



Frontispiece. Mark M. Littler and Diane S. Littler holding a rock sample with the deepest-known plant life -- a coralline alga collected from 268 m in the Bahamas (p. 306, Guinness Book of World Records, 1998).

MARINE BOTANICAL STUDIES

BY

MARK M. LITTLER AND DIANE S. LITTLER

Our good friend, Ian Macintyre, coerced (bullied?) us into doing this article on why we do the work we do—so here goes! Mark's interest in nature began as a child in the Appalachian surroundings of southeastern Ohio, where his father was a country-club golf professional. Mark spent many an hour angling for fish using his own home-made tackle (Fig. 1)—an endeavor that was to establish a sense of value for all living things aquatic and that became a life-long passion. A pivotal event occurred when Mark's father moved the family to Key Biscayne, Florida, following the blizzard of 1950. They spent the winter months there throughout his young adult life. Mark immediately became enthralled with all of the fishing, snorkeling, spearing, shelling, boating, and water-skiing opportunities to be found in Florida. He made his first scuba dive in 1955 in the upper Florida Keys at Fowey Rocks.

In 1961, Mark obtained a bachelor's degree in botany/zoology from Ohio University (OU) and then began working as a chemist for the Ohio State Highway Department Testing Laboratory in Columbus. With the money he saved, he planned to do graduate work in marine fisheries biology. However, a fortuitous encounter in 1963 with Art Blikle, a former botany professor, led him to apply for a teaching assistantship at OU and study limnology/phyecology, the closest thing to marine biology at that institution. Mark's master's studies at OU focused on the seasonal cycles of phytoplankton in a state wildlife management lake, forever sending him on a botanical trajectory. The training provided not only a classical phyecological background but also an opportunity for Mark and Diane to meet. She was taking a phyecology class and he was the teaching assistant. Diane had grown up roaming the forests (and dominating golf events) near Salem, Ohio, with a vision of pursuing a career in forest ecology. Mark eventually convinced her that seaweeds also formed interesting forests, albeit underwater. After their marriage, and being accepted into several graduate programs, Mark and Diane chose to study at the University of Hawaii (UH) because of its comprehensive curriculum in marine algal ecology.

While working for the legendary oceanographer/ecologist/phyecologist Max Doty at UH, Mark and Diane learned broadly based coral-reef ecology and state-of-the-art approaches to research, most importantly, from a "big science" perspective. One of Max Doty's quotable quotes (re. alpha taxonomy) that stuck was, "If you don't do the taxonomy, you don't know what you are talking about, but if all you do is taxonomy, you don't have anything to say". Early on, Max assigned the crustose coralline algae, at that time an extremely intractable calcareous group, as Mark's dissertation topic. This led to much struggling and little progress until Izzie Abbott, a renowned and delightful systematist, saved the situation by patiently demonstrating a useful *in situ* sectioning technique for coralline algae. This "foot-in-the-door" permitted the taxonomic pigeonholing of key coralline reef-building species and, as detailed below, ultimately



Figure 1. Mark at age 10 displaying a nice stringer of fish. The inset (right) shows that time has not changed this behavior. Immediately after Mark lands an exceptional fish, one invariably hears "Diane get the camera, get the camera!!! Diane, Diane, where the h... is Diane???"

led to rekindled interest in the importance of these calcareous plants to coral-reef biology. Because UH had a very active visiting scientist program, the Littlers also came to know most of the pioneers in coral-reef research and many other "big-name" scientists in the field of marine phycology.

Surprisingly, Mark was invited to interview for assistant professorships by faculty at the University of Washington, California State University, and the University of California—all several years premature relative to the completion of his dissertation. Furthermore, Mark was

pressed by Peter Dixon (one of Europe's "phycological giants"), who was Chairman of the Department of Ecology, into accepting a tenure track position at the University of California, Irvine (UCI), a full year prior to completion of his Ph.D. How times have changed! Mark finished his doctorate requirements at the end of the first year in residence at UCI and received tenure three years later, ultimately achieving the rank of full professor in 1980. While at UCI, Mark and Diane directed very large research programs (up to 55 full-time employees), focusing (with Roger Seapy and Steve Murray) on the ecology and physiology of rocky intertidal ecosystems (Fig. 2). They also supervised three Ph.D. candidates, Keith Arnold, Frederic Briand, and Mark Hay, who now hold full-professor positions at major universities (one other, Phil Taylor, is a division director at the National Science Foundation) and produced seven master's students who all advanced to Ph.D. programs. In 1982, Mark was recruited for the Chairmanship in Botany at the Smithsonian Institution, and Diane finally completed her masters and doctorate degrees with Pacific Western University on the functional morphology of marine algae. Mark and Diane have been at the Smithsonian Institution since that time, with Diane also holding a senior-scientist position at Harbor Branch Oceanographic Institution.



Figure 2. Diane and Mark collecting marine plants on a rocky intertidal shore.

The third member of our team, Barrett Brooks, and ourselves (Fig. 3), have been among the handful of Smithsonian scientific divers certified to a depth of 60 m. We were most fortunate in being able to add Barrett (B²) to our team shortly after arriving at the Smithsonian Institution. However, the struggle with the SI Office of Personnel (OP) had been monumental! We had advertised for a person with both biological and scuba experience. What we received was a short list of five candidates that OP had selected which were none-of-the-above, with



Figure 3. Our research team (L>R), Diane, Barrett, and Mark, entering an underwater cave on the Great Astrolabe Reef, Fiji.

one having long-since moved (no forwarding address) and, incredibly, another that was actually deceased. Luckily, B² had begun to badger OP, having just returned from his Peace Corps assignment in the backcountry of Liberia, because he was in jeopardy of soon losing his governmental noncompetitive (i.e., preferential-hiring) status. OP begrudgingly sent him to us for an interview, even though he was an experienced scuba diver with excellent phycological training from the University of Colorado. Barrett was a bit (whole lot!) noncommittal during the interview process, although we anticipated that his Peace Corps background reflected a “can-do” willingness to undertake almost any onerous assignment, including enduring work under less than tolerable conditions. This assumption could not have been more “on-the-money” and his addition to the team has led to a most productive and entertaining partnership. Unlike B², neither of us are “party-animals,” so it has often fallen on B²’s capable and enthusiastic shoulders to serve as “designated reveler” for the team, under “other-duties-as-assigned” (a caveat included in all SI position descriptions).

We decided to focus on marine plants because they are among the most important and attractive inhabitants of coastal ecosystems throughout the world. Our interests and personal satisfaction derive from being able to add in some measure to the overall picture of the unique ocean planet upon which we live, instead of narrowly focusing on human activities and services, as most non-science professions do. By contrast, the biologist perceives the relatively recently arrived human species (with both admiration and trepidation!) as the most dominant intruder among the millions of other species that have occupied the planet since the origin of the blue-green algae (Cyanobacteria) several billion years ago. Such differences in perspective are not

trivial, particularly in the restrictive intellectual atmospheres that are increasingly being fostered by politicians and administrators from the “people professions” who impose values that inhibit fundamental principals of scientific inquiry.

Having said that, we now need to provide a little background information on the organisms and ecosystems that have held our interests for more than three decades. The 25,000 described species of marine algae comprise one-third of all phyla of the plant kingdom and have been evolving longer than any other group of organisms on earth. They are responsible for building many of the world’s reef systems, contribute substantially to the planet’s primary production, permanently scrub anthropogenic and natural carbon dioxide from the atmosphere as carbonate, and their extracts are used in more than one-third of all processed food items and pharmaceuticals. We are continually amazed by coral-reef biocomplexity, with the plants alone having evolved along five dramatically disparate evolutionary lines. The variety of their sizes, shapes, and colors is remarkable, as is the versatility of their intricate life histories and species richness. We have concentrated nearly 20 yrs of collecting and curating effort into documenting the enormous morphological plasticity, variability, and taxonomic diversity within all five of these difficult phylogenetic groups. We take considerable pride in the fact that no major tropical marine-algal field guide, monograph, or serious flora could be completed successfully without consulting examples from the tens of thousands of specimens our group has added to the U.S. National Herbarium.

The biochemical and physiological complexity of coral-reef plant life is also unequalled. Tropical seas, in general, host an immense biodiversity that is critical to the world’s biogeochemical cycles and serve as an important source of foods and pharmaceuticals. However, algal natural products and metabolic pathways have not yet been explored adequately and methods for sampling the more intractable and cryptic seaweeds have only recently been developed. Because of the rapid worldwide degradation of tropical reefs, we feel that it is imperative that they be studied from all aspects in a timely, efficient, and scientifically verifiable manner. It is of paramount importance to characterize changes in the physical, chemical, and living attributes of the coral-reef environment and to understand the response of the biota to such changes. As mentioned, marine plants from five diverse phylogenetic lines dominate and, in conjunction with coelenterate corals, are the major primary producers and builders of all reef systems. Considering the critical roles these organisms play in reef ecosystems, they must be taken into account in other fields of marine sciences, whether it be the study of fisheries resources, marine chemistry, ecology, geology, or any of the associated zoological disciplines. Much remains to be discovered about the plant species on tropical reefs and how they interact with each other and with the abiotic and biotic components of their environment. We strongly believe that a better understanding of the diversity of marine plant life is a key component to preventing further damage to this living resource.

Unfortunately, the overall biodiversity research in the coral-reef realm is relatively sparse compared to that of terrestrial systems, such as rain forests, particularly as it relates to the extraordinary diversity of higher levels of taxa (Sepkoski 1995). Ecological studies also have been greatly hindered due to inadequate taxonomy but are required to understand the fundamental consequences of both anthropogenic and natural changes to the biocomplexity of marine plant life. Vastly more of the world’s genetic diversity resides among the array of different phyla than in a profusion of closely related species. The diversity of the photosynthetic

pigment apparatus of the green algae (Chlorophyta) alone greatly exceeds that of all terrestrial plants combined (Andersen 1992). The polyphyletic nature of the algae means that they embrace a much broader range of diversity than many higher plant or animal groups. For example, relatively more classes, orders, families, and genera of algae are being discovered at a comparatively rapid rate; no less than 20 new classes have been erected in the past three decades. Continuing discoveries of new families, orders, and even phyla (e.g., Prochlorophyta) of marine plants foretell a wealth of biodiversity still unrealized. Also, exciting new information, novel techniques, and heightened awareness now permit dramatically improved sampling, species identifications, and process-oriented research at larger and larger geographic scales.

Our research within this fascinating domain has been both exciting and, at times, dangerous. When the International Finance Corporation of the World Bank asked us to conduct surveys of the Moroccan coastline to assess the feasibility of their funding a new algal harvesting industry, our team found itself many hundreds of kilometers south along the West African coastline in the occupied territory of Western Sahara. Unbeknownst to us at the time, this region was at war with Morocco. We were befriended by a nomadic group of Bedouin tribesmen who cordially invited us to partake in a delightful gunpowder tea ceremony in one of their tents (Fig. 4). Later it dawned on us that this was quite likely a unit of freedom fighters, since only young men were present and because a plane was shot down inland from the same area soon afterward.

We also encountered a flourishing cottage algal-harvesting operation in the region. Its harvests of the agarophyte *Gelidium sesquipedale* were bought by an elderly gentleman in Laayoune, Morocco, who originally had been bankrolled by a large Japanese agar-producing corporation. He was proud to show us his quarterly stockpile of harvested material (Fig. 5), which we estimated to be worth approximately \$2.5 million in profit. His large home appeared quite dilapidated from the exterior but was palatial inside, where we were graciously served by a staff of servants and a daughter, home from university in Spain; his son was attending university in Switzerland. Needless to say, we immediately questioned whether or not we were in the most rewarding end of the algae business!

Since then our group has pioneered the use of shipboard expeditions specifically for marine plant systematics, i.e., collections, *in situ* photography, and inventory surveys. One of our most productive projects came as the result of an NSF grant to Diane that made possible oceanographic expeditions to the far reaches of the tropical Western Atlantic with colleagues such as Brian Lapointe, Esperanca Gacia, and Dennis Hanisak. Our 2,000+ ship-based scuba dives have taken us to the coastal ecosystems and reefal habitats of Florida, the Bahamas, Greater Antilles, Lesser Antilles, Southern Caribbean, Western Caribbean, Gulf of Mexico, Mediterranean, Morocco, Seychelles Archipelago, and many island groups in the tropical Pacific. One of our more enjoyable oceanographic cruises was the first joint USSR-USA Expedition in Marine Biology, hosted by our friend and Chief Scientist Ed Titlyanov, aboard the *R/V Nesmeyanov*. Our group, and fellow Americans Andy Benson, Phil Dustan, Len Muscatine (Fig. 6), along with 62 Russian scientists, embarked on a halcyon cruise to study primary production phenomena in the Seychelles Archipelago (published in *Atoll Research Bulletin* Nos. 365-378, 1992a). It is amusing that Diane was virtually "put under a microscope" as the first example of a "typical" American woman to be seen by most of the Russians (see Fig. 7). Such ship-based expeditions (e.g., Figs. 6 and 8) have emphasized



Figure 4. Nomadic Bedouin tribesman serving ceremonial gunpowder tea in a remote location in Western Sahara. Inset at top shows tribesmen welcoming us to their encampment.



Figure 5. Arab gentleman and a small portion of his stockpiles of the commercially valuable red alga *Gelidium sesquipedale* in Laayoune, Morocco ready for shipment to Japan.

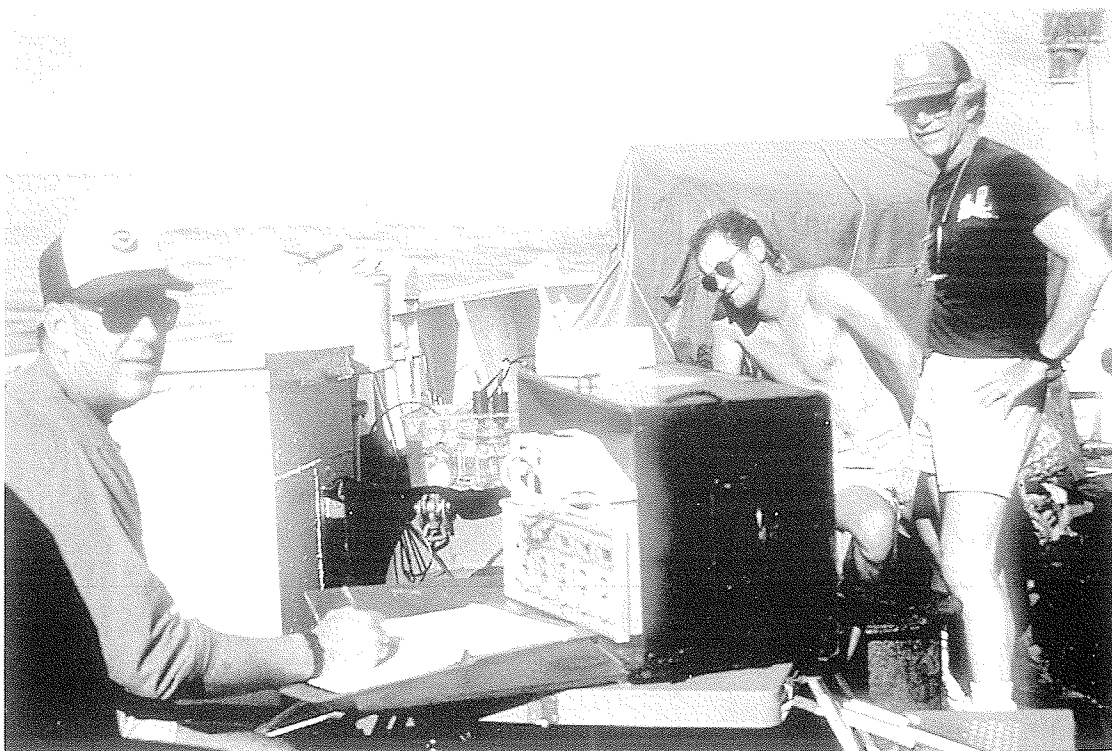


Figure 6. Mark and Barrett conducting a physiological/ecological experiment on fungiid corals with Len Muscatine aboard the *R/V Nesmeyanov* at Astove Atoll in the Seychelles Islands, Indian Ocean.

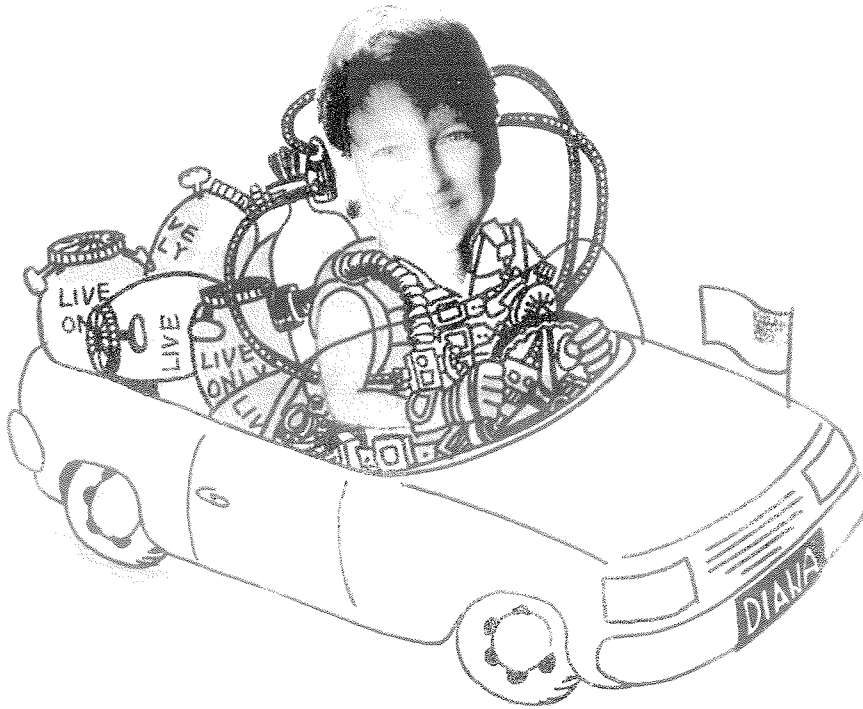


Figure 7. Russian illustrator's 1989 depiction of Diane, who has become renown in the Soviet Far East as "the woman who dives as deep as Lake Baikal".

pristine systems of extremely high biodiversity (e.g., Martinique), areas that had not been sampled well (e.g., Seychelles, southern Lesser Antilles), and environments with unique floras (e.g., Fiji, Panama). Oceanographic cruises have proven to be the most effective and efficient way to gain access to remote regions and also facilitate more thorough collecting and rapid processing than can be achieved by working only from land sites.

Lest all of this fieldwork appear too glamorous, it should be pointed out that between us we have endured a dislocated shoulder in Martinique, had an eye-ball badly lacerated in the Florida Keys, experienced severe ciguatera poisoning in Fiji, contracted malaria in the Solomon Islands, overcame amoebic dysentery in the Galapagos, and suffered through innumerable mandatory kava ceremonies in Fiji. For the uninitiated, kava is a traditional and locally revered drink (made from a plant root) that looks like muddy river water but does not taste nearly as good.

For the past 30 years, our group has addressed a broad spectrum of research topics ranging from systematics, functional morphology, and evolutionary studies of macroalgae to applied inventory and ecological work contracted by managers of tropical reef ecosystems. As an example, we were asked by the National Marine Sanctuaries Program of the National Oceanographic and Atmospheric Administration (NOAA) to initiate a rapid-response study (Littler et al. 1987) for assessing and monitoring the damage caused by the catastrophic grounding of the freighter *Wellwood* to the most popular recreational diving site in the world, Molasses Reef, Key Largo, Florida (Fig. 9). This work contributed to obtaining restitution in excess of \$3,000 per square meter of impacted reef substrate (\$22 million total). Additionally, baseline biodiversity inventories of Looe Key National Marine Sanctuary (Littler et al. 1986)

resulted in substantial penalties for the destruction of back-reef habitats following another ship grounding, a first for damage to seaweed-dominated communities. Furthermore, some of our biological inventory and survey programs (conducted for state and federal agencies such as the Bureau of Land Management, Office of Water Resources Research, State of Hawaii, NOAA, NSF, National Park Service, Minerals Management Service) culminated in the development of standard large-scale monitoring methods (Fig. 10, Littler and Littler 1985, 1987) as well as the conservation of major coastal ecosystems (Littler and Murray 1977, 1978, Littler 1979, Littler et al. 1986, 1987).

Our future research will continue to focus on complex interactions in marine ecosystems. These studies will take up both theoretical/experimental and systematic issues, often in collaboration with other researchers. As highlighted in the following selections, our studies have included the development of new theory with predictive capability as well as usable systematic field guides of applied value in shaping the management programs of environmental agencies as well as academic institutions.



Figure 8. The Littler's conducting PI vs. irradiance curve studies on Mediterranean deepwater algae aboard the *R/V Seward Johnson* (the submersible *Johnson-sea-Link II* is in the background).



Figure. 9. Underway to conduct an assessment of the Freighter *Wellwood* grounding site with colleagues (L>R) Brian Lapointe, Jim Norris, and Katy Bucher (Littler et al., 1987).



Figure. 10. Diane conducting photogrammetric/video assessments of benthic biota by open-sided helicopter (see Littler and Littler, 1987).

We regard the following as some of our most rewarding contributions (in chronological order):

(1) The first to quantitatively document the importance of coralline algae to the structure and functioning of tropical coral reefs by means of an experimental approach that combined distribution and abundance information with determinations of primary productivity and calcification rates. This resulted in one of the earliest reports of eutrophication as a cause of coral-to-algal phase shifts on tropical coral reefs, now a central theme of modern coral-reef research. Innovative photogrammetric methodologies also were developed and utilized for measuring standing stocks of benthic biota. (nineteen papers published; e.g., 1973. The population and community structure of Hawaii fringing-reef crustose Corallinaceae (Rhodophyta, Cryptonemiales). *J. Exp Mar. Biol. Ecol.* 11:103-120)

(2) Provided the first comprehensive overview of seasonal distribution and abundance patterns for invertebrate and seaweed populations for all major rocky intertidal ecosystems of the Southern California Outer Continental Shelf (OCS) and mainland from Point Conception to the Mexican border. Established the major biogeographical boundaries for the Southern California OCS and showed that these correlated with dominant oceanic currents and temperature isoclines. This program was part of a large national team effort (Bureau of Land Management) to ascertain the natural baseline levels of variability of U.S. continental shelf biotas prior to oil exploration and development. Sophisticated video and photogrammetric methods (e.g., Fig. 10) developed during this study are now in general use by marine biologists; whereas some are standardly required for marine biological inventory and monitoring studies by various U.S. federal agencies (e.g., Minerals Management Service, U.S. Park Service, NOAA). This research also was instrumental in impact prediction and helped exclude large tracts containing unique and/or sensitive marine ecosystems from lease sales. (eighteen papers published; e.g., 1991. The Southern California intertidal and littoral ecosystems. Pp. 273-296. *In* P. Nienhuis and A. C. Mathieson, eds. *Intertidal and littoral ecosystems of the world*. Vol. 24. Elsevier Sci. Pub., Amsterdam.)

(3) Major architects in the field of "marine algal functional morphology and evolution". Our 1980 model incorporating convergent anatomical, physiological, and ecological features that transcend phylogenetic lines represented a dramatic improvement in realistically explaining the evolutionary interactions that have resulted in the broad array of morphological forms shown by marine plants (Fig. 11). Now that ecologists have sufficient understanding of functional-morphological groupings, they are able to interpret patterns as well as predict environmental or biotic relationships within complex communities without having to laboriously study each component species. (seventeen papers published; e.g., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Amer. Nat.* 116:25-44.)

(4) Discovered unknown deep-sea plant communities and their ecological roles (Frontispiece), which opened up a new area of biological oceanography. Stimulated research by a diverse following (e.g., malacologists, oceanographers, sediment geologists, biomass mariculturalists, reef ecologists, physiologists) concerning deepwater macroalgal roles in primary productivity, food webs, sedimentary processes, and reef building (Fig. 8). Authors of subsequent textbooks on oceanography and general botany have included illustrations and data from this finding. (Five papers published; e.g., 1985. Deepest known plant life is discovered on an uncharted seamount. *Science* 227:57-59.)

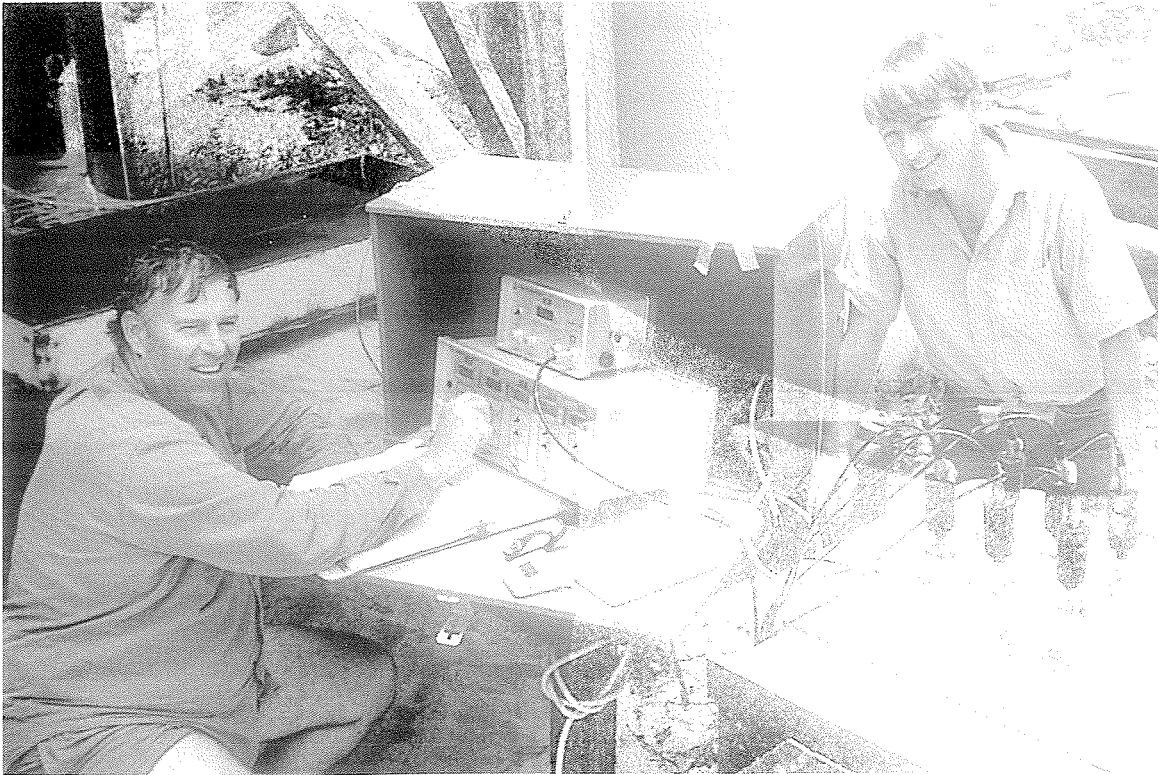


Figure 11. Performing functional morphology studies of tropical coral-reef algae in Belize.

(5) Developed and began testing a new theory of tropical reef biogenesis [Relative Dominance Model (RDM)] having major predictive significance to managers of reef ecosystems. This model posits that stable-state shifts in dominance from coral to various algal systems (accelerated by destructive forces) are ultimately a function of complex interactions between the major controlling factors of nutrient levels and herbivorous fish abundances, both of which are highly sensitive to anthropogenic modification. (Fifteen papers published; e.g., 1991. Comparisons of N- and P-limited productivity between high islands vs. low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. *Coral Reefs* 10 (4):199-209.)

In conducting the above-mentioned basic and applied research, we were amazed to learn how few of the macroalgal species from the ocean realm, particularly the Caribbean region, have yet been discovered and properly documented. We suspect that there are more macrophyte species undescribed than described. As examples, our three generic monographs, incorporating extensive scuba-depth collections (Littler and Littler 1990, 1991, 1992b), more than doubled the number of known taxa for each genus (i.e., *Anadyomene*, *Avrainvillea*, and *Udotea*) in the Caribbean and tropical western Atlantic. Consequently, we came to the conclusion that a simple identification manual was urgently needed by a broad spectrum of marine investigators and conservationists.

Since producing the popular photo guide (with Jim Norris and Katy Bucher, Littler et al. 1989), we received numerous requests to develop a systematic treatment comparable to its user-friendly design but more comprehensive, with complete specimen documentation

(morphological and anatomical), thus enabling users to key and anatomically verify their identifications. Such requests came from various colleagues in adjacent areas of research (e.g., physiology, chemistry, ecology, geology/sedimentology) as well as from numerous systematists. The result, and currently our “present most significant work”, *Caribbean Reef Plants*, written in language comprehensible to any scientist or advanced amateur, provides a source to identify tropical western Atlantic marine plants without the liability of shipping materials to dwindling numbers of overcommitted specialists for determinations (see www.erols.com/offshoregraphics). This 15-year effort has already been a “best seller” and begun to facilitate advances in (1) the ability of coral-reef researchers to identify Caribbean marine plants and document their distributions, (2) knowledge of local and regional natural patterns of plant biocomplexity, and (3) understanding the processes that create and maintain important temporal and spatial patterns.

As we enter the twenty-first century, the diversity of marine plant life is being dramatically altered by the rapidly increasing and potentially irreversible effects of human activities. Although the potential for anthropogenic degradation of coral reefs was suggested nearly three decades ago (Littler 1973), their demise has continued to escalate. Repeatedly, the attention of both the scientific community and the general public has been directed to the accelerating decline of tropical reef systems (e.g., Lapointe 1989a, 1989b, Buddemeir 1992, Wilkinson 1992, and Ginsburg et al. 1993). In particular, many picturesque and diverse coral/algal-dominated reefs (e.g., Fig. 12) are rapidly undergoing phase shifts to monotonous algal monocultures, with the formerly complex communities becoming overgrown by several undesirable species. As



Figure 12. Diane diving on a garden-like coral patch reef in Fiji.

pointed out in the RDM, the most critical vectors are eutrophication (Littler et al. 1993, Lapointe et al. 1997) and destructive alterations to herbivory (Russ 1991, Hughes 1994). We believe that these two factors are primary in determining "stable states" on reefs and controlling phase shifts following major (catastrophic) disturbances such as physical habitat alteration/destruction (Rogers 1985), diseases (Antonius 1995), invasions of exotic species, and sedimentation associated with land-based development (Kuhlmann 1988, Ogden 1988). Such stresses, along with global-warming phenomena, have the potential to cause serious and widespread social, economic, and biological problems.

Nevertheless, the situation may not be hopeless. Some governments have begun to protect significant tracts of reef systems (e.g., Australia, Philippines, Turks and Caicos, Netherlands Antilles, Belize, Mexico, and United States). We count ourselves among the increasing number of concerned coral-reef workers who are committed to providing conservation advocacy groups and governmental administrators with the tools and unbiased data needed to effect some of their management decisions. Coral reefs are remarkable ecosystems and extremely attractive to the recreational diving community (Fig. 12), but because they are under the surface of the sea, changes brought about by pollution and destructive fishing are not obvious to the casual observer. It is well known that tourism can bring a substantial economic return, and it is only by sound scientific inventories of the biodiversity of plant and other life on tropical reefs that a case can be built for establishing attractive and fully protected marine reserves. However, as human populational pressures escalate and continue to harm vulnerable coral-reef resources, it will become increasingly difficult to protect these resources unless sound scientific reasons for doing so are presented in a manner that will be convincing to conservation biologists, politicians, economists, sociologists, resource managers, governmental agencies, the general public, and, most importantly, the local populace.

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