, *Newsweek, National Public Radio, Livescience*, *Miami Herald, Tampa Bay Times, Daily Mail Online,* among others. The potential audience reach was more than 463 million people around the world. Yet, with all of these advances certain characteristics in the field remain the same. A certain level of dedication and grit are required if one is going to withstand the challenges and adversity commonly present in the advancement of science. Today's students and future researchers must understand that the world is not fair. Like me and many who have come before, they will face criticism. And like me, they need to develop academic and professional resiliency in order to respond to those who would oppose the science in favor of political or economic gain. Finally, beware of scientific fashions as it is the freedom from popular frameworks that makes the advancement of science and rationality possible.

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Several lab managers deserve mention for their outstanding service over the years. These include B. Bedford, who began as a volunteer, and helped expand my HAB program at HBOI in 2004. In 2011, L. Herren joined my program as Research Coordinator and was instrumental in the design, implementation and write—up of our Indian River Lagoon—wide research. Following Laura's departure in 2016, R. Brewton became Research Coordinator in my lab, and is currently doing an amazing job multi—tasking several research projects while assisting me with publishing papers, including this one.

Numerous sources of financial support have made my research and public outreach possible. These include the National Oceanic and Atmospheric Administration (NOAA, National Marine Sanctuaries Program), National Science Foundation (NSF), Monroe County, Herbert W. Hoover Foundation, John D. and Catherine T. MacArthur Foundation, United States Environmental Protection Agency (USEPA), National Geographic, National Aeronautics and Space Administration (NASA), Florida Wildlife Research Institute (FWRI), Martin County, Indian River Lagoon National Estuary Program, Sarasota Bay National Estuary Program, Lee County, Charlotte County, the "Save Our Seas" Specialty License Plate funds granted through the Harbor Branch Oceanographic Institute Foundation, and the Coastal Ocean Association for Science and Technology (COAST). Jim Jacoby and Capt. C. Hampp generously provided research vessel support for field work in South Florida and the Bahamas. The Florida Chamber of Commerce is gratefully acknowledged for supporting a public education and outreach program that is critical to securing Florida's water future.

This paper would not have happened without the invitation from M.S. Peterson and N.J. Brown—Peterson, and I thank them for their patience and the opportunity to tell this story. Finally, I am most grateful for the incredible support of my wife Lee and son Sebastian. Sebastian introduced me to the classic play by Henrik Ibsen (1882) *An Enemy of the People*, which describes how the search for truth concerning water pollution issues can be undermined by politics and money, and how the majority is never right, until they do right. This is contribution #2262 of the Harbor Branch Oceanographic Institute at Florida Atlantic University

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